SYMPOSIA SERIES FOR UNDERSEA RESEARCH
NOAA'S UNDERSEA RESEARCH PROGRAM, VOL. 1 NO. 1, 1983

The Ecology of Deep and Shallow Coral Reefs

Edited by
Marjorie L. Reaka
Department of Zoology
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Washington, D.C.
December 1983

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

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TABLE OF CONTENTS

CHAPTER I: INTRODUCTION

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This volume includes research contributions from participants in a Workshop on Coral Reef Ecology that is being held at the Meetings of the American Society of Zoologists in Philadelphia, December 1983. The workshop is sponsored by the Division of Ecology of the ASZ.

The goal of the workshop is to serve as a forum for researchers to debate what we currently do and do not know about functional relationships on coral reefs and to identify the most significant directions for future research. To provide a conceptual framework for our discussion of the current status of coral reef ecology, four topics were chosen for detailed consideration: 1) growth and life history patterns of coral reef organisms, 2) the dynamics of recruitment in coral reef organisms, 3) the processes that structure coral reef communities, and 4) the structure and function of coral reef ecosystems. Of particular interest also was whether or not different processes predominate in shallow *vs.* deep reef habitats and in different geographical regions. I felt that it would be especially fruitful to bring together investigators working in different laboratories and in different oceans. Each group of researchers, influenced by the unique history of their group and by the particular aspects of the reef environment(s) in which they have worked, has its own strengths and unique emphases in research outlook. The workshop presented an opportunity for a more complete exchange of ideas among these groups.

For example, following the dynamic leadership of Dr. Thomas Goreau, much of our early knowledge of the biology of deeper coral reefs (e.g., 30-100 m) came through the efforts of an active research group at the Discovery Bay Marine Laboratory in Jamaica. However, NOAA's Undersea Research Facilities, initiated with the Hydrolab program at the West Indies Laboratory of Fairleigh Dickinson University in St. Croix in 1977, have allowed more extensive observations and even experimentation with components of the deep reef community than was previously feasible. Also, through the use of its shallow water submersible, the *Makali'i*, the Undersea Research Facility operated by the University of Hawaii has made extensive observations and sampling in deep reef environments possible in Hawaii, Enewetak Atoll, and Johnston Island. Supported by NOAA's submersible program, Harbor Branch Foundation's submersible, the *Johnson Sea-Link*, has investigated the *Oculina* reefs off the east coast of Florida.

These research efforts on the ecology of deep coral reefs, many of them completed within the last 5 years, complement a rapidly growing body of knowledge on shallow reef communities and ecosystems in different parts of the world. Because many of these programs, especially those on deeper reefs, have been initiated recently, some of the results (e.g., those involving long term experimental manipulations) are not yet generally available to the scientific public. An opportunity for an up-to-date exchange of ideas and information among groups of investigators seemed highly desirable at this time. Consequently, this and the ensuing volume of The Ecology of Deep and Shallow Coral Reefs include contributions from researchers who have worked at each of the institutional sites mentioned above, as well as contributions from investigators who have studied coral reefs in a variety of other geographical locations.

The papers are organized into four chapters. The first chapter addresses the currently important topic of growth and life history patterns in coral reef environments. Sebens provides a general overview of the factors that can cause different size distributions in populations of different habitats and suggests ways of isolating these causal factors. Using long term monitoring techniques to evaluate life history patterns of corals over a depth gradient, Hughes arrives at the interesting conclusion that both recruitment and injury-mortality (but not necessarily growth) are higher in shallower (10 m) than deeper (35 m) sites on a Jamaican reef. Brakel provides an interesting biophysical analysis of the factors that influence the morphology of corals over a 27 m depth gradient. He shows that light and water movement do not directly determine, but instead place phenotypic constraints, on the possible shapes of corals in deep and shallow environments, respectively.

Providing a conceptual link between the chapter on life history patterns and the following chapter on community structure of reef organisms, the second set of papers addresses the issue about which we probably know the least in coral reef ecology: what factors control recruitment? Lobel and Robinson provide an overview of how offshore currents and particularly mesoscale eddies can influence recruitment of the planktonic larvae of reef fishes. The widespread occurrence of dispersing larvae in marine organisms, particularly in tropical species, has many important consequences for both ecological and evolutionary processes. One consequence is that kin selection should be less likely in marine organisms than in taxa which are characterized by less widespread dispersal (e.g., many species in terrestrial or fresh water environments). Shapiro addresses this question with an analysis of the processes of passive dispersion vs. the biological mechanisms that may prevent dispersion. He evaluates mechanisms that prevent dispersion, and suggests particular taxa of reef fishes that would be most likely to show the characteristics of kin selection. Also, as pointed out by Lobel and Robinson, our knowledge of the dynamics of recruitment undoubtedly will play a key role in our understanding of how communities are organized. In order to understand the structure of a community, we must know how and when recruits colonize particular sites. Using experiments on settling and metamorphosing fish larvae, Victor describes bands that identify the planktonic stage, a transition to an indistinctly banded zone that corresponds to settling and then a period of benthic metamorphosis, and distinct postmetamorphic bands. These marks on the otolith provide a valuable tool for determining the precise time of settling and metamorphosis that is independent of the first visual observations of recruits.

One of the processes thought to structure apparently saturated coral reef communities is competition for space. In many sessile species, growth is the primary mechanism of competition, and papers in this section are equally relevant to the chapter on growth and life history patterns in coral reef organisms. Suchanek, *et al.*, examine the significance of overgrowth interactions in a little studied but important assemblage of sponges that occupy open reef habitats. Interestingly, their data show that, while a gorgonacean was the most important aggressor in shallow ($\approx$ 3 m) water, in deeper water (> 10 m) four genera of demosponges were the most significant aggressors, while corals were the most frequently overgrown taxa. Chornesky and Williams provide new information on the phenomenon of sweeper tentacles, known to modify overgrowth relationships among some species of corals. Using field experiments, they show that sweeper tentacles on *Montastrea cavernosa* develop in response to competitive encounters with other species (*M. annularis*), and that these changes are relatively persistent, so that the apparently anomalous distribution of sweepers often observed in this species may reflect a history of past interactions.

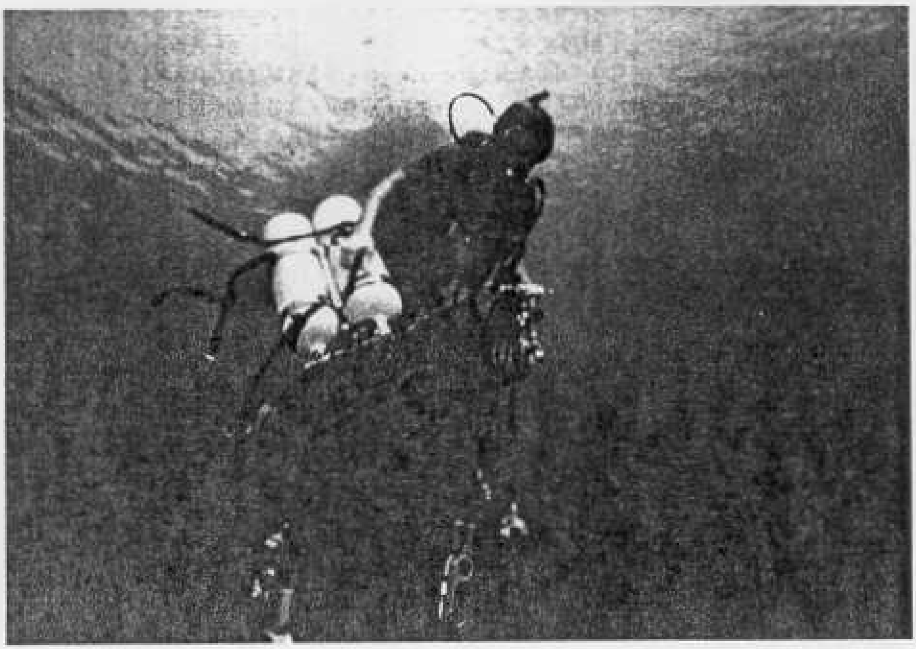
Consumers also clearly influence the structure of reef communities, an effect that appears to increase from moderate to deep water. Using experimental manipulations of artificial reef substrates to vary the numbers of fish predators and of the mobile cryptic fauna at 20 m, Wolf, *et al.*, show that colonization by fishes is influenced by the presence of cryptic invertebrates, and that fish predators in turn influence the densities of colonizing stomatopods, the largest and most mobile prey. Except for polychaetes, however, the secretive habits of the remaining taxa of mobile cryptic invertebrates appears to protect them from the effects of fish predation. Hixon provides an excellent review of the effects of fish grazers upon reef corals and algae. He shows that, while demonstrations that fishes influence the distribution and abundance of corals have been few, the effects of fishes (especially territorial damselfishes) upon reef algae are dramatic. These effects have major consequences for the structure of the entire coral reef community, since fishes directly or indirectly determine local algal abundance and diversity; accretion of the reef framework; nitrogen fixation by blue-green algae; the abundance of benthic microfauna; bioerosion of the reef framework; and the recruitment, growth, and survival of coral. Fitz, *et al.*, show that, whereas numbers of herbivorous fishes are known to decline at greater depths, these herbivores nevertheless control benthic community structure on deeper (20 m) reefs. Experimental manipulations (exclusion cages over artificial reefs) demonstrate that, while coral recruitment does not vary in the different experimental conditions, survival of recruits is reduced inside herbivore exclosures (where heavy turfs of algae predominate) compared to controls. Hay and Goertmiller use a *Thalassia* bioassay technique to show that herbivory is higher on shallow reef slopes (1-10 m) than on very shallow reef flats or on deep reef slopes (30-40 m). They also demonstrate that resistance to herbivory is greater on shallow and deep reef slopes than on reef flats (where algae occupy a spatial refuge from herbivores). Steneck uses six different techniques (including the *Thalassia* bioassay) to assess the intensity of herbivory for several functional groups. Herbivory is most intense on shallow forereef sites (1-2 m) and decreases in the shallow algal ridge, backreef, and deep wall reef habitats. Interestingly, the results of the *Thalassia* bioassay do not agree with those of the other techniques in all cases. Carpenter also provides a nice experimental analysis of the effects of different herbivores upon the algal community on coral reefs. Grazing regimes influence species composition of the algal community, leading to subsequent changes in primary production. Carpenter's study makes an important connection between herbivores, turnover rates of consumed species, and community metabolism. His study thus provides a link between the present chapter on community structure and the last chapter, which addresses the processes of nutrient flow that integrate coral reef ecosystems.

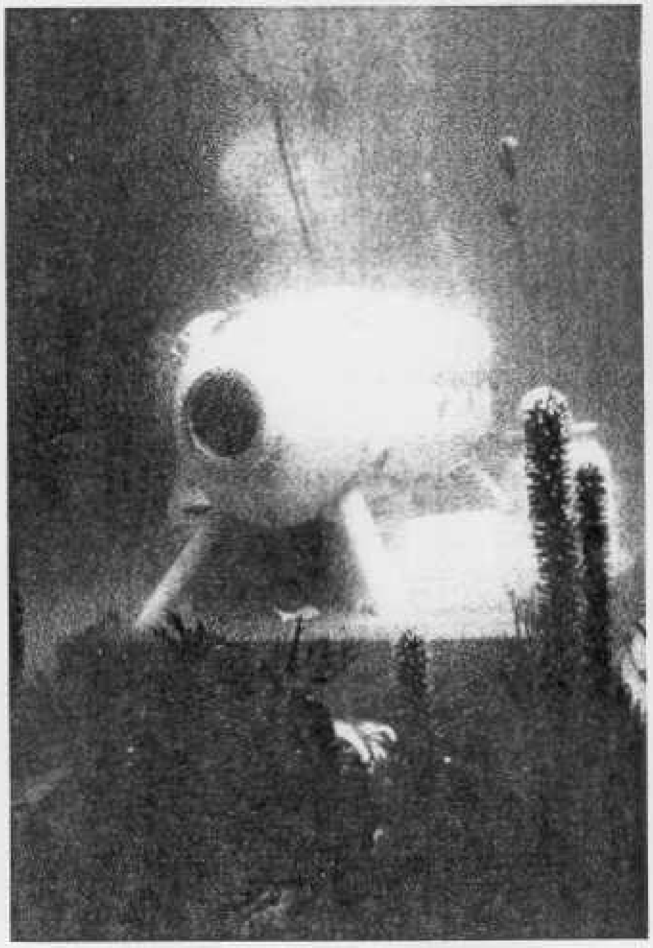
Taking a slightly different approach to the organization of coral reef communities, Reed provides valuable information on variations in the characteristics of the high latitude *Oculina* reefs off of eastern Florida along a shelf and depth gradient. Growth rates of the *Oculina* and species diversity of the associated mollusk and decapod fauna are higher on the deeper shelf-edge reefs (which are episodically subject to upwelling throughout the year) than on shallower reefs nearer shore, even though temperatures are cooler and the corals lack zooxanthellae on the shelf-edge reefs. Since it addresses both growth form and the effects of exogenous nutrients, this paper also relates to chapter 2 (growth and life history patterns of reef organisms) and chapter 5 (ecosystem processes).

The last chapter addresses the question of how such diverse communities of high biomass are maintained while sources of nutrients in tropical waters are low. Drawing upon information from several sites in the Central Pacific, West Australia, and the Indian Ocean, Smith concludes that the overall nutritional requirements of reefs do not differ greatly from those of plankton in the surrounding ocean. He suggests that, while many reef ecosystems do respond to nutrient loading, and while components within the reef ecosystem do exhibit high metabolic activities, the nutritional requirements of the entire reef ecosystem are low. The key to the high biomass and productivity of the ecosystem is efficient transfer of nutrients among different components of the system. Szmant Froelich examines sources of new *vs*. recycled nutrients to explain the high productivity of coral reefs. On the basis of her studies in the Caribbean, she concludes that efficient regeneration of nutrients, perhaps *via* sediments and feces that are concentrated, emitted from pores and caves in the reef framework and then reused, may allow the community to recycle nutrients with a high degree of efficiency. Harrison examines another interesting subsection of the coral reef ecosystem, a lagoon floor community, along a depth gradient (3-55 m) in Enewetak. Production and respiration decline but become more efficient with depth. The sediment community is heterotrophic, representing a sink for carbon produced elsewhere in the atoll ecosystem. Harrison also describes how particular macrobenthic species (alpheid shrimps in Hawaii and callianassid shrimps in Enewetak) can alter community metabolism through bioturbation. Also providing a link with the chapter on community organization and addressing some of the issues raised in Smith's paper, Dollar presents an interesting comparison of the effects of nutrient subsidy upon community structure (species composition, trophic position, diversity, abundance, and biomass) vs. community metabolism (rates of nutrient fluxes) on benthic reef communities at 10 and 70 m depths off of Hawaii. Whereas dramatic effects of a sewage outfall upon the structure of the benthic community were noted in the shallow site, they were not detectable at the deeper outfall. Community metabolism, however, responded strongly to nutrient subsidy at the deep site, indicating the sensitivity of this approach for detecting responses to perturbations in reef ecosystems.

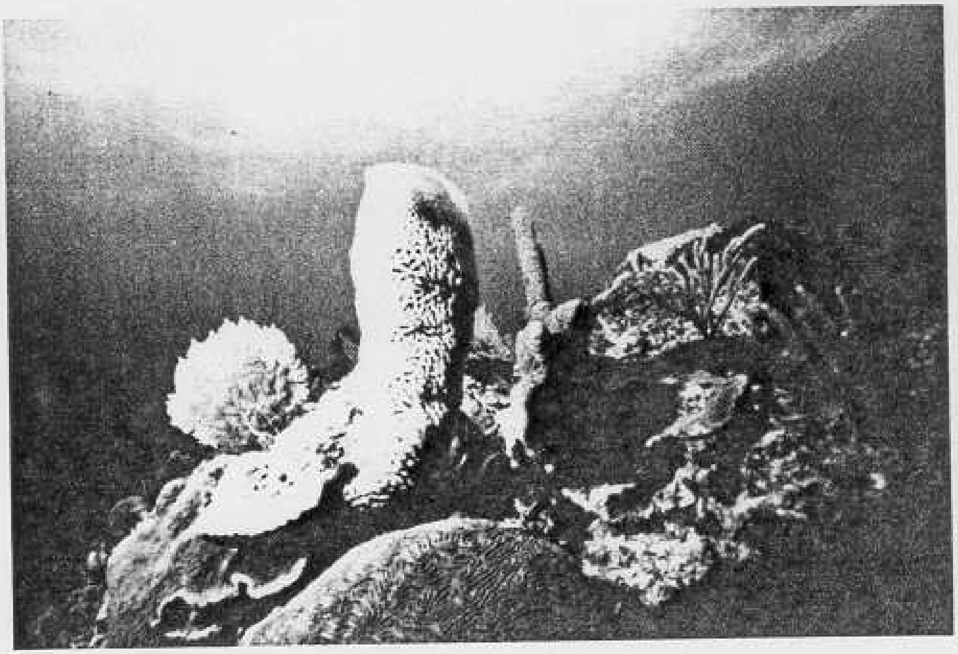
These studies, therefore, represent a series of advancing fronts, many of them new and many of them interconnected, in our knowledge of the processes that govern the marvelously diverse assemblages we know as coral reefs.

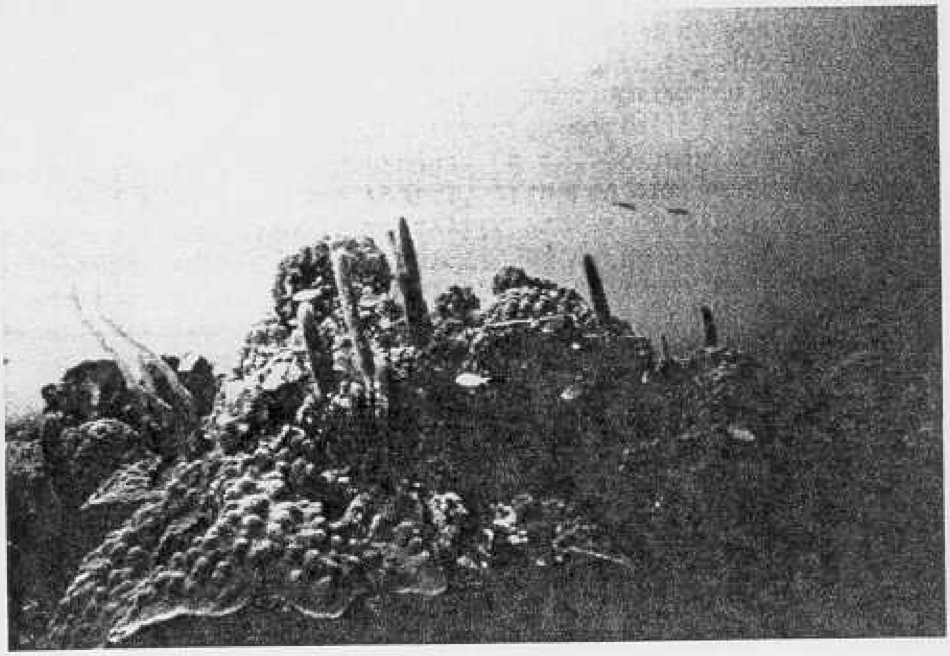
Special thanks are due Ronald Karlson, Kenneth Sebens, William McFarland, Phillip Lobel, Mark Hixon, Stephen Smith, and Alina Szmant Froelich for their primary roles in the workshop. I particularly would like to express my appreciation to Mark Hixon, Ronald Karlson, and Stephen Smith, who contributed valuable ideas, contacted additional contributors, and provided substantial extra assistance during preparations for the workshop and the publication. NOAA's Office of Undersea Research provided support for the publication. I thank Alan Hulbert, Science Director, who provided valuable suggestions and assistance throughout preparation of the volume, and I gratefully acknowledge the help of Marcia Collie, Staff Assistant, for her expert editorial assistance in all of the final stages of preparation of the volume. I am happy to acknowledge the reviewers who contributed valuable time and effort to these proceedings; many parts of the volume were substantially improved by their critiques and suggestions. I also would like to express my appreciation to the authors for their patience and cooperation, which allowed us to have this volume available in time for the workshop. The success of this volume and of the workshop depends, after all, upon the ideas and research contributions of these investigators, and they are gratefully acknowledged. Lastly, especially warm thanks are reserved for my husband, Stephen, and my 1 1/2-year-old son, Alexei, for their even more than usual support and understanding during the final stages of preparation of this volume for publication.





CHAPTER II: GROWTH AND LIFE HISTORY PATTERNS OF CORAL REEF ORGANISMS





SIZE STRUCTURE AND GROWTH RATES IN POPULATIONS OF COLONIAL AND SOLITARY INVERTEBRATES

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ABSTRACT

Benthic invertebrate populations on coral reefs and in other marine communities often occupy several habitat types and display very different size structures in those habitats. The explanation for such size differences may lie in recruitment, mortality, or growth rate differences. These possible causal factors can be separated by carefully monitoring populations of marked individuals or colonies.

INTRODUCTION

Even a brief examination of a coral reef indicates that such a community is easily divided into obvious zones or habitat types. Certain coral species, other sessile invertebrates, and many mobile ones, have distributions that span a number of distinct habitats. In such cases, the sizes of individual organisms or colonies can have radically different distributions as can the maximum sizes attained. The same is true on temperate rocky shores (Fig. 1B,C,D). However, a single period of sampling, resulting in a series of size-frequency histograms, is insufficient to explain the inter-habitat size differences and can serve only to illustrate the pattern. Conclusions arrived at by linking particular distribution types to size or age-dependent mortality patterns (e.g., Grassle and Sanders 1973) can be hypotheses at most, especially when growth is indeterminate or colonial.

A size-frequency histogram skewed to the right (Fig. 1A) reflects a population dominated by large or old individuals and may result from: 1.) constant high rates of juvenile mortality, 2.) infrequent recruitment followed by good juvenile survivorship and growth that slows and approaches an asymptotic size or 3.) rapid juvenile growth with low mortality, growth cessation at a size asymptote, and high rates of mortality only for large individuals, just the opposite of the first explanation. A skew to the left, as in a population dominated by small or young individuals, could result from either constant high mortality at all sizes or from size-selective predation on large individuals (e.g., Grassle and Sanders 1973). Such a distribution could also be found shortly after an infrequent high recruitment event, and be followed by high juvenile mortality and an eventual switch to a distribution skewed toward large individuals. When clonal or colonial organisms are considered, another explanation arises; periods of colony or individual fragmentation (Highsmith 1980, Hughes and Jackson 1980, Sebens 1983) could also produce such a pattern.

If individuals have very indeterminate growth, reaching different size maxima under various microhabitat conditions, a left-skewed distribution might result if a population spans microhabitats, within one of the distinct zones or habitats, that are mostly of poor quality (producing small individuals) with a few patches of better quality (thus larger individuals). This pattern would result even if mortality and recruitment rates were equal in all microhabitats and if mortality was size-independent. Distributions approaching a Gaussian curve could also result from any of the above processes. Finally, size-frequency histograms sometimes exhibit strong multimodolity. A bimodal distribution (Fig. 1A) is often taken as evidence of distinct age classes. Yet, the same distribution would be produced by indeterminate growth and a habitat comprising two microhabitat types 'poor' and 'good'. It should thus be clear that the shapes of size-frequency histograms do little more than illustrate existing patterns. Causal interpretations are impossible from these alone, especially when size and age are at least partially uncoupled.

Once a particular inter-habitat size pattern is determined, it is logical to attempt to find an explanation for the pattern. Assume that a sampling study shows that mean sizes of individuals (or colonies) change across habitats of increasing wave exposure (e.g., Birkeland 1973, Ebert 1982, Sebens and Paine 1978, Sebens ms). The following hypotheses (and probably others) could be proposed:

1) mortality rates are higher in habitats with smaller individuals; mortality may or may not be size-specific (greater for larger individuals).
2) growth rates and thus maximum or asymptotic sizes are greater in habitats with the larger mean individual sizes.
3) recruitment rates of juveniles are greater in habitats with smaller individuals, thus skewing the distribution and reducing the mean size.
4) fission or colony fragmentation rates are higher where the individuals or colonies are generally smaller. Biomass growth could still be as high or higher than in other habitats, but must be considered as 'clonal' growth rate.

A variety of experimental and monitoring approaches must be undertaken to test such hypotheses. Furthermore, the above hypotheses are not mutually exclusive nor are they comprehensive. All of the above causes could influence the size pattern in the same direction. The following discussion will explore the second hypothesis.

Figure 1 A. Shapes of hypothetical size-frequency histograms.
B. Diameters of the octocoral *Alcyonium* in three habitats (Sebens Ms.)
C. Mean sizes of *Alcyonium* versus wave exposure index (elevation of intertidal barnacle zone) (Sebens MS), DIA = average colony diameter
D. Sizes of 10 largest sea anemones (*Phymactis clematis*) as a function of wave exposure index (Sebens and Paine 1978), DIA = basal diameter, mm.

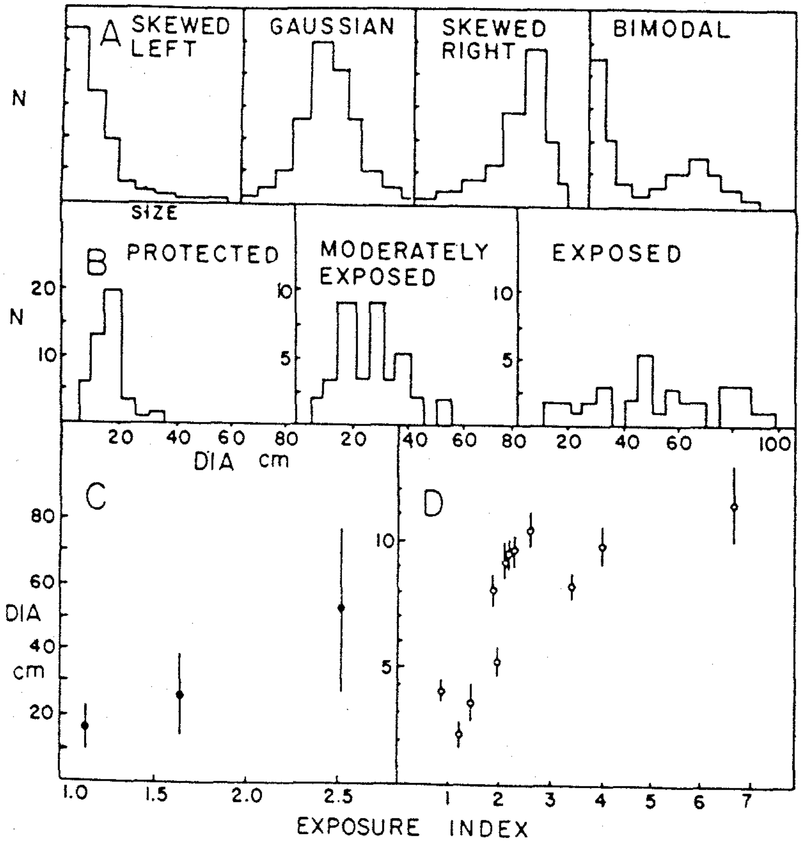
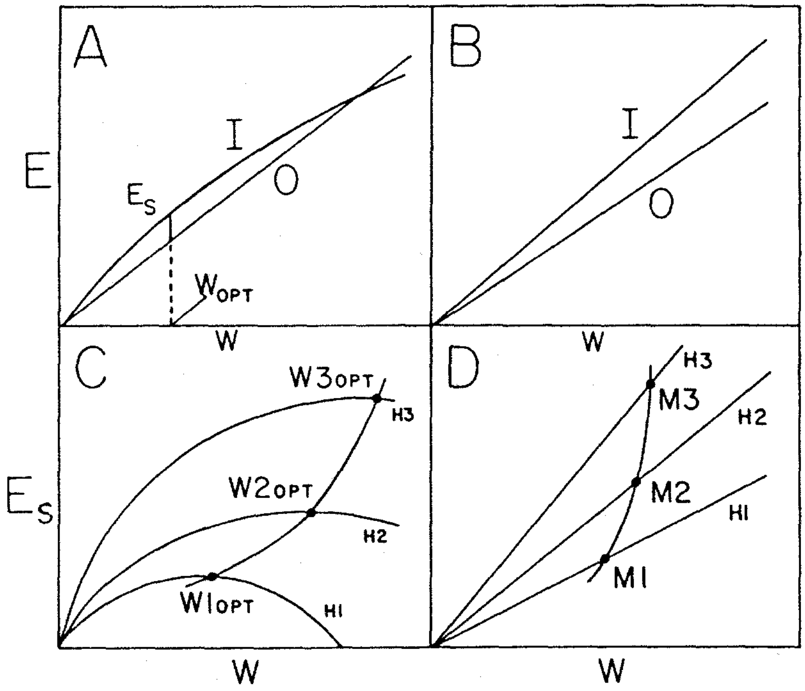


Figure 2 A. Energy intake (I) and cost (O) as functions of individual biomass (W) where $c_1 < c_2$ (see text). W_{opt} = optimum size, E_s = I-O,

B. As in A, but where $c_1 = c_2$, as in colony growth.

C. Energy surplus (E_s) as a function of W where $c_1 < c_2$. Habitats H_1, H_2, H_3 increase in food availability or decrease in physiological cost.

D. As in C but where $c_1 = c_2$, M = maximum size (non-asymptotic), set by non-energetic causal factor such as size-dependent mortality.



GROWTH RATES AND SIZE ASYMPTOTES

Growth rates depend on intrinsic factors such as the allocation of energy to metabolic activity and to reproduction, or genetically determined limits to size. Extrinsic factors that influence growth include local food availability (determining potential energy intake) and the physical nature of the habitat (determining energetic cost). Intertidal habitats with high temperature or desiccation stress, for example, generally increase metabolism integrated over time. The frequency of predators in a particular habitat can affect their prey's energy loss (e.g., escape behavior) and intake (time available for foraging). Growth rate (dW/dt) depends on the difference between energy intake ($k_1W^{c_1}$) and cost ($k_2W^{c_2}$) minus the allocation to reproduction (g(W)) (Sebens 1979, 1982)

$$dW/dt = k_1W^{c_1} - k_2W^{c_2} - g(W)$$

assuming a simple power function relationship between intake or cost and body mass (W) (Fig. 2). Under most conditions, reproductive output (g(W)) (and thus offspring number $\cong$ fitness) will be maximized when W is chosen such that when dW/dt = 0 (growth ceases), $k_1W^{c_1} - k_2W^{c_2}$ is at its greatest. In other words, this hypothetical organism should stop growing at some asymptotic size W_{opt} where $W_{opt} = (c_2k_2/c_1k_1)^{1/(c_1-c_2)}$. The parameter c_2 equals 0.7-1.0 and $c_1 \leq 0.7$ for a variety of organisms, thus producing the predicted size asymptote because energy intake scales at a lower power of mass than does cost. Colonial organisms need not conform to this pattern. If a planar colony doubles in area and mass, both its energy intake and metabolic costs could double as well. If $c_1 \geq c_2$ there is no size asymptote predicted on energetic grounds (Fig. 2B). A similar argument can, however, be used to predict the size of units within a colony (polyps, zooids, etc.) which often show quite determinate growth and a size asymptote (Sebens 1979). On energetic grounds, individuals or colonies (where $c_1 < c_2$) might thus grow to an asymptotic size that maximizes their reproduction under a given set of habitat conditions. This asymptote will be higher in habitats that are 'better' for either prey availability or physical conditions affecting metabolic rate (Fig. 2C). Mortality rates may be high enough, however, in some habitats that the energetically predicted asymptote is never reached.

Mechanisms other than energetics will lead to a habitat-dependent maximum size that is non-asymptotic (growth does not slow and cease). Size-dependent fission (e.g. Sebens 1982) could have such an effect. Size-dependent mortality will also produce a maximum size that can differ between habitats (Fig. 2D). Birkeland (1973) found that seafans in Panama have smaller maximum sizes in habitats with higher wave energy because storm waves tear off large colonies. Octocoral colonies (*Alcyonium siderium*) at wave exposed sites in New England are larger than at calmer sites, but there is no obvious growth cessation in large colonies at the most exposed sites; storm waves may also set the maximum size in this case. Size-selective predation would produce a similar pattern. In fact, Paine (1976) showed that a bimodal distribution of mussel sizes can arise because of constant seastar predation on most size classes; an escape in size occurs for the few mussels that, by chance, grow large enough that they cannot be consumed by seastars.

Figure 3 A. Growth rate differences in two habitats, H_1 and H_2, with equal asymptotic sizes (SA). S1 = initial size, S2 = size after one time interval.
B. Similar growth rates in two habitats, H_1 and H_2, with unequal asymptotic sizes (SA1, SA2).
C. Ford-Walford Plot of A. D. Ford-Walford Plot of B.
E,F. Comparison of mean size increments by size class in two habitats (see text). Bars along abscissa indicate size classes 1-6.

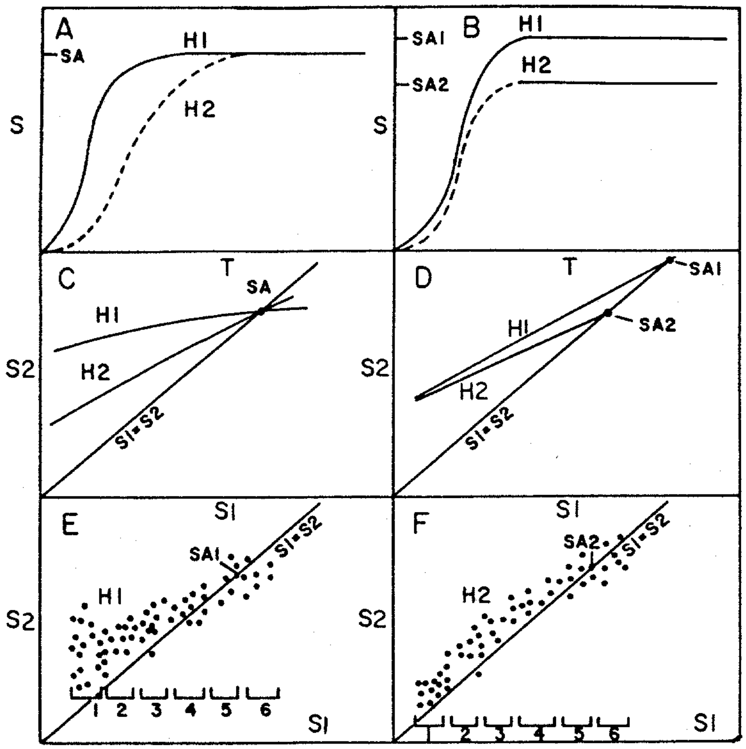
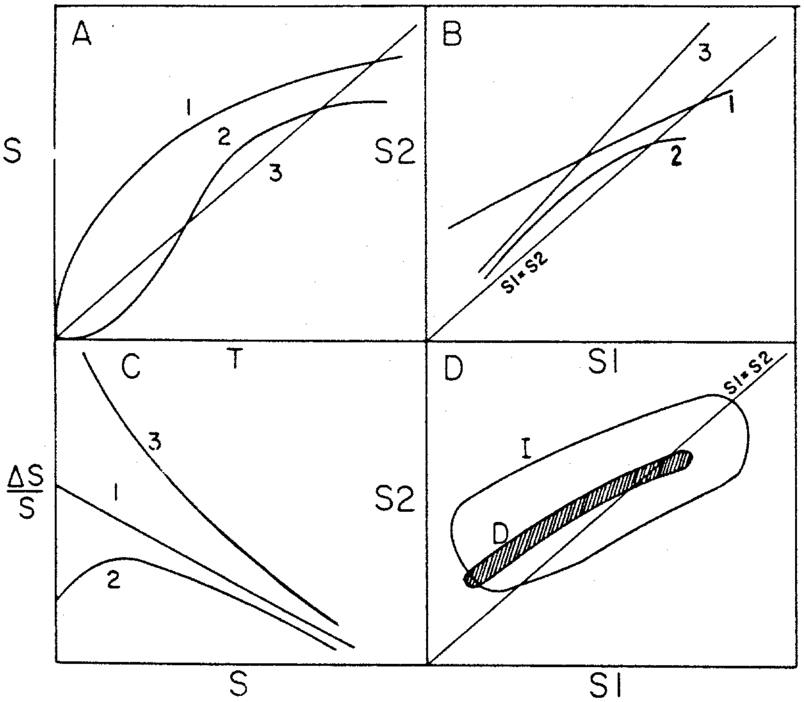


Figure 4 A. Growth models for individuals: 1. parabolic asymptotic (Von Bertalanffy), 2. sigmoid asymptotic (Gompertz), 3. linear, non-asymptotic, T = Time.

B. Ford-Walford Plot. Numbers refer to models as in A.

C. Size-specific growth vs. size (see text). Numbers refers to models as in A.

D. Ford-Walford Plot illustrating determinate growth (D) and relatively indeterminate growth (I), as envelopes around clouds of data points.



COMPARING GROWTH RATES

Testing the hypothesis that growth rates differ across habitats involves some means of tagging, mapping, or otherwise identifying individuals covering the full range of size classes. It is perfectly possible to have similar asymptotic or maximum sizes in two habitats yet to have significantly different juvenile growth rates, for example. Alternatively, statistically indistinguishable growth rates at all sizes could still lead to asymptotic sizes that differ significantly (Fig. 3 A-D). One of the most widely used means of comparing growth increments is the Ford-Walford plot (Ricker 1975; Ebert 1980, 1982; Sebens 1983) which graphs initial size on the abcissa and size after some time interval on the ordinate (Figs. 3C,D;4B,D). This presentation does not show any single individual's growth through all size classes, but instead presents a 'snapshot' of growth in the entire population over a single interval. Variations of the Ford-Walford plot can also be used to fit growth models (von Bertalanffy, Gompertz, Richards functions; Ricker 1975, Yamaguchi 1975, Ebert 1980) (Fig. 4 A, B). A regression line through the points on a Ford-Walford plot (either or both axes can be transformed to produce a linear plot) can be tested for significant differences in slope or intercept, thus testing the hypothesis that differences in growth rates exist between habitats. If a growth model is to be fit to the data, Ebert (1980, 1982) suggests that the Richards function be used because it has the ability to incorporate deviations from linearity which are especially common in the small size classes.

Growth increments can also be plotted as the specific growth rate ($\Delta S \cdot \Delta t^{-1} \cdot S^{-1}$) on the ordinate vs. size (S) at the middle of the time interval Δt on the abscissa (reviewed in Kaufmann 1981) (Fig. 4 C). This method has the advantage of allowing growth to be measured over different time periods (Δt). Such plots can also be subjected to regressions and these lines can then be used to fit various growth models. This technique has the disadvantage that size (S) is incorporated into both parameters of the regression, making statistical interpretation difficult by violating the assumption of independence (Ricker 1975). The Ford-Walford plot avoids this problem, and can incorporate a small degree of variability in Δt values by assuming short-term linear growth and normalizing all data to a constant time interval.

The Ford-Walford plot allows direct examination of growth and 'degrowth', growth rate as a function of size, and size asymptotes or maxima. The degree of 'indeterminateness' is also evident as the spread around the regression line (Fig. 4D), as is the fraction of individuals below the zero growth line (showing shrinkage or degrowth). Coral growth, measured as density bands in the skeleton, could be compared in this manner, as could whole colony size increase. Growth can also be compared statistically without resorting to either regression lines (assuming linearity) or any particular growth model. If the data are broken up into size classes (Fig. 3E, F) such that there is a reasonably large number of points in each size class, then the mean growth increments in each size class can be compared across habitats (e.g., by analysis of variance, Sebens 1983). This method allows comparison across several habitats (via a multiple comparisons test) and determines where in the size distribution the significant differences actually occur. This is the only method that would pick up differences between habitats which have equal maximum individual sizes and differ only in early growth rate.

Growth by fission and fragmentation cannot be incorporated directly into a Ford-Walford plot. A good descriptor of such growth is the rate of biomass change (e.g., exponential function) within a clone, colony, or group of colony fragments. However, some clones or colonies may have reached limits imposed by available space. Therefore, choosing experimental subjects not apparently space limited, or removing such limits experimentally (e.g., clearing space around the subject, transplanting) may be necessary to compare potential growth rates (Sebens 1983).

SUGGESTIONS AND LIMITATIONS

There is no shortcut method that allows an investigator to read causation from static samples of size distributions across populations. Mortality schedules can be arrived at only by following individuals or cohorts over time. It is theoretically possible to calculate an average overall mortality from a size distribution (e.g. Ebert 1982), but this approach assumes constant mortality and recruitment rates. It is the latter assumption that causes real problems because many sessile invertebrates have successful recruitment only rarely and sometimes many years apart. In colonial organisms, partial mortality (e.g. corals, Hughes and Jackson 1980) presents another problem for interhabitat comparisons. This process is best treated as 'degrowth' or 'shrinkage' and can be compared across habitats directly. Similarly, binary fission does not constitute 'mortality' of the original individual, even though that individual no longer exists as such. Fission rates can also be compared directly either numerically or by using biomass (Sebens 1983).

Growth rate differences, resulting from habitat or microhabitat variability, can produce some of the observed size gradients within populations. There are several methods for comparing growth and for fitting growth models; however, it is not necessary to choose a growth model if the goal of a study is only to determine whether or not growth rates differ across habitats. Ford-Walford plots of growth increments can be used for this directly, and can also illustrate growth rate variability and the extent of degrowth or shrinkage in the population. An even simpler growth comparison between habitats would be to compare only maximum size (mean size of largest N individuals) and growth at some earlier stage, for example at 1/2 the maximum size in the habitat with the smallest maximum size. This would necessitate fewer data points but would answer the basic question of whether or not growth rate differences could be causing the observed pattern. However, even if growth rate differences can be established, either mortality, recruitment, or fragmentation could still be major factors affecting size distributions across habitats, and must be investigated.

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LIFE HISTORIES AND GROWTH OF CORALS OVER A DEPTH GRADIENT

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ABSTRACT

Results from long term monitoring of coral populations from -10m to -35m show that several important life history parameters are strongly correlated with depth. Typically, coral colonies tend to settle in greater numbers in shallow water, where they are also more likely to be injured or killed compared to deeper sites. Colony extension rates were found to be very weakly dependent on depth, with some of the fastest growing colonies at -55m and -35m growing faster than many -10m specimens. The net growth rate of shallow corals may be limited by higher rates of injuries.

INTRODUCTION

One of the best studied features of coral reefs is the variation in species composition and area associated with depth gradients (see review in Stoddart 1969). Less well understood is how such changes in relative abundance are brought about. The number of colonies in a coral population is determined by the balance between sexual (and, in some species, asexual) recruitment and colony mortality, while colony size is a function of time since settlement and rates of growth and injury. In the present study, these aspects of the population dynamics of five species of foliaceous corals (*Agaricia agaricites*, *A. lamarcki*, *Leptoseris cucullata*, *Porites astreoides*, and *Montastrea annularis*) were studied on the north coast of Jamaica over a wide depth range (-10m to -55m). I present here some of the major findings; a fuller account, including species comparisons, will be presented elsewhere (Hughes and Jackson, in review).

METHODS

Twelve $1m^2$ quadrats were tied permanently to the reefs off the Discovery Bay Marine Laboratory between -10m and -20m ("shallow") and at -35m ("deep"). The quadrats, which enclosed more than 1,000 foliaceous coral colonies were photographed each year from 1977 to 1980. Analysis of the photographs yielded population structures, as well as rates of mortality and sexual recruitment. Coral growth was measured *in situ* using fixed reference points (nails) and a plastic tape measure, and at -55m by collection of Alizarin stained colonies. All colonies in the quadrats were measured regardless of colony condition, size or ease of access.

RESULTS

Many important population parameters were strongly dependent on depth. The size-frequency distribution of colonies of all species were dominated by small corals over their entire depth range, but especially in shallow water. Large colonies greater than $200cm^2$ in area constituted only 8.9% of the total colony counts from -10m to -20m, compared to 17.4% at -35m.

Depending on species, the mortality rate of whole colonies for all size classes combined was 2-6 times higher in shallow (-10m to -20m) compared to deep water (-35m) (Table 1). This reflects, in part, depth-related changes in the proportion of small colonies in the populations, since large corals are much less likely to be killed than small (e.g. Connell 1973, Loya 1976, Hughes and Jackson 1980). However, within-size class mortality rates were also invariably higher in shallow water, particularly for the largest corals. Not a single colony out of 32 greater than 200cm^2 was killed at -35m in three years, compared to the loss of 8 out of 39 colonies of the same size at -10m to -20m.

Further more, total tissue losses (from both injuries and whole colony mortality) were greater in shallow water (Table 1). The relative importance of injuries and whole mortality also varied with depth. At -35m fully 80% of the coral tissue destroyed was due to injuries, particularly to large colonies, while in shallow populations losses from injuries and whole mortality were almost equal.

The higher rates of colony and tissue losses in shallow water were compensated somewhat by enhanced amounts of larval recruitment, which was more than twice the levels of the deep (-35m) quadrats (Table 1).

Table 1. Various aspects of coral population dynamics as a function of depth for the three species common at all depths. (A) Percentage mortality of coral colonies monitored photographically from 1977 to 1980. The total number of 1977 colonies was 425 shallow (-10m to -20m), and 301 deep (-35m). (B) Total percentage area of coral tissue destroyed by injuries and whole colony mortality. (C) Number of new recruits observed settling within the permanent quadrats (equal areas shallow and deep) from 1977 to 1980.

		A. agaricites	A. lamarcki	L. cucullata
(A) % of colonies Killed	Shallow	41%	39%	63%
	Deep	21%	6%	34%
(B) Amount of tissue killed (% of '77 area)	Shallow	47%	57%	103%
	Deep	33%	9%	56%
(C) Larval Settlement (no./12m^2/3yrs)	Shallow	60	1	39
	Deep	25	3	16

Coral Growth

Within-species growth rates of foliaceous A. agaricites, A. lamarcki, P. astreoides and M. annularis were only weakly dependent on depth, and many individual colonies of corals at -35m and -55m exceeded the extension rates of specimens in shallow water (Fig. 1). Deeper foliaceous corals were less likely to have their growth interrupted by partial mortality, and also had thinner skeletons (Hughes 1982), i.e., they could increase their surface area with a smaller addition of calcium carbonate, so that they often grew surprisingly fast relative to shallow foliaceous corals.

DISCUSSION

Several previous studies have shown only a very weak relationship between lateral coral growth and depth because of considerable within-depth variation between colonies (see Highsmith 1979 for review). This variability is often artificially eliminated by collecting biased samples of undamaged colonies, which probably grow faster than colonies that have recently suffered injuries. Coral injuries were found in the present study to be common events; of 883 colonies

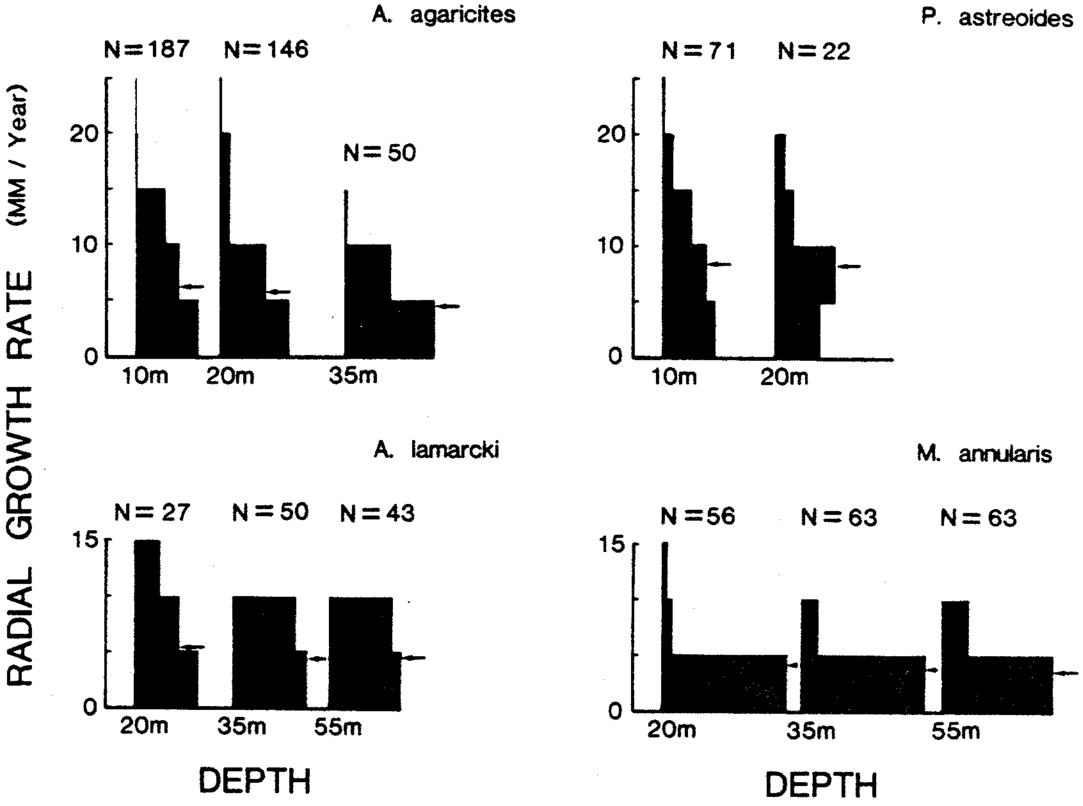

Figure 1. Frequency distribution of annual radial growth rates versus depth for A. agaricites, A. lamarcki, P. astreoides and M. annularis. Measurements at each depth were categorized into 5mm growth classes and the frequency distribution (shaded areas) standardized by dividing by the sample size. The sample sizes (N) indicate the number of colonies measured in situ or after staining and collection. The total number of colonies measured or stained over the three years was 778. Arrows signify means.

surviving from 1977 to 1980, over 75% were injured at least once. Although deeper colonies tend to be larger, they are not necessarily much older than smaller, shallow colonies, whose history of growth and injury will often be more complex. Whether similarly sized corals of different past histories will have comparable expectations of survival and fecundity remains an interesting, but untested, question.

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DEPTH-RELATED CHANGES IN THE COLONY FORM OF THE REEF CORAL PORITES ASTREOIDES

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ABSTRACT

The depth-related morphological transition of Porites astreoides colonies from near-hemispherical to flattened forms is well known, but requires closer examination. For this reason, colonies of P. astreoides were surveyed at 7 sites spanning a depth range of 27 m at Discovery Bay, Jamaica. The depth, substrate slope, and degree of exposure of each colony were assessed prior to measurements of colony shape and corallite structure. Regression analysis of quantum irradiance measurements taken throughout the study area provided equations to estimate the light available to each colony as a function of its depth, substrate slope, and exposure. Predicted wave heights and periods from wind statistics were used in conjunction with theoretical equations for the attenuation of wave motion with depth to estimate the relative water movement about each colony.

It was found that availability of light does not directly determine the shape of the colony, but only sets an upper limit to colony height, a limit that decreases with decreasing illumination. Similarly, water movement places only an upper constraint on morphological variation, with only very flat colonies possible in high energy environments. Consequently, flattened colonies were found at all depths, but were exclusively present in very shallow water (due to high turbulence) and in very deep water (due to low light). These morphological constraints were shown to be primarily the result of a phenotypic response of the colony to its environment.

INTRODUCTION

Coral reefs typically exhibit sharp gradients in environmental factors such as illumination and water movement over relatively short vertical or horizontal distances. Physical gradients in relation to depth and their effects on reef organisms are of particular interest at this workshop on deep and shallow reefs. One approach to investigating the impact of depth and depth-related variables on reefs is to examine those organisms that have somehow managed to overcome the physiological stresses imposed by the depth gradient and that have, as a consequence, achieved a relatively wide depth range. By studying the adaptations of these eurytopic reef organisms we can better understand the effects of depth on the entire biota.

Among the reef-building scleractinian corals of the Caribbean region, several species that are primarily massive in their colonial growth form exhibit broad depth ranges for light-dependent organisms. They include Montastrea annularis and Porites astreoides, both of which are common from shallow lagoons to depths of 27 m or more (Roos, 1964; Goreau & Goreau, 1973). These species, along with others such as Meandrina meandrites, Stephanocoenia michelinii, Colpophyllia natans, C. breviserialis, Dichocoenia stokesi, and Montastrea cavernosa, show a morphological transition from roughly hemispherical colonies in shallow water to flattened plates at greater depth. The consensus has been that this change in colony shape is a phenotypic response to maximize light interception by the polyps (Goreau, 1959, 1963; Roos, 1964; Macintyre & Smith, 1974). This view was reinforced by Roos (1967), who was able to relate morphological change in Porites *astreoides* colonies on Curacao reefs to measured changes in the distribution of underwater radiance, and who observed the expected morphological changes in transplanted *Montastrea annularis* in computer simulations of coral growth based on empirical measurements of light distribution and on simple assumptions about the effects of light on calcification.

As part of a larger study of the ecology and variation of the genus *Porites* (Brakel, 1976), I collected detailed information on the colony shape and distribution of *Porites astreoides* on Jamaican reefs. These data were supplemented by relatively simple, but objective and repeatable, estimates of two important depth-related variables, water movement and irradiance. The results presented below reveal that the generally recognized depth-related morphological trend is more complex than expected.

METHODS

Study area

Observations and collections were made on the north coast of Jamaica at Discovery Bay. The structure and zonation of the reefs of this region have been described by Goreau (1959) and Goreau & Goreau (1973). I selected 7 different reef habitats as study sites, encompassing a depth range of 27 m (Fig. 1). Four sites were located on the exposed seaward side of the reef crest; 3 additional sites were situated in the sheltered, more turbid waters leeward of the fringing reef. At each study site the coral fauna was surveyed in quadrats along transect lines perpendicular to the slope of the reef. For every *Porites* encountered, the following features were recorded: (1) the slope of the substrate on which the colony was growing; (2) the exposure of the colony, measured on an arbitrary scale from 0 (fully exposed, open to water on all sides) to 3 (in a deep hollow or crevice); and (3) the shape of the colony, based on a series of morphological measurements described below.

Irradiance estimates for each colony

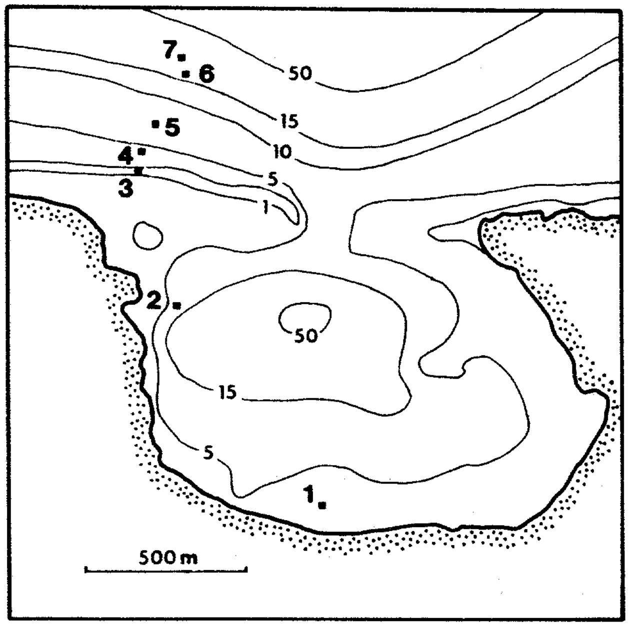

Fig. 1. Study sites at Discovery Bay, Jamaica. Depth contours are in meters.

Light measurements were made at all sites using a diver-operated Lambda Instruments L192S underwater quantum sensor coupled to an L185 quantum/radiometer/photometer mounted in an Ikelite 5910 underwater housing. In addition to downward irradiance taken with the cosine sensor pointed straight up, measurements were also taken at various angles from the vertical in the four cardinal directions, providing data on the 3-dimensional angular irradiance distribution. Results relevant to this paper are summarized below; complete details of the methods and statistical analyses are provided elsewhere (Brakel, 1979). Regression equations were obtained to describe the attenuation of light with depth. Two equations were necessary, since the water column in the bay (sites 1-3) had a light extinction coefficient significantly different from that of the fore reef (sites 4-7):

$$\ln I = 4.31 - 0.11\ d \quad \text{(bay)}$$

$$\ln I = 4.20 - 0.06\ d \quad \text{(fore reef)},$$

where d is the depth in meters. The equations predict the midday irradiance at various depths on clear, sunny days as a percentage of the surface irradiance. These expressions for I were modified to take into account the slope, s, of the substrate on which the coral was growing, using a relationship also developed from regression analysis:

$$F = \exp[(4.61 - 0.02\ s)/100]$$

The light score, L, for each coral was further modified by the exposure, E, of the coral (a measure of the amount of shading by overarching branches of neighboring corals and other reef features described above):

$$L = I\ F\ [1 - (E/6)].$$

Estimates of water movement

A relative water movement score for each coral was derived from theoretical calculations. In the belt of the NE trade winds, the winds blow from the E to NE 88% of the time with a maximum velocity of 35 km/hr (U.S. Weather Bureau, 1962). According to the wave forecasting curves of Bretschneider (1966), winds of this direction and magnitude for 8 hours would generate waves with a period, T, of 5.9 sec, and a significant wave height, H, of 159 cm on the north coast of Jamaica. Empirical observations of wave height (Reiswig, 1971:114; U.S. Weather Bureau, 1959) fall in the same range as the predictions. Under the maximum trade wind conditions specified, the fore reef (sites 4-7) would be under the influence of the surface conditions given above. On the leeward side of the reef crest (sites 1-3), the maximum fetch is 1 km, limiting wave conditions to H = 61 cm, T = 2.5 sec according to the wave prediction curves.

The effect of surface waves diminishes with increasing depth, d, below the surface, in such a manner that the major axis, A, of the ellipse traced out by a particle as the wave passes over is approximated by the following equation, modified from Eagleson and Dean (1966):

$$A = H \exp[(-4\pi^2 d)/(gT^2)],$$

where g is the universal gravitational constant. Simplifying all the constants, this reduces to:

$$A = H \exp[(-4.062\ d)/T^2].$$

The wave movement score for each colony was then defined as:

$$W = A/T,$$

to give an arbitrary, but reproducible measure of the average expected wave-induced water movement.

Measurement of colony shape

Although an elaborate multivariate analysis of various aspects of colony morphology can be done (see Brakel, 1976), for the purposes of this discussion a simple measure of the degree of flattening of the colony will suffice. I used the relative colony height, defined as the average diameter of the colony in the plane of the substrate divided by its height measured perpendicular to the substrate. For a perfectly hemispherical colony the relative colony height would be 0.5; for a very flat colony it could be as little as 0.05. To avoid the allometric complications inherent in such a ratio of morphological measurements, it was found necessary to exclude all very small colonies (less than 9 cm in diameter)

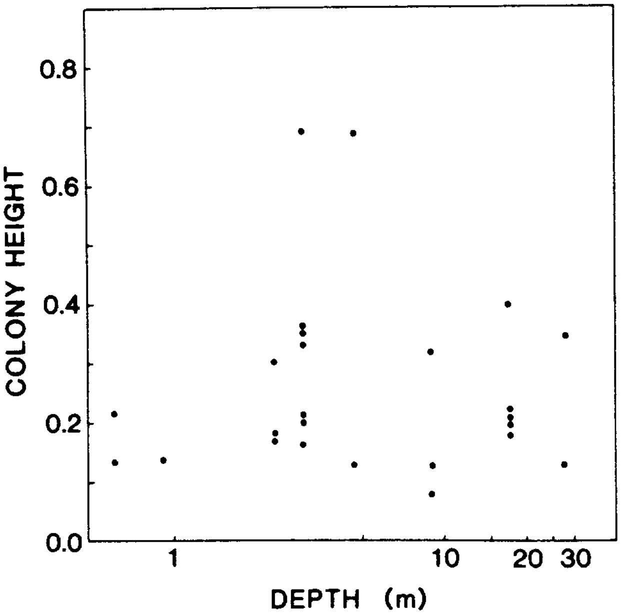

Fig. 2. Graph of relative colony height as a function of depth.

from the analysis. Those few colonies with diameters greater than 30 cm were also omitted.

The above procedures yielded data on 27 P. astreoides colonies. For each colony the relative colony height was measured and the irradiance and water movement in the immediate vicinity of the colony (based on its depth, location, exposure, and substrate slope) were estimated.

RESULTS

The mean relative colony height of the corals sampled was 0.24 with a range of 0.08 to 0.69.

A graph of colony height as a function of depth is shown in Fig. 2. Depth is plotted on a logarithmic scale to emphasize differences among the shallower sites where physical gradients are most pronounced. Surprisingly, the expected monotonic relationship between depth and colony morphology is not seen.

When irradiance, L, is plotted against colony height (Fig. 3), a linear or curvilinear relationship is still not apparent. Instead, it appears that irradiance acts only to set an upper limit to colony height: under high illumination all colony heights are possible, but as available light diminishes only increasingly flattened colonies are seen to occur. The line drawn on the graph marks the limit to colony height imposed by light regime.

The graph of colony height as a function of water movement, W, (Fig. 4) shows that this parameter also exercises a constraining effect on morphological variation without directly determining the height of the colony. At low wave energies the full range of corallum variability is seen; in more turbulent micro-environments only the more flattened forms are found.

DISCUSSION

The data on Porites astreoides illustrate that the response of organisms such as corals to changes in depth can be complex. As depth increases, different biologically-relevant physical and chemical variables such as illumination and water

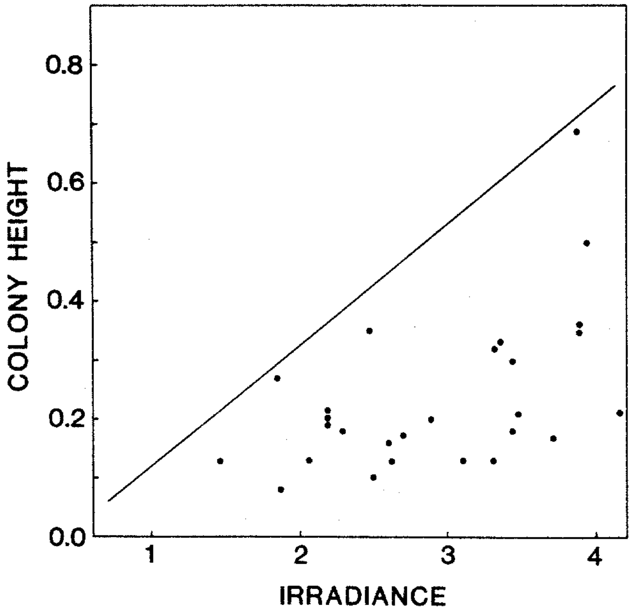

Fig. 3. Plot of relative colony height as a function of irradiance.

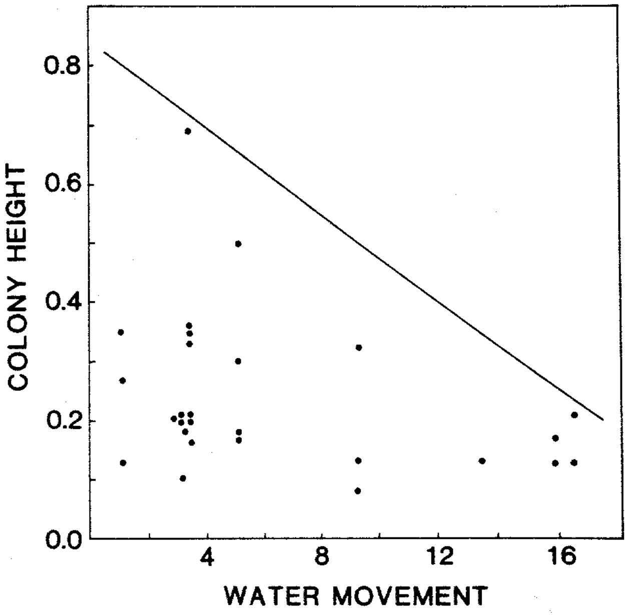

Fig. 4. Graph of relative colony height against water movement.

movement, as well as salinity, temperature, and sedimentation rates, may vary in disparate ways. When all these factors act at once, individually or synergistically, on the physiology and morphology of the benthos, the outcome is not easily foreseen.

Even when considered in isolation, an ecological variable such as irradiance or water movement does not have the expected biological effects. One might have anticipated some linear relationship between irradiance or wave energy and relative colony height, a relationship amenable to correlation or regression analysis. In actuality, the roles of light and water movement are quite different: they do not directly determine the shape of the colony, but rather set limits to the possible range of morphological variation.

A detailed discussion of the physiology of coral colony growth is beyond the scope of this paper, but one question that should be addressed is whether the observed environmental constraints on Porites colony morphology are environmentally-induced or the result of natural selection at different depths for genotypes with the requisite inherent shape characteristics. Examination of fine skeletal structures of the individual corallites known to be unaffected by environmental conditions (Brakel, 1977) showed that those colonies most flattened or constrained with respect to colony height are not genetically distinct, but constitute a random subsample of the population. This implies that their modified colony shape is the result of a direct physiological response to environmental stimuli. The observed morphological transition of P. astreoides in relation to irradiance and water movement is therefore principally due to phenotypic plasticity, not selection.

The mechanism by which this morphological transition occurs is not understood. Goreau (1963) and Barnes (1973) suggested that the form of the corallum is the result of two separate processes; skeletal accretion (dependent on light) and tissue growth (independent of light), so that at low light intensities calcification cannot keep up with tissue growth, resulting in the lateral proliferation of excess tissue to form a flattened colony. The adaptive significance of a flat colony profile in environments with high wave action has been discussed by Graus, et al. (1977), but again the mechanism by which water movement controls colony height is not clear. Jokiel (1978) has suggested that water movement influences corals by controlling the exchange of materials between the polyps and the surrounding sea water. Whatever the nature of the physiological controls on coral growth and form, it is evident that, with changes in depth, environmental factors act on the colony in intricate ways and that the adaptive response of the coral can be subtle and complex.

ACKNOWLEDGMENTS

This research was made possible with the support of the Biology Department, Yale University, and with the assistance and facilities provided by the Discovery Bay Marine Laboratory.

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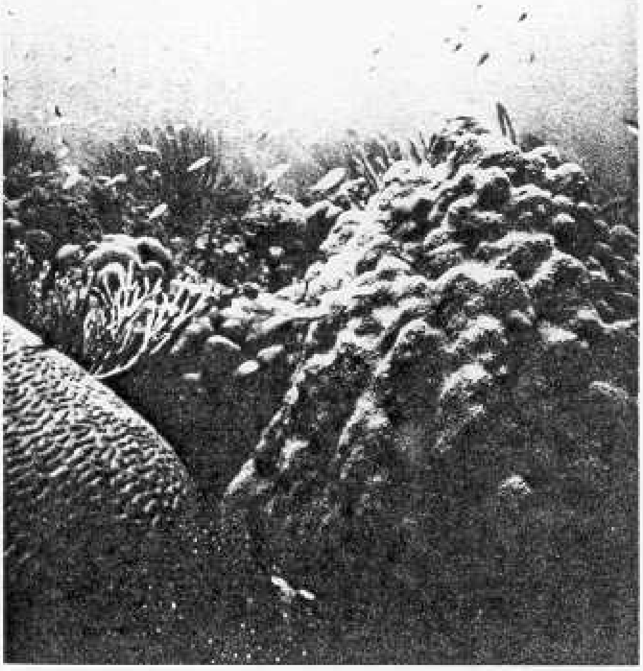
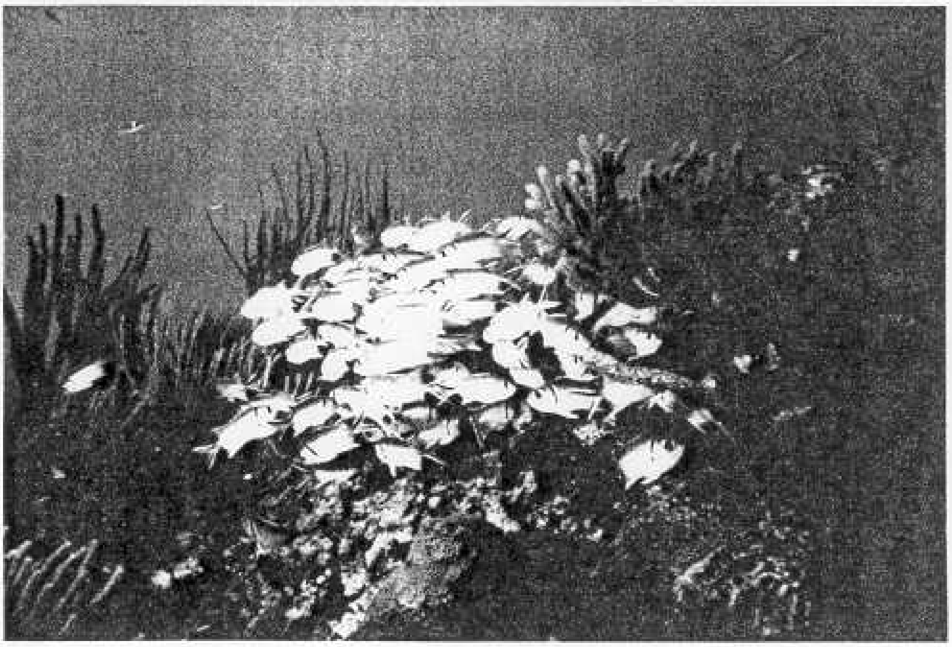
CHAPTER III: THE DYNAMICS OF RECRUITMENT IN CORAL REEF ORGANISMS





REEF FISHES AT SEA: OCEAN CURRENTS AND THE ADVECTION OF LARVAE

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ABSTRACT

This paper presents an overview of an interdisciplinary study of the kinematics and dynamics of reef fish larvae in offshore currents, especially mesoscale quasigeostrophic eddies. We develop herein the conceptual framework and background information for our on-going studies, the preliminary results of which will be presented at the 1983 ASZ meetings. The focus of this research has been to define the appropriate scales in ocean circulation relative to the developmental biology and reproductive ecology of coastal marine fishes whose larvae are planktonic.

INTRODUCTION

Interest in the topic of larval dispersal by ocean currents has been longstanding and its broad implications to ecology, evolution and fisheries are well known. Yet, the factors that ultimately limit the distribution of oceanic planktonic organisms have not been clearly specified (Wiebe 1976). The constraints upon the transport of planktonic larvae along coasts and across oceans are few. Only the direction and velocity of the prevailing currents, the timing of reproduction, and the length of the planktonic stage place limits upon where, when and how far species are transported (Scheltema 1972, 1977). One critical variable in the survival of certain shore-dwelling species may be the phase and quantity of larvae of one species relative to the phasing and quantity of another in contest for spaces sporadically open to occupancy (Sale 1977, 1978).

Determining the fate of fish larvae as plankton in open ocean currents is not just interesting with regard to the life cycle of fishes. It is also crucial to the resolution of key ecological hypotheses concerning species distributions and diversity in reef and shore communities (Helfman 1978, McFarland 1982). Furthermore, resolution of these important questions leads directly into a discussion about the evolutionary strategies of island species, one notable feature of which is the origin and maintenance of endemic species. Other aspects of this work are basic to applied fisheries and the development of effective fisheries management plans, since a majority of food, game and aquarium fishes possess planktonic larvae and/or may seek larval fishes as food (e.g., Huntsman *et al*. 1982).

The following discussion highlights the key questions and outlines significant results and references pertaining to the study of planktonic larvae of coastal marine fishes.

An overall approach for the study of physical oceanic processes affecting ichthyoplankton distributions ideally would include: 1) mapping current patterns and confirming the appropriate scales of variability, 2) strategic sampling of plankton in and out of specified currents, 3) relating the time scales of current variability to the duration of pelagic lifespans of larvae by aging techniques (especially otolith ring counts), 4) monitoring spawning and recruitment of shore fishes in relation to the dynamics of the offshore current field. Some other aspects for such an interdisciplinary study also have been discussed by Richards (1982).

OCEAN EDDIES AND PLANKTON

Mesoscale eddies, in general, are the features of ocean circulation which most likely entrain planktonic organisms, thereby affecting their transport (Wiebe et al. 1976, Cox and Wiebe 1979, Angel and Fasham, 1983). In particular, recent findings on the variable nature of ocean circulation around islands and along coasts (for review see Chopra 1973, Hogg et al. 1978) and the increasing understanding of eddy entrainment and advective processes provide a potential solution to the anomolous spawning seasons of tropical marine fishes at some locations. The variable occurrence of mesoscale ocean eddies (on the order of monthly and perhaps seasonal periods) and the peak reproductive season of coastal marine animals (with planktonic larvae) may be synoptic. We are studying such a case in the Hawaiian Islands.

We will discuss the potential role of eddies in marine biology as a general phenomenon. Among the specific details yet to be carefully considered are any potential differences that may exist according to the type of eddy involved (Angel and Fashman 1983). Two types of eddies are known: warm-core or anticyclonic eddies and cold-core or cyclonic eddies. In the northern hemisphere anticyclonic eddies rotate clockwise and cyclonic eddies rotate counterclockwise. Eddies develop by a variety of physical mechanisms including wake phenomena in the lee of islands and by extreme meanders of a strong stream current. Whether or not the way in which an eddy is generated has a subsequent impact on its biological function is unknown. Robinson (1983) recently has compiled a comprehensive review of the role of eddies in marine science.

A more general physical feature relating to the distribution of pelagic fishes and ichthyoplankton are thermal fronts. Thermal fronts are sharp gradients of temperature with distance. The expression of fronts can result from several sources, including the edges of eddies, upwellings, current shears, convergence and divergence zones, jet streams and, vertically, at the thermocline. To what degree pelagic larvae of shore fishes are able to select locations within currents by temperature or other cues is unknown. The overall correlation of fish distributions across fronts in general has yet to be determined. The possibility also exists that various fronts may differ in some physical way that is detectable by fishes but which we have not yet recognized. There are, however, good examples of the distribution of myctophid fishes consistent with thermal patterns across fronts and eddies (Brandt 1981, 1983; Brandt and Wadley 1981). Myctophids are mesopelagic fishes whose entire lifespans are spent in the open sea.

It is not our intent here to review past works on plankton communities. The open ocean dynamics of plankton migrations and global distributions are well known and have been extensively discussed by others (e.g., Reid et al. 1978, Wiebe et al. 1976, Cox and Wiebe 1979, Wiebe and Boyd 1978, Boyd et al. 1978). Among the remaining questions is how the physical dynamics interact with the biological dynamics (e.g., reproductive patterns, swimming and energetic abilities of the plankton,etc.) to form and maintain a "patch" (Haury et al. 1978). Evidence for the role of ocean eddies in trapping planktonic organisms can be obtained by sampling zooplankton densities inside and outside of eddies. In the few cases where such discrete sampling has been done, the general result has shown higher abundances of zooplankton in eddies than in surrounding waters (Uda 1957, Uda and Ishino 1958, Wiebe et al. 1976, Ortner et al. 1978). Other planktonic populations can become trapped inside eddies and transported out of the species' normal range as the eddies move (Wiebe et al. 1976, Ortner et al. 1978, Boyd et al. 1978, Wiebe and Boyd 1979, Cox and Wiebe 1979). Loeb (1979) presented data on larvae and mesopelagic fishes which accumulate inside the North Pacific Gyre (also, Reid et al. 1978).

REEF FISHES SPAWNING STRATEGIES

The longstanding belief that tropical marine animals spawn continuously throughout the year without seasonal variation no longer appears generally valid. Distinct peaks of reproduction have now been documented for marine fishes in several tropical localities (Munro et al. 1973, Watson and Leis 1974, Johannes 1978, Lobel 1978, Nzioka 1979). In the absence of strong and recognizable seasonal fluctuations characteristic of the temperate latitudes, annual periods of peak reproduction by tropical coastal marine species are difficult to explain.

We have collected data and examined evidence which suggests that seasonal reproduction by certain tropical species may be in phase with variable offshore quasigeostrophic mesoscale circulation. This circulation is a major environmental factor determining the fate of the planktonic larvae of coastal species. The model species is one which lives its adult life in coastal marine habitats but whose larvae are planktonic in offshore waters. This is typical for a majority of reef fishes. Such species may spawn seasonally in response to natural selection acting on the survival of planktonic offspring. These offspring float with ocean currents which advect and disperse them.

Past emphasis has been on the idea that widespread transport of planktonic larvae across long distances is an evolutionary adaptation reducing the susceptibility of a population or lineage to extinction by local catastrophes (Vermeij 1978). The ecology of some shore fishes, however, suggests the possibility that transport of offspring far from the site of origin or native habitat may not always be favored by Natural Selection. The "lottery" hypothesis, described by Sale (1977, 1978, 1982), is based on experimental field evidence showing that the availability of living sites limits the numbers of pomacentrid fishes and that similar species utilize the same kind of space. Priority of arrival as recruits, rather than subtle differences in ecological requirements or competitive abilities as adults, appears to determine which species occupy each site (Sale 1978). Thus, Natural Selection should favor those individuals of a species who maximize the return of their offspring to home reefs. Sale's lottery hypothesis has stirred considerable debate (Smith 1978, Dale 1978, Anderson et al. 1981). It is clear that the resolution of whether to accept or reject it as a viable hypothesis lies, in part, in determining the fate of the planktonic larvae in the ocean currents (Helfman 1978, McFarland 1982).

Even though an extensive literature deals with the genetics and evolutionary consequences of dispersing offspring (Gadgil 1971), little strategic sampling has been done to ascertain the frequence of dispersal in natural animal populations in general, and in marine populations in particular (Leis 1983). Recent advances in knowledge of the ocean circulation make this just now a feasible scientific undertaking.

The Hawaiian fauna has a high percentage of endemic species, emphasizing that many species have clearly delineated and limited distributions. Conversely, the life history strategy of some species may be to colonize distant habitats. A mechanism whereby such larvae are transported en masse would increase the chance of successful colonization elsewhere. Hawaiian eddies appear to remain stationary near the islands up until several months and then, perhaps, to move off into the open ocean. Thus, eddy mechanisms could be responsible for transporting fish larvae through the open ocean as well as maintaining populations near shore. Any feature of the ocean circulation which would accumulate larvae is likely to accumulate other planktonic particles also. Larvae in eddies are transported in microcosm ecological communities (Wiebe et al. 1976, Wiebe 1976, Ortner et al. 1978). The duration of existence and extent of movements of eddies are important factors determining whether or not eddies function to retain plankton near islands or to transport plankton away. An especially important relationship which needs to be examined is the comparative lifetimes of mesoscale eddies and the planktonic phase of shore fishes.

FISH LARVAE IN EDDIES

We have investigated whether or not offshore ocean eddies near Hawaii play a key role in the life cycle of coastal marine species by functioning to retain planktonic larvae near the islands until such larvae metamorphosize and return to inshore habitats. In general, the peak period of eddy formation and movement appears to coincide with the peak season of reproduction by Hawaiian shore fishes. In the following sections we will develop the ideas, discuss the mechanisms related to the prototype model, and present relevant biological and physical evidence. We will present preliminary results of our field investigations at the December 1983 meeting of the ASZ.

The possibility that ocean eddies near islands might function as reservoirs for planktonic larvae of coastal species was indicated early by Boden (1952). He commented that animals in Bermuda breed during months when wind driven circulation is at a minimum. At this time, a convergence between warm and cold water currents occur, and anticyclonic eddies form. Boden discovered that plankton accumulated in this region of the convergence. Emery (1972) reported a similar situation for the island of Barbados, West Indies, and provided evidence for the existence of eddies in the island's lee. Planktonic larvae in these eddies ostensibly avoid being swept away from the island (Emery 1972). Eddies discovered in Hawaiian waters have been similarly implicated by Jones (1968). Evidence for the function of eddies in preventing loss of larvae from Hawaiian waters and maintaining fish larvae of the family Acanthuridae near shores was later obtained by Sale (1970). He presented data suggesting that the surface eddies were effective in trapping planktonic larvae which then were revolved past the island of Oahu (about 25 to 50km from shore) every five to six days (see also Leis and Miller 1976). A key feature of the Hawaiian eddies is that some remain in the vicinity of the islands for at least 65 days, (Patzert 1967, Lobel and Robinson, in prep.), which is sufficient time for development of some larvae into a stage capable of migrating back to the inshore habitat (eg., *Acanthurus triostegus sandvicensus*, Randall, 1961; *Chaetodon milaris*, Ralston 1976).

The biological importance of retaining planktonic eggs and larvae near shore to the maintenance of island populations is obvious. However, the behavioral and physical mechanisms by which planktonic larval fishes return have not been elucidated and the potential role of eddies has not been widely recognized.

It is well known, for example, that the larvae of fishes which dominate Hawaiian inshore habitats (e.g., labrids, scarids, acanthurids, and chaetodontids) are nearly absent from inshore waters, but instead are found offshore many kilometers away (Miller 1973). Many Hawaiian fishes display a collective spawning peak in the spring (Watson and Leis 1974, Lobel 1978). Watson and Leis (1974) suggested that the spring spawning peak was an adaptation to local currents. A general shift in the prevailing large scale currents around the Hawaiian Islands occurs in late spring and again in the fall (Barkley *et al*. 1964). Watson and Leis (1974) proposed "These shifts, which should be associated with weaker currents, occur with spring and fall spawning peaks. Synchronization of spawning with periods of reduced current flow would allow development and metamorphosis of the pelagic larvae before they were swept out to sea" (see also Johannes 1978). Additional evidence suggests that it is not the shifts in prevailing currents, *per se*, but the offshore eddies and other variable mesoscale currents which form during those times which may be the important factor involved (Lobel 1978).

We have suggested a relationship between the occurrence of ocean eddies and the distribution and abundance of coastal marine larvae. If this relationship is approximately true, then we expect the following, given two alternative environmental circumstances:

I. If ocean eddies or other currents acting to reduce dispersal are predictable in time and space and meet other basic criteria (i.e., the eddies persist at least 2.5 months and remain near islands) then:

   A. Spawning of coastal marine species with planktonic larvae is expected to be synoptic with the time that eddies are most probably present.

   B. Recruitment of pre-juveniles to the reef also will be concurrent with eddies in time and space.

II. If eddies occur but are unpredictable, dissolve sooner than 2.5 months, or move far away, then:

   A. Spawning will be independent of eddy occurrence.

   B. Recruitment probably will be greatest when eddies occur near shore but also will be unpredictable.

The complex process of offshore transport and return of larvae to coasts involves quasi-continuous exchange of recently spawned eggs being swept offshore and older larvae being brought back. Ocean currents affecting the transportation of larvae must not only bring fish to hospitable coasts but also must do so within time scales appropriate to larval developmental periods. Larvae must not merely be brought back nearshore but must be returned at a time when they can undergo metamorphosis and settle onto reefs. Among the significant questions remaining are: What is the mechanism by which larvae return to coastal habitats? Are pre- juveniles (post-larvae) able to "home-in" on some cue and actively swim some distance from sea to shore or is passive drift the sole mechanism?

A CONCEPTUAL MODEL FOR THE EFFECT OF MESOSCALE OCEAN CURRENTS ON THE LIFE CYCLE OF REEF FISHES

Our research to date has led us to formulate a working conceptual model for the processes discussed above. In summary, reproduction and recruitment of coastal fishes occurs to some degree all year but with peaks during the spring-summer months in Hawaii, with a phase lag of a few months between first reproduction and first recruitment. The offshore currents are variable in both space and time (fairly rapid to quasi-steady), and typically consist of one or more eddies and/or fronts and currents. These mesoscale features will, in certain places, make contact with sections of coasts on islands in the Hawaiian Archipelago. This creates locations where offshore water is swept onto the reef and locations where water is swept off. Thus, reef habitats may be either near the source of steady incoming offshore water or be situated further down stream along the same path. While an eddy is quasistationary in adjacent offshore waters, all nearby coastal currents are dominated by the eddy flow field, and drifting particles are likely to be entrained. At other places or times, the mesoscale features are absent, the currents are weak and simple tidal oscillations occur (except during episodes of occasional oceanic events, e.g., storms, tsunamis, errant eddies, etc.). Under these conditions, oceanic and coastal waters mix mainly in regions of flood divergence and ebb convergence flows associated with tidal processes. The overall picture will change with time and location especially when a large eddy is present and moves along or away from the coast. An eddy is expected to act as a major entrapment and near-island retention mechanism. Thus, depending on the location of a reef relative to offshore mesoscale features, the larvae produced by the residing fauna may be swept over stretches of reef before moving offshore, move quickly offshore, or be trapped nearshore. Once offshore, larvae may be carried out to sea and lost or trapped in an eddy which, if it remains near an island, will enable larvae to return to suitable adult habitats. Recruitment may depend, in part, on those mesoscale eddies and currents bringing larvae near to shore. If the seasonality of such currents is predictable in time and space, then potential exists for species to adapt by developing a peak in reproduction at times when the offshore mesoscale field most favors nearshore retention of larvae.

Research supported by National Science Foundation grants No. OCE-80-09554 and No. OCE-81-17891.

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ON THE POSSIBILITY OF KIN GROUPS IN CORAL REEF FISHES

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ABSTRACT

This paper concerns the widely-held assumption that members of schools of coral reef fishes are unlikely to be related because of pelagic dispersion of their eggs or larvae. The most direct way for adult schools to contain kin would be for siblings to remain together throughout the pelagic period and then to settle together as juveniles. For pelagic sibling groups to endure, mixing and dispersion by turbulent diffusion must be counterbalanced by biological processes for the formation, maintenance or selective survival of discrete egg or larval aggregations. I argue that there are sufficient hints of the existence of such processes to warrant examination of the possibility of kin groups in coral reef fishes. For example, demersal spawners may reduce the period of passive dispersion almost to zero by laying benthic eggs that release developmentally advanced larvae with the sensory and motor ability to aggregate actively soon after hatching. Other likely places to look for kin groups are among mouthbrooders, livebearers and pelagic spawners like lionfishes or species like *Anthias* whose young juveniles occupy large, sedentary groups.

With rare exception, eggs and/or larvae of coral reef fishes undergo a pelagic phase during which many are thought to travel large distances in open ocean. It is generally assumed that pelagic eggs and larvae are thoroughly mixed, so that recruits at any particular site on a reef represent a random sample of the reproductive products entering the local gene pool. If mixing occurs, kin are unlikely to settle together or find one another after metamorphosis. Hence, it is widely assumed that kinship plays no role in the evolution of coral reef fish behavior, schools or social groups (e.g., Thresher, 1977).

However, at the beginning of, during, and at the end of the pelagic phase, eggs and larvae are clumped. Eggs are initially released in the sea by pelagic spawners or laid on the substrate by demersal spawners in a small, tightly-clumped mass. Thus, at the outset sibling eggs are closely aggregated. Little is known about patterns of pelagic dispersion for coral reef fishes, but among commercial temperate water fishes pelagic eggs and larvae are often found in patches (Hunter, 1980). Among these species patchiness is sufficiently prevalent that Hewitt (1981) concluded that patchiness is an important characteristic of larval existence with strongly positive survival value. At the end of the pelagic phase, coral reef fish larvae metamorphose and settle on the reef. Larvae of at least 23 species in several families settle in aggregates (Luckhurst & Luckhurst, 1977; Talbot, *et al*., 1978), often in bursts of recruitment over short periods of time (Victor, 1983). Thus, one finds patches in all pelagic stages. The most direct way for adult social groups, colonies or schools to contain kin would be for siblings to remain together throughout the pelagic period and then to settle together as juveniles. The aim of this paper is to outline some of the factors determining whether or not sibling aggregations will persist through the pelagic phase.

To place dimensions on the problem, I will first treat eggs as though they were a passive, inert substance, such as dye, that is dispersed by diffusion. Assume that 2,000-40,000 neutral or positively buoyant eggs are released in the water column at a depth of 10 m in a single spawn as a sphere 10-20 cm in diameter. If (1) the eggs are non-adherent, (2) horizontal turbulent diffusion is radially symmetric, and (3) vertical diffusion is Fickian with a constant vertical diffusivity (Okubo, 1974), how large a volume will the eggs occupy 24 hours later? Calculations (Okubo, pers. comm.) are based on diffusion diagrams that plot horizontal variance σ_x^2 (i.e., the mean square distance from the center of mass) of dye distribution as a function of time since point release of dye in the ocean. Horizontal diameter of the egg patch is considered to be $2\sigma_x$, i.e., twice the standard deviation (Okubo, 1971), and vertical height of the patch is $2\sigma_z$. After 24 hours, eggs would be spread 3-9 m vertically and 400-1000 m horizontally. Mean separation between neighboring eggs would be 24-71 cm vertically and 28-70 m horizontally for a spawn of 2,000 eggs with zero mortality, and 9-26 cm vertically, 10-26 m horizontally for 40,000 eggs. The average density of 40,000 eggs spread horizontally in a circle 700 m in diameter, and neglecting vertical spread, would be 0.10 eggs/m^2. Assuming the eggs are dispersed at random within the circle according to a Poisson distribution, the probability of two or more eggs occupying a 1 m^2 portion of the circle is 0.004679. We could expect 1800 units, each 1 m^2 in size, within this circle each to contain $\geq$ 2 eggs.

What factors operate to make aggregation of sibling eggs more or less likely than this simple model suggests? Firstly, eggs probably do not behave like dye in the ocean. While the chorionic surface of fish eggs may often be smooth (Hemple, 1979), 27 tropical species (e.g., Robertson, 1981) produce eggs with external chorionic hooks, tendrils, spikes, or raised hexagonal ridges. In some cases these structures hold fertilized eggs in compact sheets. In others, chorionic sculpturing increases drag (Robertson, 1981). Female lionfishes of the family Pteroidae produce transparent mucous balls containing 2,000-15,000 eggs that remain in the mass until hatching 36 hours later (Fishelson, 1975).

Turbulent motion is customarily broken into Fourier components with different length scales. Components with length scales smaller than or equal to the egg patch tend to break the patch and mix and spread the eggs. Components with length scale larger than the patch move the patch as a whole (Okubo, 1971). "As a result, the apparent power of the mixing which acts on a diffusing patch increases with patch size or, to put it another way, with the time elapsed since the patch first began to mix." (Okubo, 1971: 91). Empirically, horizontal variance is a function of diffusion time raised to the power 2.34 (Okubo, 1974). Thus, any tendency for newly spawned eggs to adhere to each other or otherwise remain in an aggregated cloud would delay the time at which any particular eddy length became capable of dispersing it and produce an inordinately large reduction of egg patch dimensions 24 hours later.

Species in many families lay demersal eggs that have adhesive structures or properties that maintain their benthic attachments (Thresher, 1980). Dispersion does not begin for demersal spawners, for mouthbrooders such as cardinalfish and jawfish, or for livebearers such as some clinids, until after hatching or live birth. The period of completely passive egg dispersion is by-passed in these species.

The simple model predicted an egg density 24 hours after spawning of 0.10 eggs per m^2. Much higher egg densities have been recorded: up to 46,000 eggs/m^2 in temperate fishes and up to 12 eggs/m^2 in tropical fishes (Hunter, 1980; Watson & Leis, 1974). Inter-egg distances may be as low as 1-2 cm at spawning and 15-20 cm several days later (Hunter, 1980). These distances are an order of magnitude lower than those in the above model. While these field observations suggest that egg clumping may be more likely than expected by the above model, very high egg densities almost certainly result in part from superposition of egg products from multiple spawns. I will return to the effect of multiple spawns on sibling aggregation later.

Unlike an assumption of the model, dispersion is not uniform throughout the egg patch, but is Gaussian with densities greater at the center than at the periphery

(Hunter, 1980; Walsh, et al., 1981). This distribution will accentuate aggregation. On the other hand, passive dispersion will continue longer than 24 hours, at least among pelagic spawners. The actual duration will depend on the time of hatching, the onset of larval swimming, and perhaps on the overall length of the pelagic period. In cold-water fishes, the egg stage may endure from 2-4 days to 2 years (Hempel, 1979), but the precise time is species- and temperature-dependent. In coral reef fishes, where incubation temperatures are high, pelagic eggs hatch generally after 15-36 hours (Thresher, 1980). Demersal eggs usually require longer to hatch, up to 12 days in coral reef fish, but, since dispersion does not begin in these species until emergent larvae enter the water column, the duration of the egg stage does not influence spread.

Once young larvae begin actively swimming, the possibility exists for behavioral mechanisms to influence dispersion. Swimming begins between 0.5-3 days post-hatching in coral reef fishes (Thresher, 1980) and 1-3 days after hatching in anchovies and Pacific mackerel (e.g., Hunter & Kimbrell, 1981). Larvae hatch from demersal eggs at a more advanced stage of development than larvae from pelagic eggs. Sensory and motor systems are more fully functional in the former and new larvae swim and catch prey very soon after hatching (Iwai, 1980). The short time interval, for these larvae, between hatching and onset of swimming provides short purchase for turbulent diffusion to act. Hence, we should expect dispersion to be far less in larvae from demersal than from pelagic eggs.

Finally, very little is known about the total length of the pelagic period. Estimates vary from 3 days to 10 weeks in some coral reef species (Thresher, 1980; Brothers & McFarland, 1981). The density of eggs and larvae, whether aggregated or not, will clearly vary with mortality. During the pelagic egg stage, mortality varies between 2-95% per day, with larval mortality running 2-15% per day (Jones & Hall, 1975; Hempel, 1979).

In spite of the large area covered by eggs in the model, eggs did aggregate within some 1 m^2 units simply from random processes. The probability of finding eggs or larvae in aggregates would be substantially increased if selective forces favored their survival over that of isolated eggs or larvae (Hewitt, 1981). On theoretical grounds, the probability that a predator will detect aggregated eggs may be less than the corresponding probability for dispersed eggs (Rubinstein, 1978). The same phenomenon will favor aggregated larvae as well. Larval aggregation may also increase the difficulty of prey capture for a predator (Milinski, 1977). The larger the larval aggregation, the less likely it is that any particular larva will be eaten, provided the predator is incapable of eating the entire patch. It is not known whether more active anti-predator behavioral adaptations occur in fish larvae or not, e.g., increased total vigilance as aggregate size increases, but such processes are well documented for adult social groups of terrestrial animals and for some marine insects (Treherne & Foster, 1980).

Food densities necessary for larval survival and growth tend to be substantially higher than mean densities of food in the open sea. Consequently, there should be strong selective pressures for larvae to locate and remain in high-density food clumps (Hunter, 1980). One way to achieve this is through local enhancement: larvae in clumps should find food patches faster than isolated individuals because each larva could watch its neighbor's behavior as well as look for food. When a larva begins feeding, the observant neighbor could swim to the feeding site and itself begin feeding. Since (1) young larvae feed largely through visual mechanisms of perceiving prey (Iwai, 1980), (2) perceptive distance increases with the size of the perceived object (Hunter, 1980), and (3) neighbors are much larger than food items, a larva should see neighbors at greater distances than food. The effect will be a substantial increase in the search volume for food by each aggregated larva. Search volume, currently estimated at 0.1-1.0 liter/hour for individual larvae (Hunter, 1980), will be determined by larval swimming speed. In general, early larval cruising speeds range between 1-3 body lengths per second and speed increases as larvae grow (Hunter, 1980; Hunter & Kimbrell, 1981). These figures provide a starting point for evaluating how far away a larval neighbor might be and still provide positive local enhancement.

Larval food patches commonly occur in the open sea (Owen, 1981) and fish larvae do find food patches (Sherman, *et al*., 1981). When turbulent sea conditions disrupted food aggregations and diluted potential food items to below densities needed for larval survival, first-year anchovy recruitment declined markedly (Lasker, 1981).

Once in a food patch, larvae tend to remain there by employing non-random search patterns. When larval anchovies entered dense food patches they decreased swimming speed and time spent swimming, and increased their turning probability by a factor of 5-6 (Hunter, 1980). The result was a substantial increase in the probability of staying within the food patch.

The onset time of these oriented search patterns influences dispersion. The sooner they begin in larval development, the less widely dispersed larvae will be at the moment mechanisms for maintaining patchiness become operative. This leads to a consideration of the time of first feeding by young larvae. Generally, first feeding precedes or coincides with onset of swimming (Hunter & Kimbrell, 1981). Temperate fishes begin to feed 2-4 days after hatching. Since development is faster in tropical than in temperate waters, and armed with the above estimates of onset of swimming, we can estimate that feeding in coral reef fishes begins 0.5-3 days after hatching.

We see, then, that there should be strong selective pressures for eggs and larvae to aggregate, as an anti-predator device, for local enhancement of food-patch searching, or simply to remain with food patches once they are found. In order to form or remain in patches, larvae must have appropriate motor and perceptual skills and we have seen that swimming ability and feeding emerge early in larval development.

Another mechanism by which larvae may limit dispersion is by diurnal vertical migration. Surface waters in the mixed layer suffer greater turbulent diffusion than deeper waters (Okubo, 1974). Particulate organic matter and many planktonic organisms concentrate at the boundary between layers. While vertical stratification of coral reef fish larvae has scarcely been studied (Watson & Leis, 1974), larvae may find a rich source of food if they migrated to the boundary, and there they would undergo less turbulent diffusion than if they remained near the surface.

Regardless of the mechanisms, dispersion of fish larvae apparently does not continue throughout the entire pelagic period. Temperate larvae disperse for a limited period and then re-aggregate (Hunter, 1980; Hewitt, 1981). Thus, the duration of passive dispersion may be relatively short.

Thus far, discussion has been directed to processes influencing dispersion of a single spawn of eggs or larvae. Spawning, however, generally involves all or part of a local population reproducing during the same period. Turbulent diffusion operating on multiple egg masses will mix offspring from adjacent spawns. The larger the number of egg masses that are mixed and the greater the thoroughness of mixing, the lower will be the probability that small clumps of eggs or larvae late in the pelagic phase will contain kin.

The amount of mixing will depend on slightly different factors for pelagic and demersal spawners. For pelagic spawners, critical factors will be the time and distance separating successive spawning events, and current speed. For example, if current speed over a reef is a modest 6.2 m/min (0.2 knots), pelagic spawnings 1-4 hours apart, as in some parrotfish (Clavijo, 1982), would initially produce egg masses separated by 0.4-1.5 km due to current plus whatever distance separated the spawning sites. With eggs concentrated 24 hours later in the center of a circle 700 m in diameter in a Gaussian distribution, eggs from early and late spawns would mix relatively little. Similarly, eggs from spawning sites 500 m apart will mix substantially less than those from closer sites. Coral reef fishes often spawn at sites openly exposed to current that quickly sweeps eggs off the reef (Johannes, 1978; Barlow, 1981) and away from later egg masses. These current conditions could restrict genetic mixing.

In demersal spawners, degree of genetic mixing will be influenced by spatial separation between benthic egg masses, current speed, and the degree of asynchrony of hatching within and between egg masses. If all eggs within one mass hatch synchronously, then young larvae will form a tight clump as they enter the water column. If intra-spawn hatching is asynchronous, sibs will enter the water column at intervals and will be more widely spaced by the currents. If adjacent egg masses hatch hours or days apart, currents will space emergent larvae with relatively little mixing.

In summary, the eggs of coral reef fishes begin their pelagic existence in small, discrete patches. Egg and larval patches subsequently are found at various stages throughout pelagic life and newly recruiting juveniles or post-larvae may settle in or form aggregations. There are tantalizing hints of strong selection pressures for pelagic eggs and larvae to aggregate, either to increase protection from predation or to enhance the search for food patches. The perceptual and motor apparatus to support active aggregation are available within a few days of hatching. Since coral reef fish eggs hatch rapidly in tropical seas, the total time for which eggs and young larvae are susceptible to passive turbulent diffusion, prior to onset of the ability to form or remain in patches, is short, on the order of 2-5 days. This time is substantially reduced, perhaps to zero, for demersal spawners, mouthbrooders, livebearers, and lionfishes, whose eggs remain together throughout egg development and whose larvae hatch at a large size and at a relatively advanced stage. Mixing of eggs released by separate spawning pairs within a local population will be limited to spawning episodes occurring close together in time and space. The stronger the current at the time of spawning, the closer in space and time successive spawns can be without substantial mixing. All of these factors render it possible, for at least some members of some species, that eggs will remain together throughout pelagic life and release larvae that settle aggregately to form kin groups or groups containing kin on the reef.

Few of the factors influencing the possibility of kin groups have been thoroughly examined in coral reef fishes. However, genetic relatedness among individuals on a reef can be studied with existing electrophoretic techniques. Likely places to look for kin groups are among colony-forming demersal spawners, lionfishes, mouthbrooders, livebearers, and fish like Anthias whose young juveniles occupy large, sedentary groups.

ACKNOWLEDGMENTS

I wish to thank A. Okubo, A. Mercado and P. Yoshioka for calculations, and R. Appeldoorn, J.Corredor, D. Hensley, M. Leighton-Shapiro, J. Morell, and Y.Sadovy for helpful discussion of ideas and criticism of the manuscript. Work was supported by NIH grant S06RR08103.

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SETTLEMENT AND LARVAL METAMORPHOSIS PRODUCE DISTINCT MARKS ON THE OTOLITHS OF THE SLIPPERY DICK, HALICHOERES BIVITTATUS

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ABSTRACT

Early in the sequence of daily increments on wrasse otoliths there is a transition from clear increments to a band of very faint, often indecipherable, wide increments. After about five of these wide increments clear increments resume. Planktonic larvae do not have the transition on the edge of their otoliths, while newly-metamorphosed juveniles have both the transition and the subsequent band on theirs. Experiments showed that metamorphosis takes about five days, during which the larva remains buried in sand. The transition therefore corresponds to settlement of the planktonic larva onto the reef, and the band is formed during the process of metamorphosis. These findings demonstrate that 1) it cannot be assumed that newly-appeared fish on the reef settled that day and 2) experiments are necessary to ascertain the meaning of marks on the otolith.

INTRODUCTION

Reef fish ecologists have only recently begun to focus their attention on the early life history of reef fishes. These fishes are unusual in that virtually every one of the many thousands of species that live on coral reefs has a planktonic larval stage. The interest in the ecology of larvae and the process of recruitment is indeed timely, for it is becoming increasingly apparent that many of the patterns of diversity and abundance of coral reef fishes are being determined by processes occurring in the plankton. Several studies have demonstrated that reef fish populations are limited by the supply of larval recruits, rather than by some resource on the reef (Williams,1980; Doherty,1983; Victor,1983). Furthermore, some of my recent findings (in prep) indicate 1) that species-specific larval behaviors determine when successful recruitment occurs in some Caribbean wrasses and thus promote the coexistence of species on the reef, and 2) that the duration of the planktonic larval stage affects the distribution of wrasse species in the Indo-Pacific and may well account for the differing degree of speciation that has occurred within wrasse genera.

Much of the progress that has been made on this subject is a result of the power of the daily otolith increment aging technique (Brothers,1981; Brothers & McFarland,1981). Because there are both daily increments and a mark corresponding to the settlement of the planktonic larva on wrasse otoliths (Victor,1982), the date of settlement for any individual can be calculated by subtracting the number of daily increments between the settlement mark and the edge of the otolith from the date of capture. The duration of the planktonic larval period can also be estimated by counting the number of increments between the center of the otolith and the settlement mark. The settlement mark appears under the microscope as a transition where the previously prominent dark lines that delineate each increment abruptly disappear. Regular increments only reappear after a band without clear increments is formed (see Fig. 1C). It is, however, often possible to discern several (usually five) faint increments making up this band in some areas of the otolith. The aim of this study is to clarify which events during the process of settlement account for the transition and the subsequent settlement band on the otoliths of the slippery dick, Halichoeres bivittatus, one of the most abundant wrasses in the Caribbean.

METHODS

Planktonic larvae of the slippery dick were captured at a nightlight with an aquarium dipnet on Ukubtupo reef in the San Blas Islands of Panama. They were identified both by fin ray counts and by raising in an aquarium. Only larvae that had their full complement of fin rays and were of a size ready to settle were present at the nightlight. Some of those captured were preserved in ethanol immediately, while others were transferred to a ten-gallon aquarium containing sand and sea-water. Collections of juvenile slippery dicks also were made on Ukubtupo reef about the same time.

The otoliths of all individuals captured were obtained by first removing the top of the cranium and then extracting the larger pair, the sagittae, from the base of the skull and the smaller pair, the lapilli, from the sides of the skull with fine forceps. The otoliths were then cleaned and dried and placed in a drop of immersion oil on a glass slide. They were subsequently examined under a compound microscope with transmitted light and a polarizing filter at magnifications of 400X to 1000X.

RESULTS

All twenty of the slippery dick larvae captured at the nightlight and preserved immediately had no settlement transition on their otoliths. In these fish the alternating light and dark lines that make up daily increments continued all the way out to the edge of the otolith (Fig. 1A).

Those larvae that were put into an aquarium had all disappeared into the sand at the bottom of the tank by the next morning. After a number of days these fish emerged from the sand and after some exploring took up residence in a corner or near some rubble. During those days in the sand they had lost the transparency and the melanophore pattern of larvae and developed the stripes, spots, and colors typical of juveniles of this species. The juvenile slippery dicks usually emerged on the fifth day (mean of 5.5, n=17,

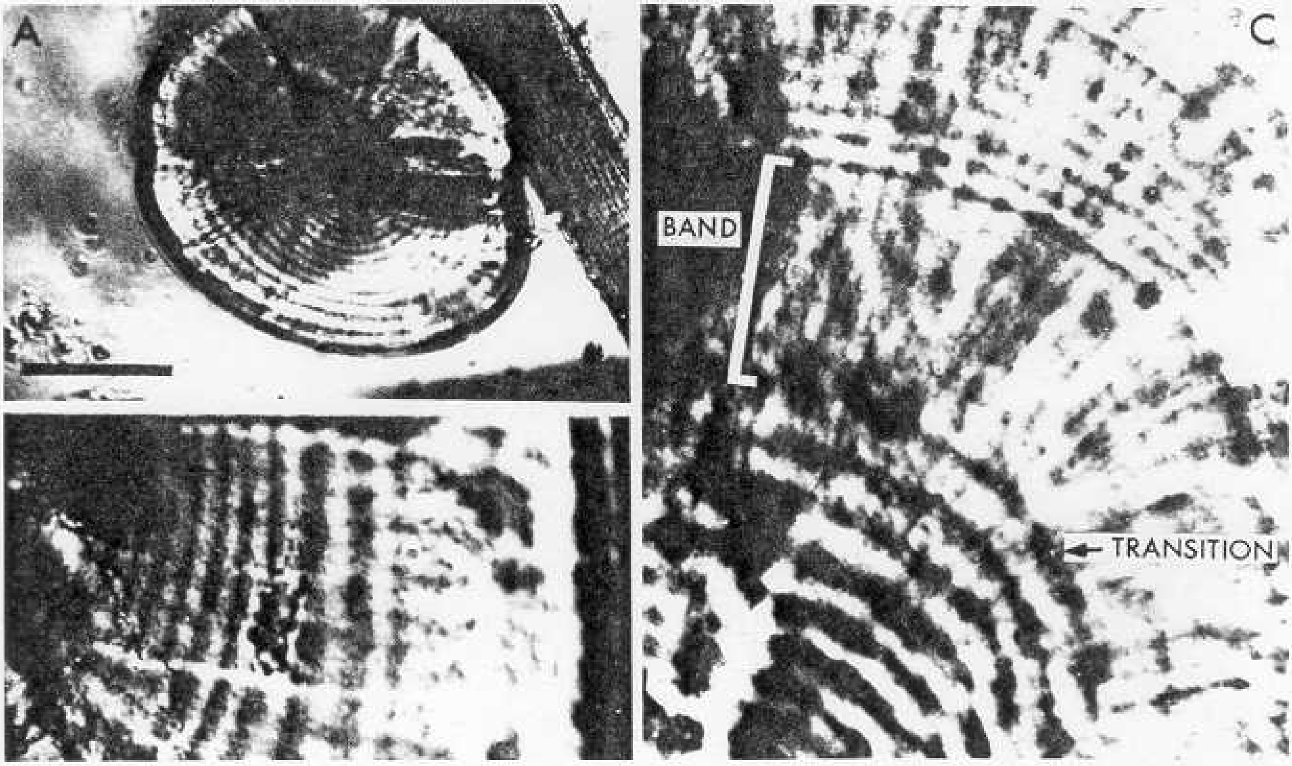

Fig. 1: Otoliths of slippery dicks. A: 9.9 mm SL, bar=100 microns. B: 10.1 mm SL, bar=20 microns. C: 21.0 mm SL, bar=30 microns.

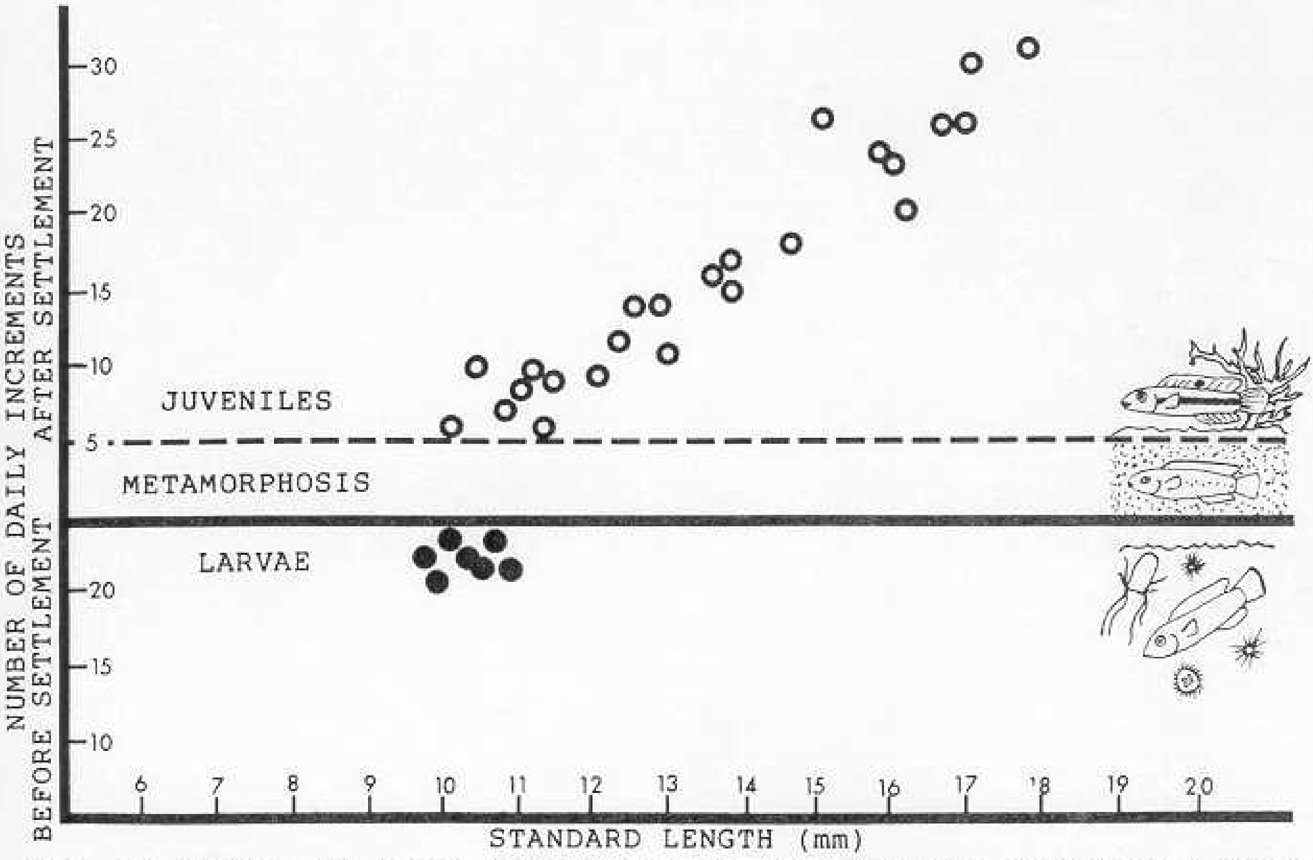

Fig. 2: Number of daily increments on the otoliths of slippery dicks.

SD=.87, range=4 to 7). Individuals killed immediately after emergence had a completed settlement band after the settlement transition (Fig. 1B). Juveniles captured on the reef had the settlement band as well as some number of clear increments after the band (Fig. 1C and 2). The smallest fish captured had only one increment in addition to the five faint increments making up the band.

Clearly, the abrupt settlement transition occurs when the planktonic larva settles onto the reef and buries itself in the sand to metamorphose. The settlement band of five faint increments corresponds to the five days during which the larva metamorphoses into a juvenile. Regular increments resume when the juvenile emerges. The faint increments within the settlement band should, therefore, be included when counting the number of post-settlement increments in order to determine the settlement date for an individual.

DISCUSSION

These results demonstrate that it cannot be assumed that juvenile fish caught at their first appearance on the reef settled that day or the previous night. Furthermore, marks should not be interpreted as settlement marks unless they have been experimentally demonstrated to occur at the time of settlement rather than during the process of metamorphosis, which could take place at some other time. Many fishes metamorphose (i.e., take on the body form and color of juveniles) before settlement; as in the barracudas (Sphyraenidae), butterflyfishes (Chaetodontidae), angelfishes (Pomacanthidae), some damselfishes (Pomacentridae), scorpionfishes (Scorpaenidae), filefishes (Monacanthidae), triggerfishes (Balistidae), and pufferfishes (Tetraodontidae). Others metamorphose after settlement, as in the wrasses (Labridae), parrotfishes (Scaridae), and some of the drums (Sciaenidae)(Victor, unpublished data). Sciaenids of the genus *Pareques* in the Caribbean not only settle when very small and transparent, but even before their full complement of fin rays have developed (Powles & Burgess, 1978).

The settlement transition is particularly clear on the otoliths of wrasses, probably because the transition from life in the plankton to entombment in the sand is so profound. More subtle changes in life style have been demonstrated to produce quite subtle changes in the character of increments in grunts (Brothers & McFarland, 1981). The increments that can often be discerned within the settlement band in wrasses are unusual in being fainter and often wider than increments anywhere else on the otolith. If the width of otolith increments were a measure of the daily growth rate, it would mean that during metamorphosis the larva is growing quickly, even though it is, presumably, not eating. Since light, temperature, and food cycles appear to control the formation of daily increments in fishes (Mugiya, *et al*., 1981; Neilson & Geen, 1982), and wrasse larvae remain buried in the sand while increments are produced, it is quite possible that some entrained circadian rhythm continues during metamorphosis. Juvenile wrasses that are maintained unfed in a dark insulated container for several days put down a very different kind of mark on their otoliths (Victor,1982). It is much narrower than the settlement band and does not show any internal pattern of light and dark lines.

Further confirmation of a five day period of metamorphosis during which wrasse larvae remain hidden comes from my data on the pattern of settlement of bluehead wrasses, Thalassoma bifasciatum, onto patch reefs in the San Blas Islands. Settlement was monitored by daily censuses of an area of coral outcrops in a seagrass bed for two years. At the same time, nightly collections of fish larvae were made at a nightlight. A preliminary analysis of the data indicates that a lag of about five days occurs between peaks of larval fish abundance and diversity and subsequent peaks of juvenile wrasse appearances.

Despite the fact that the process of settlement is such a critical period in the life of an individual and can greatly influence the abundance and distribution of adult populations, it remains both one of the least understood and least examined phases in the life history of reef fishes. The settlement strategies of reef fishes are probably as varied and complex as any other feature of this notably diverse assemblage, and clearly deserve closer and more rigorous attention.

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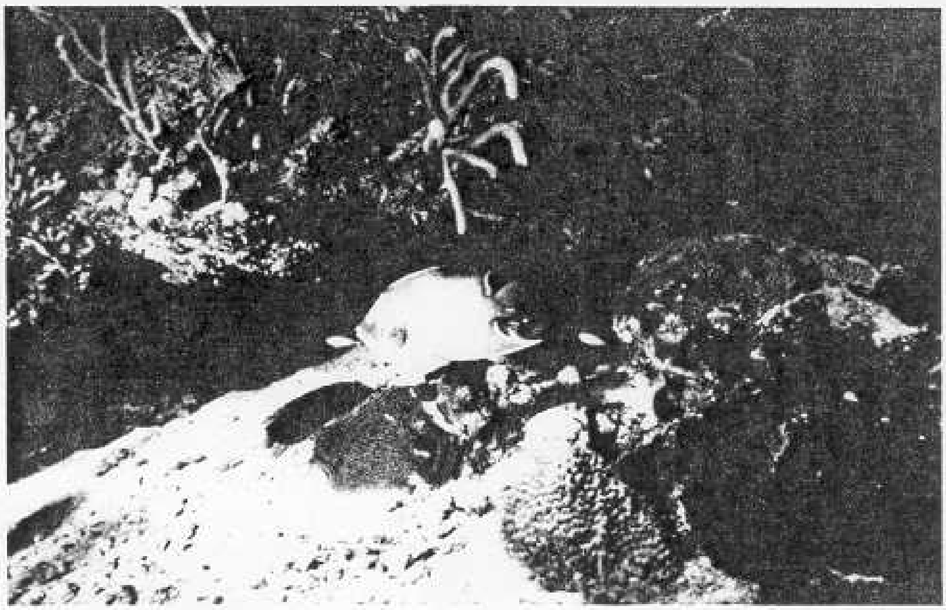
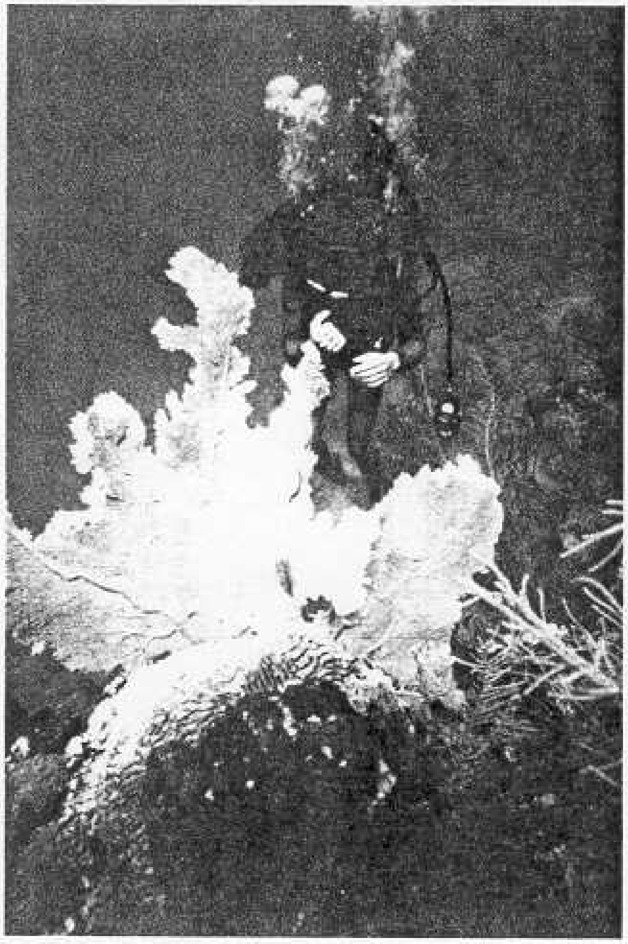
Note: Photos by B. Victor

CHAPTER IV: THE ORGANIZATION OF CORAL REEF COMMUNITIES





SPONGES AS IMPORTANT SPACE COMPETITORS IN DEEP CARIBBEAN CORAL REEF COMMUNITIES[1]

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ABSTRACT

Demosponges are diverse and aggressive competitors for space in deep open-reef habitats. Sponges comprise nearly half (30/63) of all encrusting taxa recorded in this study and are significantly more diverse than corals at 90' and 120' ($p < .001$). Analyses of m^2 quadrats (total $N = 111$) from depths of 10', 30', 60', 90', and 120' reveal that a gorgonacean (Erythropodium) was the most frequent aggressor at 10'. Below this depth, four genera of demosponges (Chondrilla, Hemectyon, Ircinia and Verongia) were the most significant aggressors. Below 30', scleractinian corals were the taxa most frequently overgrown. Sponges should be recognized as important contributors to the organization and dynamics of open coral reef communities.

INTRODUCTION

Competition for space has gained the attention of a wide variety of investigators interested in making long-range predictions about community structure (Dayton, 1971; Lang, 1973; Jackson & Buss, 1975; Osman, 1975). In tropical coral reef communities, heavy emphasis has been placed on the transitive nature of competitive interactions between scleractinian corals and the contribution of such "competitive hierarchies" to the structure of these communities (Lang, 1973; Sheppard, 1979). Although other invertebrate groups are well-known to exist within these communities, they are known mostly from the cryptofauna (those species that inhabit the undersides of foliaceous corals or cave-like environments) where competition has been reported to be non-transitive in nature, producing "competitive networks" (Jackson & Buss, 1975; Buss & Jackson, 1979).

For "open-reef" assemblages (defined here as those reef species existing out in the open, as opposed to those in cryptic habitats) relatively little attention has been given to non-scleractinian components of the community and their contribution to reef diversity and dynamics.

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Despite this situation, it is becoming increasingly evident that non-scleractinian invertebrates such as encrusting sponges, zoanthids, ascidians, gorgonians and soft corals also compete aggressively for space in these open-reef habitats, and may often be the dominant space occupiers (Rutzler, 1970; Reiswig, 1973; Jackson & Buss, 1975; Karlson, 1980, 1983; Benayahu & Loya, 1981; Birkeland, *et al.*, 1981; Bunt, *et al.*, 1982; Sebens, 1982; Sheppard, 1982; Suchanek & Green, 1982; Sammarco, *et al.*, 1983).

Here we present a set of preliminary results from a study of such competitive interactions between scleractinian and non-scleractinian components of an open-reef habitat at a site in the U. S. Virgin Islands from depths of 10' to 120'. Specifically, we focus a) on the significant contribution made by demosponges to the species diversity of such an assemblage and b) on the quantitative and qualitative aspects of competition between demosponges and other encrusting colonial invertebrates, especially scleractinian corals.

METHODS

Data on depth distribution, species richness, percent cover and competitive interactions for encrusting colonial invertebrates were obtained with the aid of SCUBA during two NOAA NULS-1 Hydrolab Missions at Salt River Canyon, St. Croix, U.S. Virgin Islands (17°47'N;64°45'W): Mission I (=NOAA# 81-12) in Oct/Nov 1981 and Mission II (=NOAA# 82-12) in Aug/Sept 1982. See Suchanek (1983) for a location map. A fixed camera frame (quadrapod), outfitted with a Nikonos IV camera and 15mm lens (fully corrected for parallax), was used to photograph 0.5m^2 areas (85.75cm X 58.31cm) of coral reef substrate at 60', 90' and 120' depths. Random locations were chosen for the beginning of three contiguous transects (with 10 replicated photo-quadrats in each transect), yielding 30 possible photo-quadrats for each depth contour. Resulting color photographs (8" X 12") were analysed for percent cover of sessile organisms by tracing the outline of each species using a Houston Instuments HIPAD digitizer linked to an APPLE II computer; resolution using this technique was ca. 0.5cm of the original substrate. Because of equipment failures some quadrat-photos were lost, resulting in the following number of analysed replicate quadrats (and associated total areas) for Mission I: 29 @ 60' (=14.5m^2), 28 @ 90' (=14.0m^2), 27 @ 120' (=13.5m^2).

Quantitative and qualitative data on competitive interactions between encrusting colonial fauna and flora were taken at 10', 30', 60', 90' and 120' using a 1.0m^2 quadrat. A random point was chosen for the start at each depth and replicate quadrats were then placed contiguously along that depth contour (number of replicates at each depth = 30 @ 10', 30 @ 30', 20 @ 60', 14 @ 90' and 17 @ 120'). Each interaction was scored as a) an overgrowth encounter or b) a standoff.

RESULTS

Digitized photographs from Mission I demonstrate that sponges comprise the most diverse taxonomic group, representing nearly half (30/63) of all species recorded, as well as dominating the total species richness (SR) values at each depth (Fig. 1). The mean SR of sponges and corals in the photo-quadrats was not significantly different at 60', but sponges were significantly more diverse on the

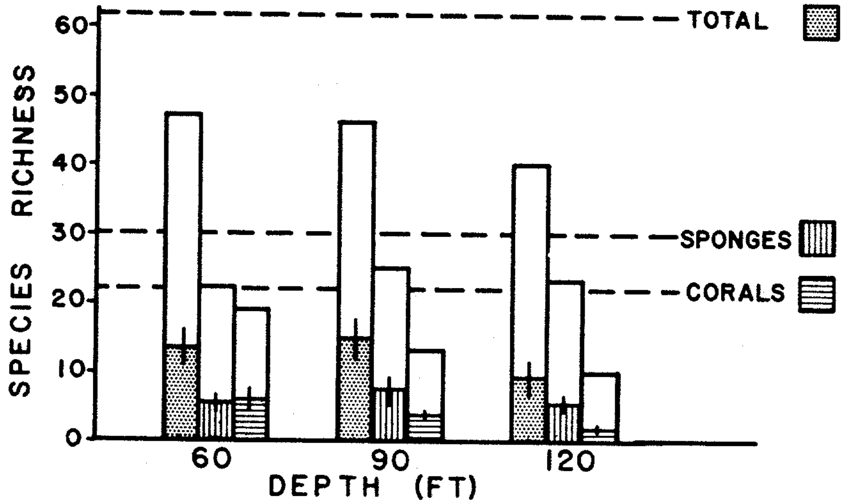

Figure 1. Species richness (SR) values obtained from digitized photo-quadrats of Mission I. Dashed lines = SR values pooled over all depths. Open histogram bars = SR values pooled for each depth. Shaded bars = mean SR values for $0.5m^2$ quadrats ± S.D. line.

deeper reefs (t-test: $p < .001$ at 90' (df=27) and 120' (df=26)). Interestingly, although the percent cover of sponges (8.0 ± 4.9 at 60', 19.1 ± 12.5 at 90' and 12.3 ± 9.5 at 120') and corals (18.3 ± 10.6 at 60', 23.8 ± 13.2 at 90' and 39.1 ± 23.1 at 120') was not significantly different at 90', corals occupy considerably more area than sponges at both 60' and 120' (t-test: $p < .001$).

The greatest number of both total interactions and overgrowths (per m^2) occurred at the 120' depth (Fig. 2). While the frequency of standoffs was relatively consistent over all depths, overgrowths increased to a mean of 9.0 ± 5.4 at 120'. The frequencies of overgrowths at 10', 60' and 90' were not significantly different from each other, but at 120' were much greater than at all other depths (t-test: $p < .01$ for 30'; $p < .001$ for 10', 60' and 90').

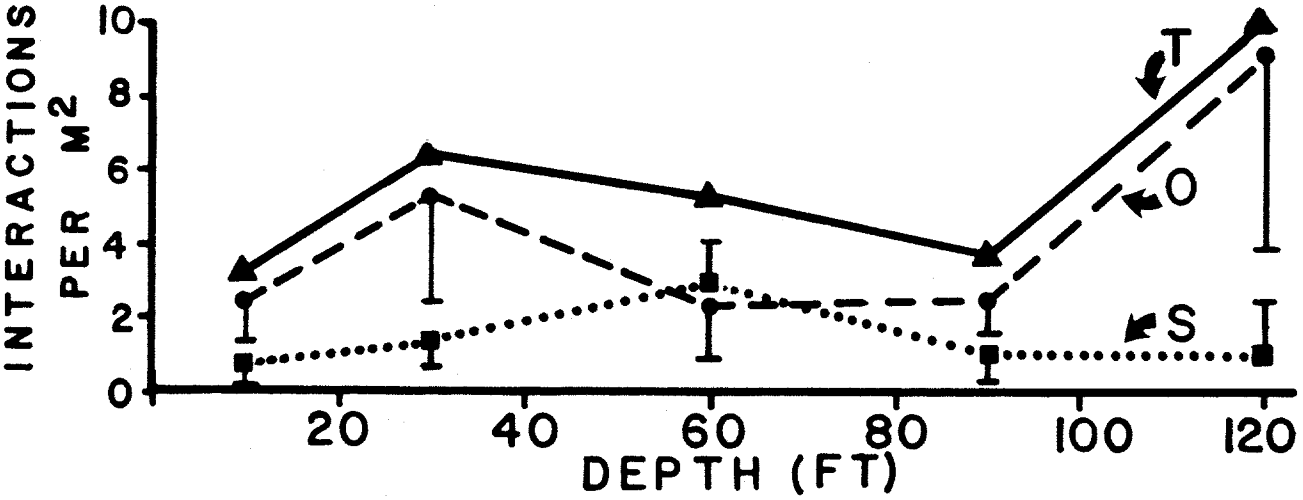

Figure 2. Number of interactions per m2 (+ or - S.D. lines) versus depth. T = total number of interactions, O = overgrowths, S = standoffs.

The relative contribution of the three most frequent interactors is given in Figs. 3A & 3B. Clearly sponges were the most common aggressors, monotonically increasing both the frequency of their overgrowths and their relative standing as aggressors with depth (Fig. 3A). Corals on the other hand were by far the most frequently overgrown species, especially at depth (Fig. 3B). Several other taxonomic groups were also frequently involved in these overgrowth interactions. Their relative contributions are given below as the (% of all interactions as aggressors)/(% of all interactions as subordinates) for depths of 10', 30', 60', 90' and 120' respectively for each taxonomic group: millepore corals - 12/34, 16/5, 0/0, 0/0, 0/0; zoanthids - 12/0, 4/0, 0/0, 0/0, 2/0; ascidians - 1/1, 10/1, 6/0, 0/0, 1/3.

With increasing depth the relative importance of various aggressors changed substantially. At the shallowest depth studied, 10', the gorgonacean Erythropodium was the most dominant aggressor, but was never recorded as an aggressor in any observations below this depth. At 30' the demosponge Agelus was the most influential aggressor, initiating 25% of all aggressive interactions at that depth. Similarly, at 60', 90' and 120', those species that initiated 10% or greater of all overgrowths were demosponges; these genera are listed below with the percentage of the total overgrowth that they themselves initiated at each depth: 60' = Chondrilla (34%), Hemectyon (23%), Ircinia (11%); 90' = Chondrilla (40%), Hemectyon (23%), Verongia (11%); 120' = Verongia (34%), Chondrilla (26%).

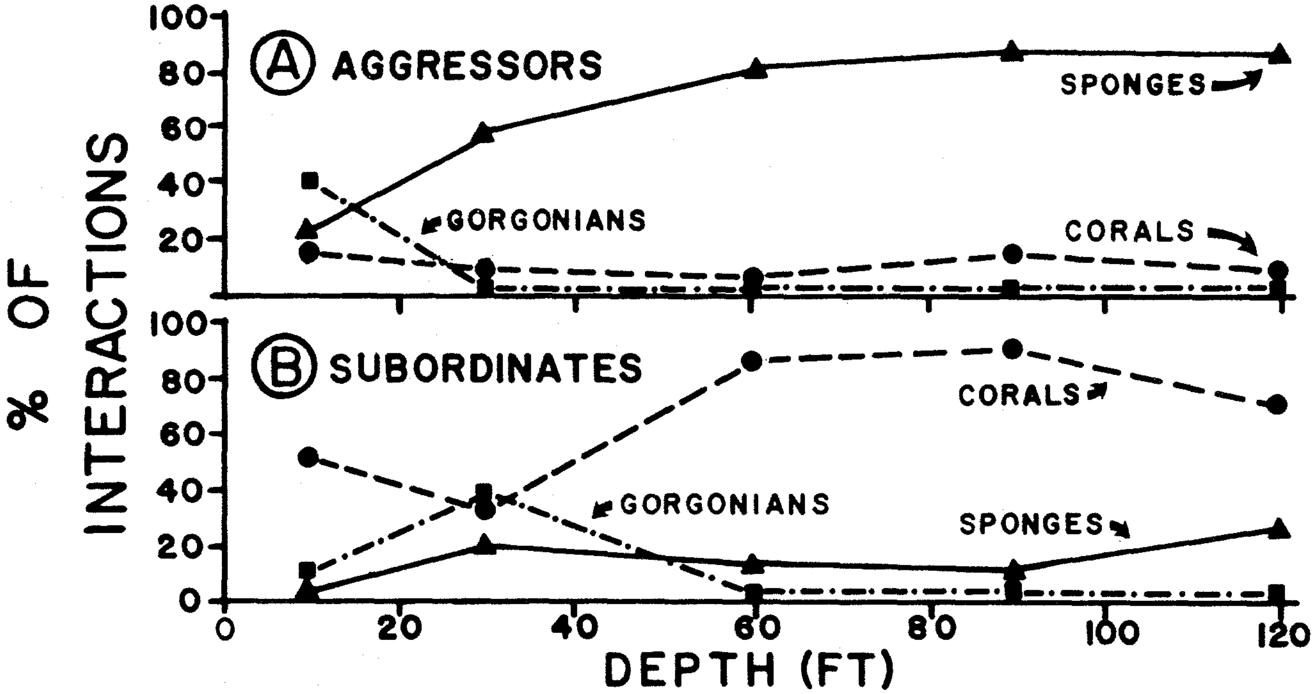

Figure 3. Percent of all interactions versus depth. Each taxonomic group was scored as either A) an aggressor (was overgrowing another species) or B) a subordinate (was being overgrown).

DISCUSSION

We present evidence here that demosponges play an important role in open-reef communities of the Caribbean, not only in terms of species richness, but also with respect to the intense competition for space that occurs in these environments. Demosponges are known from open-reef habitats (Reiswig, 1973), but until now virtually no quantitative data have been available on sponge/coral interactions from these communities. Although the relative aggressiveness of demosponges appears to be correlated with depth, reaching a maximum in our study at 90' and 120', it is interesting to note that coral cover increases from a mean of 18.3% at 60' to 39.1% at 120'. Nevertheless, the total species richness of sponges clearly overwhelms that of corals at 90' and 120'. The processes that permit both a high diversity of sponges and a high frequency of aggressive overgrowths on corals, while allowing such a high % coral cover, remain obscure at this time.

Mechanisms by which sponges can acquire, maintain and expand their space are likely to involve rapid growth rates and/or allelochemicals. Some sponges are known to possess virulent toxins (Bakus & Green, 1974), although these have typically been considered anti-predatory in nature (Bakus, 1981). The use of allelochemicals by sponges for aggressive growth over corals has been suspected (Bryan, 1973; Jackson & Buss, 1975), but only recently has a sponge toxin that inhibits coral growth been identified (Sullivan, *et al*., 1983).

Whether corals themselves use allelochemicals to ward off attacking sponges is uncertain, but this seems unlikely (or at least ineffective) because of the high frequency of aggressive overgrowths by sponges at depth. However, predation on sponges, especially by the angelfishes *Pomacanthus arcuatus* and *P. paru* (Randall & Hartman, 1968; Hourigan, *et al*., in prep.) may help to limit the influence of aggressive sponges on corals, but further research is needed to test this hypothesis.

ACKNOWLEDGMENTS

Special thanks go to M. W. Colgan and D. L. Green for assistance in collecting field data at Salt River Canyon and to the personnel of NULS-1 Hydrolab for their excellent operations program and unselfish help during both missions. We also thank J. C. Ogden, D. K. Hubbard and J. Bayes for help with various logistic and/or computer problems. This study was funded by NOAA grants NA81AAA02690, NA82AAA00470, NA82AAA00872 and NA82AAA01344 to T.H.S. and by funds from the West Indies Laboratory.

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DISTRIBUTION OF SWEEPER TENTACLES ON MONTASTRAEA CAVERNOSA

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ABSTRACT

In direct competition among reef corals for limited substrate space, some species utilize elongate tentacles with specialized cnidae, or sweeper tentacles, to damage opponents. On species described thus far, these tentacles are not generally present, but develop as competitive interactions progress. Colonies of the Caribbean reef coral *Montastraea cavernosa* frequently have sweeper tentacles distributed over colony surfaces in patterns which do not necessarily correspond to ongoing competitive encounters. Nevertheless, we found that, when injured by the congeneric species *M. annularis*, colonies of *M. cavernosa* increase both the number of polyps with sweeper tentacles and the number of sweeper tentacles per polyp on colony regions close to the encounter.

INTRODUCTION

Reef corals are known to use a variety of mechanisms to compete for limited substrate space in crowded reef environments. Two of the best described are the use of mesenterial filaments (Lang, 1971, 1973; Sheppard, 1979) or of "sweeper tentacles" (Richardson, *et al*., 1979; Wellington, 1980; Bak, *et al*., 1982; Chornesky, 1983) by some corals to damage the tissues of neighboring corals.

Mesenterial filaments are normally present in all polyps of every coral. When corals of different species are placed into direct contact, these digestive filaments are deployed rapidly and extracoelenteric digestion of opponent tissues may take place within hours (Lang, 1971, 1973; Sheppard, 1979). The immediate "winner" (i.e., the animal remaining undamaged) in such interactions is generally predictable among various species pairs. Unlike mesenterial filaments, sweeper tentacles (elongate tentacles with specialized cnidae) are found only on certain species of coral (see Lewis and Price, 1975; Bak and Elgershuizen, 1976). Moreover, within these species, sweepers may not be present on all colonies, and, when present, may be erratically distributed over the colony surface. On some corals, sweeper tentacles develop specifically after damage by mesenterial filaments (Wellington, 1980; Bak, *et al*., 1982; Chornesky, 1983) or after contact with recognition (Chornesky, 1983) of other corals. In natural interactions, this delayed development, and thus the ability of the coral to utilize sweepers against a neighbor, occurs some time after the interaction has begun (on the order of a month--Wellington, 1980; Bak, *et al*., 1982; Chornesky, 1983). However, on at least one species of coral, sweeper tentacles are routinely present and are therefore "ready" to participate in competitive interactions with neighboring corals which grow too close (depending, of course, on their location on the colony relative to that of nearby competitors).

Sweeper tentacles commonly are seen on colonies of the Caribbean coral Montastraea cavernosa (Linnaeus). Descriptive patterns of the location of sweeper tentacles on M. cavernosa variously include: concentration around colony perimeters (den Hartog, 1977; Richardson, et al., 1979); maximal expansion in response to water currents (Price, 1973, in den Hartog, 1977); or a less predictable pattern of distribution over colony surfaces (J.C. Lang, unpub. data). Perhaps in part because they are usually present, sweepers on M. cavernosa have been described as feeding appendages (Lewis and Price, 1975), defensive structures to deter close growth of adjacent competitors (Richardson, et al., 1979), and "polyfunctional" structures which might serve both functions (Lang, 1979). Here we present preliminary data on the behavior and development of sweeper tentacles on M. cavernosa in artificial competitive interactions with the congeneric species M. annularis (Ellis and Solander).

MATERIALS AND METHODS

These experiments were conducted at a depth of 60 feet in Salt River Canyon, St. Croix. They were initiated during a saturation dive in the NOAA NULS II Underwater Habitat in March of 1982. Colonies of M. annularis and M. cavernosa (N=8) were cemented to cinder blocks using underwater epoxy-putty (see Chornesky, 1983, for methods). Corals were arranged so that a gap of about 1 cm remained between paired colonies of M. annularis and M. cavernosa when their polyps and tissues were contracted during the day.

Our initial intent was to examine whether introduction of other corals close to colonies of M. cavernosa would affect the expansion patterns of its sweepers. Thus, prior to introducing colonies of M. annularis, locations of existing sweeper tentacles on the M. cavernosa colonies were carefully mapped. The first night after corals were cemented into place, all colonies of M. annularis digested nearby expanded polyps of M. cavernosa in contact with their tissues. Subsequently, polyps of the digested M. cavernosa remained contracted in the area surrounding the resulting wounds. This unpredicted behavioral response made it impossible to observe the behavior of their sweeper tentacles during the remainder of the saturation dive.

Nevertheless, we were provided with the opportunity to follow the longer-term consequences of such interactions for colonies of M. cavernosa on which the location of sweeper tentacles was already well documented. These interactions subsequently were observed on six nights over the following two months. During each observation, the positions of sweepers on the M. cavernosa colonies were carefully mapped and the behavior and condition of both corals were recorded. For data analysis, each colony of M. cavernosa was divided into regions adjacent to and not adjacent to the M. annularis. Boundaries of these "adjacent" and "non-adjacent" regions were designated arbitrarily on maps resulting from the first set of observations, and then held constant for all subsequent observations. Data were analyzed by contrasting changes in the relative proportion of polyps with sweeper tentacles on adjacent and non-adjacent regions of colonies. Adjacent regions were consistently smaller than non-adjacent regions on the same colonies (approximately a third of the size). Therefore, comparison of the absolute number of polyps with sweepers between adjacent and non-adjacent regions yields a conservative estimate of their density on adjacent regions (i.e., when adjacent and non-adjacent regions have equal numbers of polyps with sweeper tentacles, adjacent regions actually would have greater densities of sweeper tentacles than non-adjacent regions).

RESULTS

Figure 1 compares the number of polyps with sweeper tentacles on: A) tissues adjacent to the M. annularis, and B) tissues not adjacent to the M. annularis. The median and a quarter of the range is plotted on this graph since these data were clearly non-normal and sample sizes were small (7-8). There is a significant correlation between the number of polyps with sweeper tentacles on adjacent tissues and time after initiation of the experiment

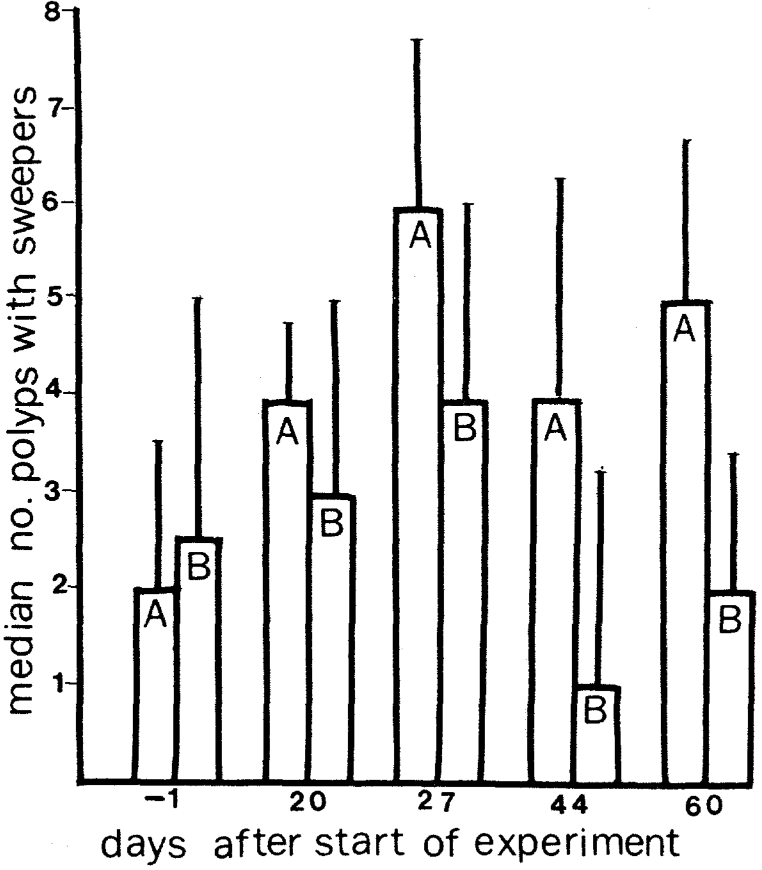

FIGURE 1. For M. cavernosa, change in number of polyps with sweepers on regions that are adjacent (A) or non-adjacent (B) to opponents (M. cavernosa). Vertical bars indicate quartile ranges.

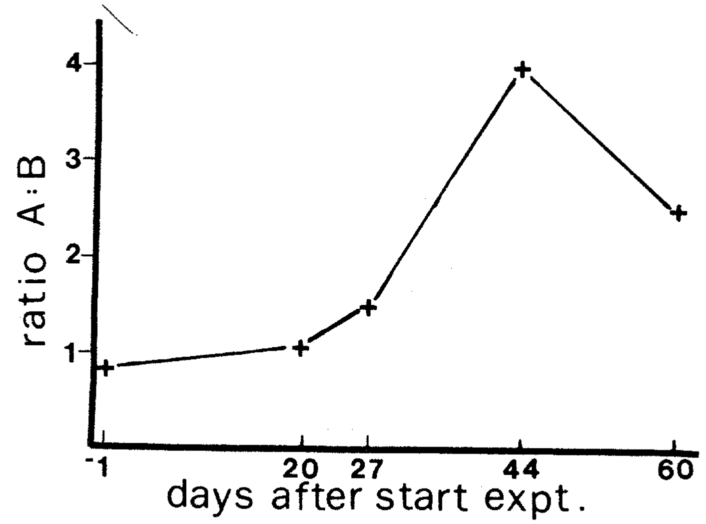

FIGURE 2. Increase in relative proportions of sweepers on adjacent regions over time.

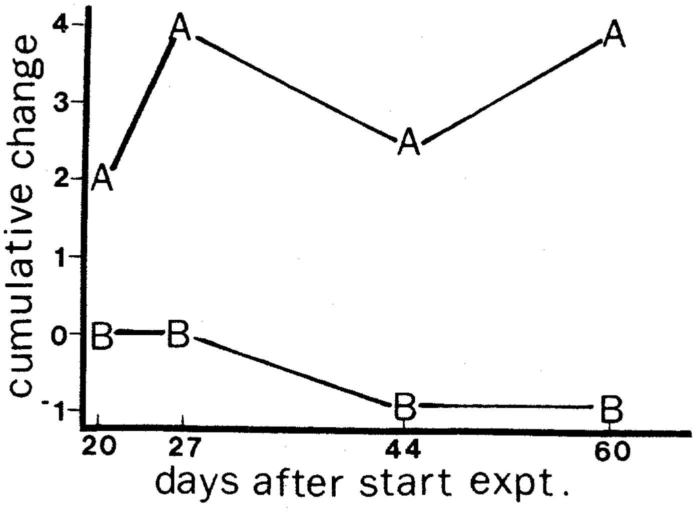

FIGURE 3. Cumulative changes in the number of polyps with sweepers on adjacent (A) and non-adjacent (B) regions. Each value incorporates summed changes from all previous observations.

(Spearman rank correlation $r_s = .333$, $P < .05$). The correlation for non-adjacent tissues is not statistically significant ($r_s = -.133$, $P > .05$). The ratio of A:B is plotted in figure 2 and demonstrates that the relative proportion of polyps with sweeper tentacles on adjacent regions increased during the observation period. Figure 3 shows the cumulative changes (median) in the number of polyps with sweepers on adjacent (A) and non-adjacent (B) regions at various times after initiation of the experiment. These data suggest a cumulative decrease in the number of sweepers on tissues not adjacent to colonies of *M. annularis*. This was clearly true for at least two colonies of *M. cavernosa* on which sweeper tentacles on non-adjacent tissues disappeared after the experiments were begun (4 and 6 weeks, respectively).

Necrotic wounds appeared on most colonies of *M. annularis* close to the colonies of *M. cavernosa*. Most (5 of 6) wounds formed in intervals between observations, during which time the number of *M. cavernosa* polyps with sweeper tentacles adjacent to the *M. annularis* also increased. Sweeper tentacles of the *M. cavernosa* often were observed touching live *M. annularis* tissues close to necrotic regions.

DISCUSSION

M. cavernosa apparently can increase the number of polyps with sweeper tentacles close to the site of competitive encounters with other corals. Although our data specifically reported the number of polyps having sweeper tentacles, observations by one of us (SLW) suggest that, in addition, the number of sweeper tentacles per polyp and the size of the acrospheres on existing sweeper tentacles may increase close to the site of such encounters.

Moreover, our data suggest that either the number of polyps with sweeper tentacles or expansion of sweeper tentacles on portions of colonies not involved in competitive interactions possibly may decrease as the number of expanded sweepers close to the interaction increases. If so, this might reflect a "cost" incurred by the production and/or expansion of additional sweeper tentacles close to the site of competitive encounters.

Although caution should be exercised in ascribing causes for wounds in coral-coral interactions (see Bak, *et al.*, 1982; Chornesky, 1983), it appears that the sweeper tentacles of *M. cavernosa* were capable of damaging tissues of *M. annularis* within their reach. Whether the course of natural interactions is similar to these experiments (i.e., digestion of *M. cavernosa* by *M. annularis* development of sweeper tentacles by *M. cavernosa* damage to *M. annularis* by *M. cavernosa* sweepers) is less clear. For example, if colonies of *M. annularis* and *M. cavernosa* grow gradually into contact, *M. cavernosa* may be able to develop sweeper tentacles prior to digestion by *M. annularis*. Similarly, at a greater distance than the 1 cm gap in these experiments, *M. cavernosa* sweeper tentacles might efficiently deter close growth by *M. annularis* and/or digestion by *M. annularis* (*sensu* Richardson, *et al.*, 1979; see Chornesky, 1983, for discussion of how natural and experimental interactions sometimes may differ).

On other corals for which the development of sweeper tentacles during direct competition has been documented, sweepers are not generally present, but appear in response to the encounter and may later regress (Wellington, 1980; Chornesky, 1983). Since colonies of M. cavernosa normally possess sweeper tentacles distributed in seemingly disordered patterns over colony surfaces, it is particularly interesting that interactions with other corals seem to affect the distribution of sweepers within colonies--increasing in density on adjacent tissues and perhaps decreasing on tissues away from the zone of the interaction. Since sweeper tentacles on M. cavernosa apparently do not necessarily regress after an interaction ceases and may remain on a colony for an extended period of time, the distribution of sweeper tentacles over a colony may reflect at least a short-term historical record of past competitive encounters.

ACKNOWLEDGMENTS

We thank the staffs of the NULS II Hydrolab and the West Indies Laboratory for essential surface support before, during, and after our saturation mission. We also thank C. Brunet, B. Nyden, and C.M. Wahle for their enthusiasm and moral support during the mission; and J.C. Lang and C.M. Wahle for many helpful discussions and useful comments on earlier drafts of this manuscript. We are especially grateful to Bruce Nyden to extraordinary and generous assistance with all aspects of the field work. This reseach was funded by a NOAA Hydrolab grant to E.A. Chornesky and C.M. Wahle.

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RELATIONSHIPS BETWEEN FISHES AND MOBILE BENTHIC INVERTEBRATES ON CORAL REEFS

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ABSTRACT

Observations of 3 types of artificial reefs at 20 m depths show that fish predation alters the pattern of colonization of stomatopods, the largest and most mobile members of the cryptic reef fauna. Recruitment by polychaetes probably is adversely affected by the presence of fish predation also. Possibly because of their secretive habits, the densities of the remaining taxa of cryptic invertebrates were unaffected by fish predators. The data also suggest that the presence of an invertebrate biota influences the colonization and abundance of invertebrate-eating fishes.

INTRODUCTION

The importance of predator-prey interactions in governing community structure has been demonstrated for some marine systems (e.g., Paine, 1966; Dayton, 1975; Menge and Sutherland, 1976; and many others), but their role in coral reef communities remains poorly understood. Coral-eating fishes can influence the structure of coral reefs (Kaufman, 1977; Neudecker, 1979; Wellington, 1982), and herbivores exert both direct and indirect effects upon coral reef communities (Ogden and Lobel, 1978; Hay, 1981; Hixon and Brostoff, 1983). In laboratory microcosm experiments, Brock (1979) showed that parrotfish grazers influence the abundance and diversity of the benthic flora and fauna, and that the presence of refuges (3-dimensional surfaces) is an even more important determinant of benthic community structure than the densities of consumers. Additionally, it has been suggested that a variety of structural, behavioral, and chemical defense mechanisms found in benthic reef organisms represent adaptations to strong predation pressures in reef environments (e.g., Bakus, 1966, 1981; Vermeij, 1978; Reaka, 1980a, 1980b; Reaka and Manning, 1981). However, astonishingly little experimental and quantitative information is available regarding the relationships between fish predators and the abundant invertebrate fauna that inhabits the reef substrate in the field. Most of this benthic biota lives in cryptic refuges under and within the coral substrate. Jackson and Buss (1975) have suggested that the cryptic sessile fauna currently does not experience strong predation. Many of these encrusting organisms grow in inaccessible sites, and particularly the colonial organisms exhibit chemical defenses that are used in competitive interactions (see also Buss and Jackson,

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1979). However, virtually no field studies have quantatively investigated the effects of fish predators upon the teeming mobile cryptic fauna that inhabits this environment. Also, while these invertebrates are the primary food source for many reef fishes (Randall, 1967), no studies have experimentally examined the importance of this mobile invertebrate fauna for the colonization and maintenance of populations of reef fishes. In July 1980 we initiated a 2½ year of study that experimentally investigated reciprocal interactions between fishes and the mobile cryptic invertebrate fauna in Salt Canyon, St. Croix. A preliminary analysis of the first 6 months of the data is presented here. A more thorough analysis of data from the entire 2½ year period is in progress.

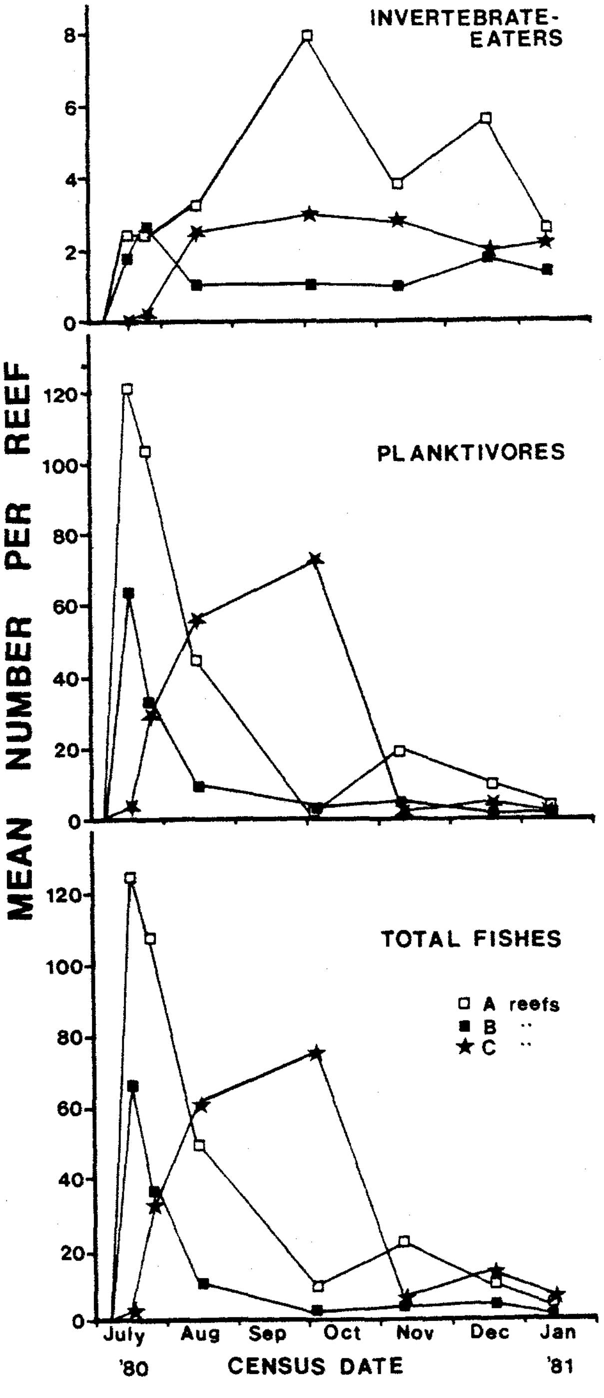
MATERIAL AND METHODS

Using the Hydrolab, an underwater habitat operated by NOAA on St. Croix, U.S. Virgin Islands, 15 artificial reefs were established at a depth of 20 m in Salt River Canyon in July 1980. Salt River Canyon is a submarine canyon 70-100 m wide with a sand floor flanked by a vertical and a sloping coral reef wall. Five reefs provided habitat for fishes and invertebrates (A reefs); each consisted of 11 cinderblocks arranged in a pyramid 2 blocks wide and 3 blocks high, with 6 pieces of sun-dried dead coral rubble placed around the pyramid base. The components were tied together with nylon rope and anchored in place with iron reinforcement bars. Five reefs consisted of a cinderblock pyramid without rubble, providing habitat for fishes but little shelter for invertebrates (B reefs). Five reefs, each composed of rubble arranged in the same pattern as in the A reefs but lacking a cinderblock pyramid, provided habitat more suitable for cryptic invertebrates (C reefs). The 15 reefs were arranged serially (ABCABC...) 10 m apart and 10 m out from the sloping east wall of the canyon. Fishes on the reefs were censused visually one week after establishment, and at approximately 30-day intervals thereafter. Using information from the literature (Randall, 1967; Clavijo, et al., 1980) and personal observations, we assigned each individual to a feeding guild (planktivore, herbivore, piscivore, piscivore-invertivore, invertivore) based on its size class (postlarval, juvenile, adult) and species (Appendix Table 1). We have included fishes that eat only invertebrates and those that eat both invertebrates and smaller fishes here as "invertebrate-eaters", since both prey on invertebrates. The invertebrate-eaters and planktivores (which prey upon invertebrate larvae as well as holoplankton) are the fishes most likely to influence benthic prey populations; hence, these taxa are emphasized in this report. After 6 months, cryptic invertebrates in half of the rubble from each of the A and C reefs were sampled quantitatively by sealing the rubble in plastic bags *in situ*. On shore, the rubble was chiselled into small pieces and sieved (0.7 mm mesh), retaining all of the resident cryptic biota. These samples were preserved in formalin and sorted, counted, and measured microscopically (see Reaka, 1981, 1983, for more details).

RESULTS

All fishes colonized both types of cinderblock reefs (A,B) quickly, while >2 months passed before fishes on the rubble reefs (C) reached peak abundances (lower graph, Fig. 1). On all 3 types of reefs, total numbers of individuals subsequently declined (and remained low throughout the winter; numbers increased again following spring recruitment; Reaka, 1981, 1983). Planktivores (mostly juvenile grunts, Haemulidae) were by far the most abundant guild, so their pattern of colonization followed that described above for total numbers of fishes (Fig. 1). Invertebrate-eating fishes were less abundant than planktivores. The number of invertebrate-eating fishes on reefs with rubble-dwelling invertebrates (A, C) did not peak until 2-5 months after establishment of the reefs. This period coincided with the time

FIGURE 1. Mean numbers of fishes observed on different types of reefs. All 5 guilds are included in total fishes. Species included in these guilds are listed in Appendix Table 1. The A reefs (open squares) are comprised of cinderblocks and rubble, the B reefs (closed squares) are built of cinderblocks only, and the C reefs (stars) are made of rubble only. For purposes of illustration, error bars are omitted here, but they are included in Reaka, 1981, 1983.



required for full colonization of the new rubble habitat by invertebrates (Reaka, 1981, 1983). In all guilds, fishes on the C reefs generally were smaller than those on the cinderblock reefs (Wolf, Bermingham, et al., unpub. data).

The data in Figure 1 suggest that reefs with habitat for invertebrates (A) generally were characterized by higher numbers of fishes than reefs without habitat for invertebrates (B). Specifically, the number of invertebrate-eaters per reef was significantly higher on A reefs than on B reefs in August and October, and the data showed a strong tendency in that direction in November (Mann Whitney U tests; $p < 0.02$, $p<0.01$, and $p<0.058$, respectively). In addition, the total numbers of invertebrate-eaters per census on the 5 type A reefs were consistently higher than those recorded on the 5 type B reefs for the 6 month interval (Wilcoxon matched-pairs signed-ranks test, $p <0.01$).

Population levels of invertebrates may be affected by invertebrate-eaters that prey upon reef residents, and by planktivorous fishes that eat invertebrate larvae swimming near or settling on the reef. The total numbers of invertebrate-eating fishes per census on the 5 type A reefs were consistently higher than those on the 5 type C reefs throughout the study period (Wilcoxon matched-pairs signed-ranks test, $p < 0.01$). However, there was no significant difference in the numbers of planktivorous fishes per census on A vs. C reefs over the 6 month interval (Wilcoxon matched-pairs signed-ranks test, n.s.). The number of invertebrate-eaters per reef was lower on the C than on the A reefs in the first two censuses (July 1980) (Mann Whitney U tests; $p < 0.02$, $p < 0.058$, respectively). Although fewer planktivores were recorded on A than on C reefs in July and November, individual C reefs were populated by more small planktivores than were the A reefs in October 1980 (Mann Whitney U tests; $p < 0.0001$, $p < 0.03$, $p < 0.05$, respectively).

TABLE 1. Numbers of individuals of major invertebrate taxa collected per piece of rubble in control (natural reef) and experimental reefs (A and C reefs) in January 1981 (6 months after establishment of the experimental reefs). Results of a one-way classification analysis of variance (df = 2,37) are given under F value. Means and standard errors (in parentheses) are based on raw data. All data were tested for homogeneity of variance (Bartlett's test), and, if necessary, transformed by ln (x+1). A superscript t indicates that test results are based on transformed data. Superscripts a and b indicate means that are significantly different by a Student Neuman Keuls test; means with the same subscript are not significantly different.

Taxon	Control Reef Wall	A Reefs (cinderblock + rubble)	C Reefs (rubble only)	F value (df=2,37)		Bartlett's Test Value	
Stomatopods	0.5(±.2)^{b}	1.0(±.2)^{b}	1.8(±.3)^{a}	3.31	$p<0.05$	4.29	N.S.
Snapping shrimps	7.1(±1.3)	6.3(±1.1)	8.3(±.9)	0.90	N.S.	1.26	N.S.
Other shrimps (non-alpheids)	10.3(±1.5)	10.7(±2.0)	10.3(±1.6)	0.02	N.S.	2.30	N.S.
Crabs	17.9(±2.0)	12.5(±2.4)	13.7(±2.0)	1.90	N.S.	0.69	N.S.
Peracarids	73.3(±17.5)	62.7(±13.6)	87.3(±15.2)	0.74	N.S.	0.16	N.S.
Sipunculans	18.5(±5.8)	17.8(±4.6)	11.7(±2.5)	0.80	N.S.	5.47	N.S.
Polychaetes	180.0(±60.7)^{a}	55.6(±12.2)^{b}	76.9(+16.8)^{ab}	4.54^{t}	$p<0.05$	6.32^{t}	N.S.
Ophiuroids	4.9(±0.7)^{a}	2.3(±0.6)^{b}	2.1(±0.4)^{b}	9.53	$p<0.05$	2.89	N.S.
Gastropods	6.2(±0.5)	6.5(±0.9)	6.5(±0.8)	1.28	N.S.	4.87	N.S.
Bivalves	10.5(±2.1)	9.4(±1.9)	6.8(±0.9)	0.84^{t}	N.S.	1.30^{t}	N.S.
Chitons	0.2(±0.1)	0.1(±0.1)	0.1(±0.1)	0.10	N.S.	1.02	N.S.

Examination of the invertebrate fauna in the rubble from A reefs (with fish predators) and C reefs (with fewer fish predators), and in naturally occurring rubble from the east canyon wall adjacent to the experimental reefs (with fish predators) revealed several patterns. Although the abundances of 8 of the 11 major revealed taxa did not differ in the 3 sets of rubble, stomatopods showed a significant increase in numbers on C reefs compared to either A reefs or rubble from the canyon wall (Table 1). The naturally occurring rubble from the wall contained species of stomatopods characteristic of shallow to moderate reef habitats (*Gonodactylus oerstedii*, *G. spinulosus*, *Meiosquilla schmitti*), while the experimental rubble (A and C reefs) was inhabited by different species (*Gonodactylus* sp. nov., *Meiosquilla* sp. nov., *M. tricarinata*, *Pseudosquilla ciliata*). Several of the latter species are generalists, occurring in grassbeds as well as rubble

(M. tricarinata, P. ciliata), and others (particularly Gonodactylus sp. nov.) are characteristic inhabitants of our deeper (35-50 m) control and experimental reef sites. These opportunists reached higher densities in the new rubble habitat (particularly in the absence of predation) than the populations that normally inhabit rubble on the reef slope at this depth. There were no differences in the species of stomatopods found in the A vs. C experimental reefs. Numbers of polychaetes were significantly lower on the experimental reefs exposed to predation (A) than in the control rubble from the reef wall, and intermediate numbers of polychaetes were found in rubble from the C reefs. Ophiuroids also showed relatively low recruitment to the new habitat on the experimental reefs, but were equally abundant on A and C reefs (Table 1).

DISCUSSION

Does the presence of cryptic invertebrates in rubble influence colonization by fishes?

Coral rubble harbors hundreds of invertebrates (Table 1), providing an abundant food source for some fishes. Many authors have argued that living space is more important than food in limiting (or structuring) populations of reef fishes (e.g., Sale, 1978; Smith, 1978). Although evidence of the importance of space comes from several sources (discussed in Sale, 1980), other studies show that space is not always limiting (e.g., Talbot, et al., 1978; Robertson, et al., 1981). Evidence that food directly influences numbers of fishes is limited (Tsuda and Bryan, 1973). In the present study, however, the timing of colonization suggests that fish recruitment to reefs is related to the availability of benthic food. On those reefs with rubble-dwelling invertebrate fauna (A, C), the number of invertebrate-eaters peaked after 2-5 months, which coincides with the colonization rate of invertebrates in coral rubble at this depth (Reaka, 1981, 1983, and Reaka, et al., in prep.). In addition, cinderblock reefs with rubble had more invertebrate-eating fishes than cinderblock reefs without rubble. Rubble around the base of the A reefs gave the latter a slightly more complex structure than the B reefs, but whether or not this contributed to the observed differences in fish populations is unclear. Other variations in the structure of small artificial reefs (differences in the sizes of available holes) have not been related to number of fishes present or species composition (Molles, 1978; Talbot, et al., 1978). Separation of the effects of food vs. habitat complexity in the present study would require an experiment comparing colonization of reefs with rubble initially containing a natural complement of invertebrates to that of reefs with sun-dried (defaunated) rubble.

Does the presence of fish predators influence invertebrate colonization?

Stomatopods appear to be strongly influenced by the presence of fish predators in this habitat (Table 1). After 6 months, these mantis shrimps were more abundant on the experimental reefs with fewer invertebrate-eaters (C) than on those with more and larger fish predators (A). This could not have been due to differences in location or habitat, since the positions of A and C reefs were alternated regularly down the canyon at equal distances from the reef wall. Except for octopuses (which in this habitat are very rare compared to the rubble fauna reported here), stomatopods are the largest and most active of the mobile cryptic fauna. Due to periodic movements on the surface of their rubble (Reaka, 1980b; Dominguez and Reaka, in review), stomatopods may be more exposed to predators than are many of the smaller, more secretive taxa. Ophiuroids had slow rates of colonization, but appeared unaffected by the fishes. Although recruitment of polychaetes to the new rubble also was slow, the effects of fish predators upon polychaete population levels are enigmatic. Invertivorous and planktivorous fishes possibly are responsible for decreased survivorship of settling polychaete larvae.

Cage experiments in shallow water (3 m) confirm that polychaete recruitment occurs slowly (probably via larval settlement), and that numbers of recruits are strongly decreased by exposure to fish predation compared to controls (Reaka, unpub. data). The remaining groups of major invertebrate taxa appear to be unaffected by fish predators. Finer taxonomic resolution of these taxa (in progress) may yield additional effects. It is also possible that a greater difference in predation pressures between the A and C reefs would have shown a more pronounced effect. At the moment, however, we conclude that the secretive habits of many of these cryptic invertebrates protects them from pronounced effects of predators upon their populations at this study site.

ACKNOWLEDGMENTS

This work was supported by grants from the NOAA National Undersea Research Program (NA80AAA03715, NA81AAA01500) and the National Science Foundation (OCE-78-26605) to M.L. Reaka. In addition, we are grateful to Frank Pecora, Joseph Landsteiner, Cheryl Van Zant, Jane Dominguez, David Moran, Hugh Reichardt, Joseph Dineen, and Miriam Smyth for their assistance as either aquanauts or members of the surface research team during our Hydrolab missions. We particularly thank the Hydrolab staff for their support and cooperation throughout the study. This is Contribution No. 111 from the West Indies Laboratory.

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APPENDIX TABLE 1. Trophic categories of reef fishes censused on our artificial reefs (3-34 m) in Salt River Canyon, St. Croix. Assignments to trophic categories were based on data in Randall (1967), Clavijo, *et al*. (1980), and personal observations. Fish names are in accordance with Robins, *et al*., 1980.

INVERTIVORES

- HOLOCENTRIDAE, squirrelfishes
  - *Adioryx coruscus*, reef squirrelfish
  - *Flammeo marianus*, longspine squirrelfish
  - *Holocentrus ascensionis*
  - *Holocentrus rufus*
- SERRANIDAE, seabasses
  - *Serranus tabacarius*, tobaccofish juveniles
  - *Serranus tigrinus*, harlequin bass
- MALACANTHIDAE, sand tilefishes
  - *Malacanthus plumieri*, sand tilefish
- LUTJANIDAE, snappers
  - *Lutjanus synagris*, lane snapper
- GERREIDAE, mojarras
  - *Gerres cinereus*, yellowfin mojarra
- HAEMULIDAE, grunts
  - *Haemulon aurolineatum*, tomtate
  - *Haemulon flavolineatum*, French grunt
  - *Haemulon plumieri*, white grunt
- SCIAENIDAE, drums
  - *Equetus acuminatus*, high-hat
  - *Equetus lanceolatus*, jackknife-fish
- MULLIDAE, goatfishes
  - *Pseudupeneus maculatus*, spotted goatfish
- CHAETODONTIDAE, butterflyfishes
  - *Chaetodon sedentarius*, reef butterflyfish
- POMACENTRIDAE, damselfishes
  - *Pomacentrus planifrons*, threespot damselfish
- LABRIDAE, wrasses
  - *Halichoeres bivittatus*, slippery dick
  - *Halichoeres garnoti*, yellowhead wrasse
  - *Halichoeres maculipinna*, clown wrasse
  - *Halichoeres poeyi*, blackear wrasse
  - *Halichoeres radiatus*, puddingwife
  - *Thalassoma bifasciatum*, bluehead
- CLINIDAE, clinids
  - *Labrisomus nuchipinnis*, hairy blenny
  - *Malacoctenus* sp.
- BALISTIDAE, triggerfishes and filefishes
  - *Balistes vetula*, queen triggerfish
- OSTRACIIDAE, boxfishes
  - *Lactophrys polygonia*, honeycomb cowfish
  - *Lactophrys triqueter*, smooth trunkfish
- TETRADONTIDAE, puffers
  - *Canthigaster rostrata*, sharpnose puffer

APPENDIX TABLE 1 (continued, p.2)

INVERTIVORES-PISCIVORES

SERRANIDAE, sea basses
- *Epinephelus adscensionis*, rock hind
- *Epinephelus fulva*, coney
- *Epinephelus guttatus*, red hind
- *Serranus tabacarius*, tobaccofish adults

GRAMMISTIDAE, soapfishes
- *Rypticus saponaceus*, greater soapfish

LUTJANIDAE, snappers
- *Lutjanus analis*, mutton snapper
- *Lutjanus buccanella*, blackfin snapper

PLANKTIVORES

HOLOCENTRIDAE, squirrelfishes
- *Myripristis jacobus*, blackbar soldierfish

SERRANIDAE, seabasses
- *Paranthias furcifer*, creole-fish
- *Serranus tortugarum*, chalk bass

PRIACANTHIDAE, bigeyes
- *Priacanthus arenatus*, bigeye

LUTJANIDAE, snappers
- *Ocyurus chrysurus*, yellowtail snapper
- juvenile snappers

HAEMULIDAE, grunts
- juvenile grunts

POMACANTHIDAE, angelfishes
- juvenile angelfishes

POMACENTRIDAE, damselfishes
- *Chromis cyaneus*, blue chromis
- *Chromis multilineatus*, brown chromis
- *Pomacentrus partitus*, bicolor damselfish

LABRIDAE, wrasses
- *Bodianus rufus*, Spanish hogfish juveniles
- *Clepticus parrai*, creole wrasse
- *Halichoeres radiatus*, puddingwife juveniles
- *Hemipteronotus splendens*, green razorfish

CLINIDAE, clinids
- *Acanthemblemaria* sp.
- *Emblemaria pandionis*, sailfin blenny

GOBIIDAE, gobies
- *Isoglossus helenae*, hovering goby

All post-larval, pre-juvenile fishes

APPENDIX TABLE 1 (continued, p.3)

HERBIVORES

- POMACENTRIDAE, damselfishes
  - *Pomacentrus dorsopunicans*, dusky damselfish
  - *Pomacentrus leucostictus*, beaugregory
  - *Pomacentrus variabilis*, cocoa damselfish
- BLENNIIDAE, combtooth blennies
  - *Ophioblennius atlanticus*, redlip blenny
- BALISTIDAE, triggerfishes and filefishes
  - *Cantherhines pullus*, orangespotted filefish

PISCIVORES

- MURAENIDAE, morays
  - *Gymnothorax* spp.
- SYNODONTIDAE, lizardfishes
  - *Synodus intermedius*, sand diver
- SERRANIDAE, sea basses
  - *Epinephelus cruentatum*, graysby
  - *Epinephelus striatus*, Nassau grouper
- CARANGIDAE, jacks and pompanos
  - *Caranx ruber*, bar jack
- LUTJANIDAE, snappers
  - *Lutjanus mahogoni*, mahogany snapper
- BOTHIDAE, lefteye flounders
  - *Bothus lunatus*, peacock flounder

FISH GRAZING AND COMMUNITY STRUCTURE OF REEF CORALS AND ALGAE: A SYNTHESIS OF RECENT STUDIES

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ABSTRACT

This paper reviews major studies published over the past 5 years on the impact of fishes upon the major components of tropical reef benthos. With one notable exception, virtually no studies have demonstrated a strong effect of fish corallivores upon coral communities, although at least one coral genus is certainly affected by fish predation. On the other hand, herbivorous fishes strongly affect the distribution and abundance of reef algae, with recent studies elucidating temporal and spatial variations in herbivore impact. Of all reef fishes, territorial damselfish have especially widespread direct and indirect effects. By establishing and defending distinct algal mats, they affect: (1) coral growth, recruitment, and bioerosion; (2) algal abundance and local diversity; (3) local microfaunal abundance; and (4) nitrogen fixation by blue-green algae. These and other interactions are summarized on a synthetic flowchart.

INTRODUCTION

The dominant benthic organisms on tropical reefs are scleractinian corals and various algae. That grazing fishes can affect the local distribution and abundance of such organisms was first demonstrated by the caging experiments of Stephenson and Searles (1960) and Randall (1961). More recently, ecologists have focused their attention on the role of fishes and large invertebrates in determining the structure of benthic communities, that is, how differential foraging can alter competitive relationships and thus the local species diversity of reef benthos. Recent reviews have been published on the impact of sea urchins (Lawrence and Sammarco 1982) and the crown-of-thorns seastar (Birkeland 1982). The goal of this paper is to briefly review and synthesize major studies on the effects of fishes upon the community structure of reef corals and algae published during the past 5 years (1978 through part of 1983). Due to textual constraints, this overview is necessarily of limited scope. Those seeking more comprehensive reviews of marine plant-herbivore interactions are referred to Ogden and Lobel (1978), Borowitzka (1981), and Lubchenco and Gaines (1981). Sheppard (1982) includes a general taxonomic review of corallivores.

FISHES AND CORALS

Despite observations that members of about ten families of fishes eat coral polyps (Randall 1974, Patton 1976), surprisingly few studies have demonstrated that such corallivores influence the distribution and abundance of hermatypic corals. For example, although butterflyfishes (Chaetodontidae) are apparently the major reef-fish corallivores (e.g., Reese 1977), recent data from the Red Sea suggest that these fishes consume a negligible portion of the total standing crop of live coral (Harmelin-Vivien and Bouchan-Navaro 1981). However, at least one coral genus, _Pocillopora_, is strongly affected by fish predation. Neudecker (1979) found that colonies transplanted from a relatively fish-free lagoon (1 m depth) to reef slopes (15-30 m depth) in Guam survived well when caged, but were extensively fed upon by butterflyfishes and balistid triggerfishes when exposed. Using a similar experimental design, Wellington (1982) found that Pocillopora colonies exposed to predation by mainly tetraodontid pufferfishes off the Pacific coast of Panama suffered strongly reduced growth rates relative to protected controls. These studies suggest that Pocillopora colonies may be generally rare where fish corallivores are abundant.

Perhaps more important to coral distribution and abundance than direct predation by fishes are the indirect effects of certain damselfishes (Pomacentridae). These fish defend permanent individual territories about 1 m in diameter, resulting in locally decreased grazing by other fishes, and thus increased algal growth as distinct mats used as food sources and nesting sites (see next section). Field observations have shown that damselfish kill coral either directly by removing polyps, thus providing open substrate for their algal mats (Kaufman 1977, Wellington 1982), or indirectly by the reduced grazing within territories allowing algae to smother corals (Potts 1977). In either case, bioerosion of corals may be accelerated within territories, apparently because the algal mats provide refuges and/or food sources for settling boring organisms, which subsequently reduce the ability of the coral to withstand wave shock (Risk and Sammarco 1982). Thus, the algal mats within damselfish territories are generally detrimental to coral colonies (see also Lobel 1980). However, small corals located within the periphery of a territory but still outside the algal mat can be protected from corallivores by the resident damselfish (Wellington 1982).

How damselfish territoriality affects the recruitment of coral larvae is unclear. Previous work has shown that algal mats inhibit settlement by corals (e.g., Birkeland 1977). However, Sammarco and Carlton (1981) reported enhanced recruitment of mostly Acropora on substrates placed inside damselfish territories on the Great Barrier Reef for four months relative to caged substrates or those exposed to grazers outside territories. Unfortunately, the ultimate fates of these recruits were not followed. Using a similar experimental design in Hawaii, Hixon and Brostoff (in prep.) found the recruitment of Pocillopora over the course of a year on caged surfaces to be greater than that on exposed surfaces either inside or outside damselfish territories. However, there was indication of low survival of these recruits due to smothering by algae. Moreover, in a laboratory microcosm experiment at the same site, Brock (1979) found an inverse relationship between the density of grazing scarid parrotfishes and coral recruitment on exposed tank walls. Bak and Engle (1979) have also attributed the high mortality rates of juvenile corals to grazing by parrotfishes, which are typically excluded from damselfish territories. It appears that on open surfaces, coral recruits may initially experience enhanced survival where they are protected from extensive fish grazing, either inside cages or within damselfish territories, but will eventually be overgrown by algae. Those larvae settling where exposed to fish grazing may initially suffer high mortality, being consumed along with the fishes' other prey, but some individuals will eventually reach an invulnerable size class where they are both immune to incidental predation and freed from competition with algae (Birkeland 1977).

Very few data have been reported on how fishes alter competitive interactions between corals. Sammarco and Williams (1982) have hypothesized that the algal mats of damselfish territories may act as refuges for some rarer corals, thus increasing the local evenness of relative abundances among coral species. By far the most extensive published study of the effects of fishes on coral community structure is that of Wellington (1982), who worked on a fringing reef off the Pacific coast of Panama. In this system, branching Pocillopora spp. dominated shallow areas (0-6 m depth), while the massive Pavona gigantea dominated deeper areas (6-10 m depth). Using a clever series of experiments and observations, Wellington discovered an interactive feedback loop whereby the damselfish *Eupomacentrus acapulcoensis* may directly and indirectly cause this zonation. When establishing territories in the shallow zone, damselfish differentially kill *Pavona* by polyp removal and maintain their algal mats on the exposed substrate; *Pocillopora* is apparently protected by its tightly branched morphology and rapid polyp regeneration. Moreover, as discussed above, *Pocillopora* colonies within the periphery of territories are protected from fish corallivores. These factors enhance the ability of *Pocillopora* to competitively dominate *Pavona* in shallow areas. The *Pocillopora* framework, in turn, provides the damselfish with shelter, a necessary requisite for a territory. In the deep zone, shelter sites and thus damselfish densities are low because overall coral cover (and thus inter-coral competition) is low, apparently due to physical factors. Here, transient fish corallivores (mostly puffers) differentially eat *Pocillopora*, whose branches they can ingest and masticate, leaving *Pavona* as the dominant coral. Overall, it seems that territorial damselfishes in general have a far greater impact on hermatypic corals than do true fish corallivores per se.

FISHES AND ALGAE

Considerably more data have been gathered on the effects of fishes on reef algae than on corals. This may reflect the fact that herbivorous fishes, especially parrotfishes (Scaridae), surgeonfishes (Acanthuridae) and territorial damselfishes (Pomacentridae), are together among the most diverse and abundant of reef fishes (e.g., Ogden and Lobel 1978). Indeed, Hatcher (1981) has empirically estimated that about half the net algal production on One Tree Reef, Australia, is consumed by fishes. Although some excellent studies have investigated the impact of these fishes on subtropical rocky reefs (e.g., Montgomery 1980a,b), I will necessarily limit this discussion to true coral reefs.

Recent studies have substantiated earlier caging experiments (e.g., Stephenson and Searles 1960; Randall 1961) showing that herbivorous fishes strongly affect the distribution and abundance of reef algae. Typically, heavily grazed dead coral surfaces become dominated by grazer-resistant crustose coralline algae (e.g., Vine 1974; Wanders 1977; Brock 1979; Hixon and Brostoff 1981, 1982), while caged but otherwise identical surfaces become covered by high standing crops of erect algae (e.g., above studies plus: Lassuy 1980, Miller 1982, Sammarco 1983), which apparently competitively exclude corallines. While grazing algae, fishes also affect interspersed assemblages of sessile animals (e.g., Day 1977, 1983). Attention has shifted lately to temporal and spatial variations in these general patterns. Hatcher and Larkum (1983) demonstrated that algal standing crops at One Tree Reef were controlled by grazing fishes all year (autumn and spring) on the reef slope (10 m depth), but only during spring in the lagoon (2 m depth). In autumn, inorganic nitrogen limited the standing crop of lagoon algae despite the continued presence of fishes.

In addition to seasonal variations, an apparently general trend within reefs is that the spatial distribution of fish grazing intensity varies inversely with tidal exposure and/or wave action (e.g., Van den Hoek *et al*. 1978) and directly with the availability of shelter for the herbivores from predatory fishes (e.g., Hay 1981a, Hay *et al*. 1983). Thus, as documented in Guam (Nelson and Tsutsui 1981) and the Caribbean (Hay *et al*. 1983), the depth distribution of grazing intensity may often be unimodal: low in very shallow water due to limited accessibility by fishes, high at intermediate depths due to high accessibility and shelter, and low in deep reef areas, where the abundance of coral shelter typically decreases. This pattern may explain the bimodal zonation of erect algal cover found on reefs such as those in Curacao (Van den Hoek 1978): high cover in the eulittoral zone (0-1 m depth), low on the upper reef slope (1-30 m), and high again on the lower slope (30-50 m). The lack of shelter for grazing fishes probably also explains the existence of extensive algal plains occurring on sand bottoms below and between reefs (e.g., Hay 1981b, Hay _et_ _al_. 1983).

As might be expected, the impact of fish herbivory strongly influences the community structure of reef algae. Hay (1981b) and Hay _et_ _al_. (1983) suggested that selection for resistance to grazing may compromise competitive ability. They found that, off the Caribbean coast of Panama, fishes prevent competitively dominant (but highly palatable) sand-plain species from displacing competitively subordinate (but grazer-resistant) reef algae. This dichotomy may act to maintain between-habitat diversity in algae (Hay 1981b).

Within-habitat algal diversity is strongly affected by territorial damselfishes. As discussed in the previous section, these fishes establish and maintain dense mats of mostly filamentous algae on dead coral surfaces by defending small individual areas against other herbivores, including sea urchins (Williams 1980, 1981). By differentially grazing these mats (Irvine 1982, Hixon and Brostoff in prep.) and/or by "weeding" undesirable species (Lassuy 1980), damselfishes can affect the local diversity of algae. This effect has been demonstrated by three similar experiments in Guam (Lassuy 1980), Hawaii (Hixon and Brostoff 1981, 1982, 1983), and Australia (Sammarco 1983). Each experiment compared algal diversity on substrates exposed to three different treatments: accessible to mostly damselfish grazing inside territories, accessible to intense grazing by other herbivores outside territories, and protected within fish-exclusion cages outside territories. Although strict comparisons are precluded by differences in experimental design and laboratory analyses, some general patterns do emerge. For both damselfish species he studied, Lassuy (1980) found that, of the three treatments, caged surfaces exhibited the greatest algal diversity after 2 months. Both Hixon and Brostoff (1981, 1983) and Sammarco (1983) obtained the same result from samples taken after 2 to 6 months and 3 months, respectively. However, after a year both these studies found that algal diversity was greatest inside damselfish territories. These data, combined with the fact that Sammarco studied one of the same species as Lassuy, suggest that Lassuy's (1980) samples may have represented early successional stages. In any event, Hixon and Brostoff (1982, 1983) further showed that grazing intensity was of intermediate intensity inside territories relative to the other two treatments. These results thus supported the "intermediate-disturbance hypothesis" (_sensu_ Connell 1978). At low levels of grazing disturbance within cages, a few dominant competitors (especially the red alga _Tolypiocladia_ in the Hawaii study) were capable of locally excluding most other species. At high levels outside territories, many local extinctions occurred. Algal diversity thus peaked at intermediate grazing intensity inside damselfish territories, where the coexistence of many species was maintained because their densities were apparently kept below levels where resources became limiting. Note, however, that not all damselfishes enhance local algal diversity; some species maintain near monocultures within their territories (e.g., Montgomery 1980a,b).

Regardless of whether or not damselfishes enhance local diversity, the greatly increased standing crop of erect algae within their territories has important secondary effects on reef communities. The algal mat serves as a refuge for invertebrate microfauna and/or various epiphytes (Lobel 1980, Hixon and Brostoff 1982 and in prep.). Also, because accretion by coralline algae adds to the reef framework and such algae (along with corals, see above) are overgrown by the algal mat, damselfish territories are probably sites of weakened reef structure (Vine 1974, Lobel 1980). Finally, damselfish territories may indirectly affect nitrogen fixation on reefs, although available data are somewhat contradictory. During the same study as Sammarco (1983) described above, Wilkinson and Sammarco (1983) found that nitrogen fixation by blue-green algae was positively correlated

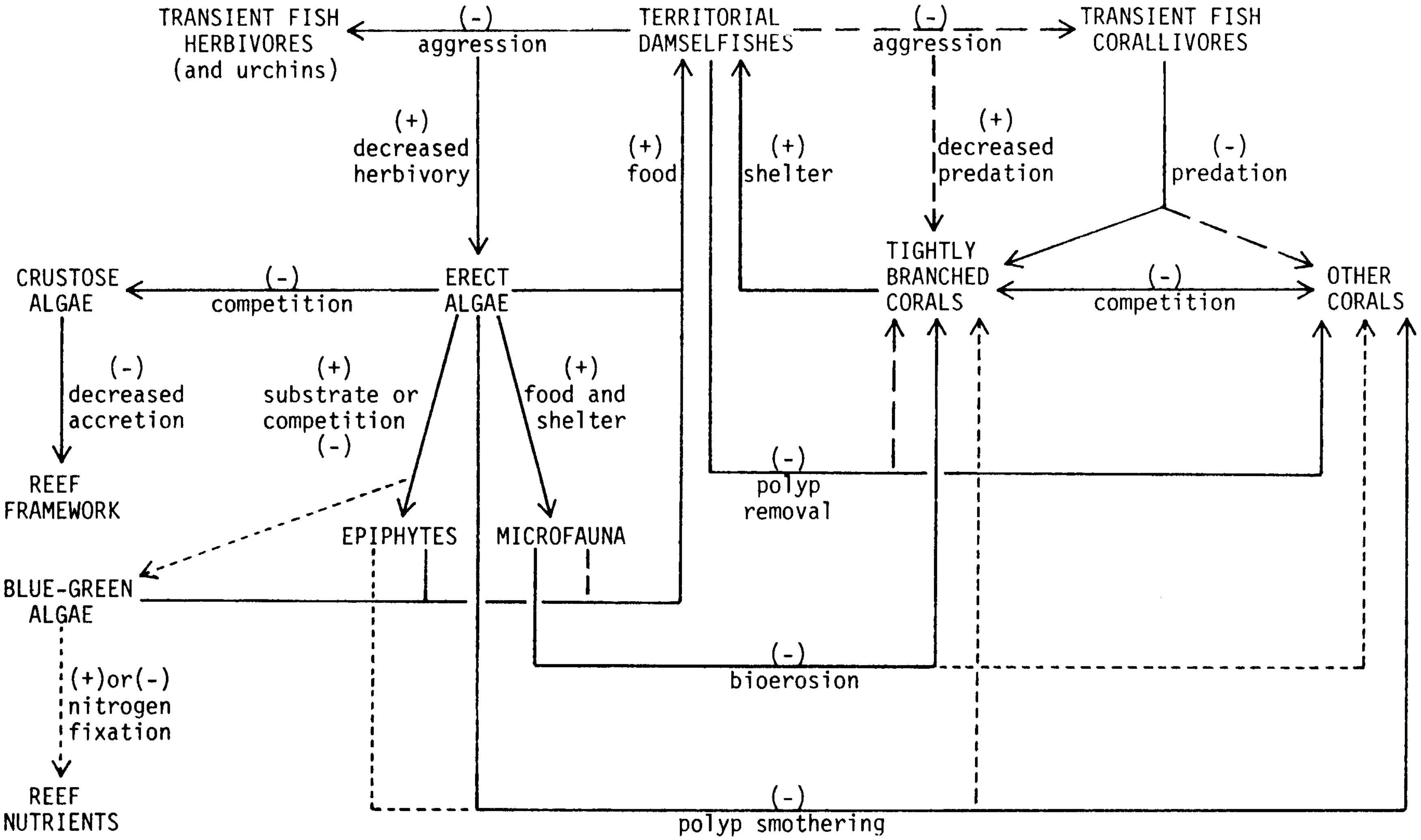

Figure 1. Flowchart summarizing interactions between fishes and benthos on a "typical" coral reef where territorial damselfishes are abundant. Arrows indicate the direction of interaction; (+) and (-) indicate positive and negative effects, respectively. Dashed lines indicate relatively weak interactions, and dotted lines indicate interactions that are poorly documented and/or controversial. Where damselfishes are rare, some of these interactions reverse. In particular, erect algae and their associates often are replaced by grazer-resistant crustose algae and their associates. See text for further explanation.

with grazing intensity on the Great Barrier Reef, being lowest within cages, intermediate within damselfish territories, and greatest outside territories. However, both Lobel (1980) and Hixon and Brostoff (in prep.), working in Hawaii, found considerably more blue-green algae inside than outside territories. These discrepancies suggest possible regional differences in local distributions of blue-green algae. In any event, herbivorous fishes, especially territorial damselfishes, extensively affect reef algae in a variety of ways.

SYNTHESIS

Attempting to synthesize the above studies into a single conceptual framework can be done only at the realized risk of over-generalization and over-simplification. So be it. In general, fishes appear to strongly influence the community structure of reef algae, much more so than that of corals. This difference may be due to coral polyps and their surrounding calcareous skeletons being less available, palatable, and productive than many algae. Indeed, Randall (1974) has indicated that truly corallivorous fishes are among the most highly evolved of fishes, suggesting that this form of predation has appeared only recently in evolutionary time. However, many algae are inferior sources of nutrition (e.g., Montgomery and Gerking 1980), and chemical defenses in algae are being discovered at an increasingly rapid rate (e.g., Norris and Fenical 1982, Paul and Fenical 1983).

In any event, while transient grazing fishes certainly control the distribution and abundance of many algae and some corals, the direct and indirect effects of territorial damselfishes appear to strongly alter a variety of components of reef benthos. These fishes truly can be considered "keystone species" (*sensu* Paine 1969) where they are abundant (Williams 1980, Hixon and Brostoff 1983). I thus submit Figure 1 as a flowchart summarizing the general scheme of fish-benthos interactions on a "typical" coral reef where damselfishes are common. Some of these interactions are well documented; others are not. This "synthesis" should therefore be considered a set of working hypotheses rather than a list of facts. All that can be stated unequivocally is that, first, fishes do indeed affect benthic community structure on tropical reefs, and second, more data on this important topic clearly are needed.

ACKNOWLEDGMENTS

Many thanks to F. Lynn Carpenter for her eleventh-hour review and Pam McDonald for her twelfth-hour typing of the manuscript.

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CORAL RECRUITMENT AT MODERATE DEPTHS: THE INFLUENCE OF GRAZING

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ABSTRACT

The effects of grazers on the biomass of algae and coral recruitment have been investigated extensively in shallow water, yet the dynamics of this interaction in deeper water have received, by comparison, relatively little attention. Fifteen cement artificial reefs were established at a depth of 20m in Salt River Canyon on the north coast of St. Croix. One third of the reefs were exposed to all grazing organisms, one third were protected from macrograzers by exclusion cages, and one third had partial cages (controls). After a year-long immersion, 267 corals of two genera were found, and comparisons were made between the three reef treatments. Numbers of newest coral recruits (3mm diameter and less) were similar on all types of reefs, indicating similar rates of settlement. However, caged reefs, with visibly greater algal biomass, had significantly fewer of the larger juveniles than those that were uncaged and exposed to (primarily fish) grazers. Though relatively few herbivores occur at these depths, herbivory nevertheless appears to indirectly control the survival of coral recruits, and hence determines the structure of coral communities on moderately deep reefs.

INTRODUCTION

Coral reefs and their primary structural component, scleractinian corals, have been the focus of intensive study, with numerous investigators analyzing some aspect of the ecology of the corals. Yet an understanding of the factors influencing coral distribution is far from complete. The present study attempts to elucidate the effects of fish (and echinoid) grazing on the settlement and survival of scleractinian corals at intermediate (20m) depths.

The effects of competition for space between algae and coral planulae or settled corals has received some attention (e.g.,Dart 1972, Vine 1974, Kaufman 1977, Potts 1977, and others cited below), particularly in shallow water. Sammarco (1980) manipulated densities of the echinoid *Diadema antillarum* in shallow water, finding that ungrazed areas of high algal biomass (free from predation or disturbance by *Diadema*) allowed the highest rates of coral settlement. Subsequent survival, however, was highest in areas subject to moderate grazing pressures: competition from algae in ungrazed areas -- and predation/disturbance in heavily grazed areas -- reduced coral survivorship. Certain fishes also crop the algae and/or prey on small corals. Brock's (1979) microcosm study revealed low rates of coral recruitment in areas exposed to grazing scarids. Given adequate spatial refuges for the corals, however,

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the highest recruitment was then found in the presence of the fishes, which cropped the algal competitor without harming the corals. Also, damselfishes, maintaining territories that form algal mats, can have either positive or negative effects on corals, depending upon the location of the coral relative to the territory (see Vine 1974, Kaufman 1977, Wellington 1982).

Observing the browsing activities of Caribbean acanthurid and scarid fishes, Birkeland (1977) found evidence that fishes avoided corals as small as 3mm; yet Bak and Engel (1979) saw no such avoidance. Moreover, Neudecker (1977, 1979) observed fishes selectively preying on corals transplanted to different areas on Pacific reefs. The extent to which urchins and fishes prey upon corals may depend to a great extent on the availability of the preferred food resource. *Diadema*, for instance, shift to feeding on corals as the preferred algal food is diminished through grazing (Carpenter 1981). The differing observations reported above may be a reflection of different grazer densities and/or algal biomass in the various study sites. Manipulative studies such as Sammarco's (1980) and Brock's (1979) indicate the existence of optimal levels of grazing for coral survival, with these grazer densities apparently being closer to those commonly found on the reefs.

We sought to determine the influence that grazers naturally present at intermediate depths have on populations of juvenile corals. As a large number of cement artificial reefs were constructed and censused, extensive underwater time was required and the work would not have been feasible without the saturation diving facilities of NOAA's underwater habitat, NULS 1 (Hydrolab).

The study area is off the north coast of St. Croix, US Virgin Islands, in Salt River Submarine Canyon. The canyon extends seaward from a small estuary, with the canyon walls being variously covered by hard corals and coral rubble, sponges, gorgonians, etc. (see Rogers *et al*. 1983). The artificial reefs were established on the sandy floor of the canyon, well removed from the reef complex of the walls. This is an area of shifting sand uncolonized by benthic macroflora; during periods of heavy swells on this exposed coastline, sand scouring around the reefs is evident.

METHODS

Artificial reefs were established during NOAA Hydrolab Mission #81-1 in January 1981. Each reef structure was identical, consisting of 11 cement cinder blocks stacked and lashed together in three layers of 6, 4, and 1 block per layer. Total censused surface area of each reef was $0.93m^2$ vertical and $0.46m^2$ horizontal substrate. Corals inside the holes of the cinder blocks were not censused. Cage enclosures were composed of 2.5 X 5cm wire mesh over a 1.5 X 3 X 1.5m frame.

A total of fifteen reefs were constructed at a depth of 20m on the canyon floor along a line a constant 15m distance from the junction of the sandy floor and the east coral wall. The reefs were divided equally into three treatment types, with each reef along the line being an alternate treatment. Uncaged reefs were exposed completely to fishes and invertebrates; caged reefs were totally enclosed by cages; and cage controls had cages with two sides and the top partly-open, allowing access by macrofauna.

In January 1982 during Hydrolab Mission #82-1, all of the reefs were censused *in situ* for juvenile scleractinian corals. Maps of each reef were employed to record the location of the corals, its identification to genus and sometimes species, and its length and width (± 0.5-1mm). Deterioration of all the cages during storms in February 1982 did not allow repeat censuses of the corals on the caged reefs.

After initial establishment of the reefs, periodic fish censuses were performed to quantify the number of resident fishes on the reefs. Transient fishes (including herbivorous fishes around the reefs) were not quantified. Numbers of *Diadema antillarum*, being low, were recorded during only one census in February 1982.

Analyses of variance (ANOVA), both completely randomized and randomized block design, and Student's t-tests were employed for statistical analysis as was appropriate. Where the ANOVA indicated significant differences ($p<0.05$), Tukey's Studentized Range Test was used to determine which cells differed significantly ($p<0.05$).

RESULTS

Cage effects: corals

After the year-long immersion, a total of 267 corals were found on the fifteen reefs, all being on vertical edges. This included only two genera of corals: *Porites* and *Agaricia* formed 19% and 81% of the total number of corals, respectively. Difficulty with *in situ* identification of corals less than approximately 6mm in diameter prevented assigning species to the smallest corals. However, of the larger *Agaricia* sp., approximately 2/3 were *A. agaricites* and 1/3 *A. lamarki*. All *Porites* were *P. astreoides*.

A Student's t-test indicated no significant differences in the numbers of *Porites vs. Agaricia* on any reef treatment; thus all further analyses pooled both genera. Substantially more corals settled on uncaged and cage control reefs (totals of 123 and 90 respectively) than on caged reefs (54 total). However, a one-way ANOVA showed that the mean number of corals on the three reef types was not significantly different, nor was the mean diameter (Table 1).

Table 1. Number of corals on each reef; total number and mean for each treatment type; mean diameter of corals for each treatment type. Numbers in parentheses are standard deviations; n.s. = not significant ($p<0.05$).

	Caged		Uncaged		Cage Control
Rep.#1	10		12		14
Rep.#2	19		26		28
Rep.#3	9		41		20
Rep.#4	1		34		10
Rep.#5	15		10		18
Total	54		123		90
Mean number	10.8 (±6.8)	n.s.	24.6 (±13.5)	n.s.	18.0 (±6.8)
Mean diameter (mm)	5.3 (±3.0)	n.s.	6.8 (±3.0)	n.s.	5.4 (±2.6)

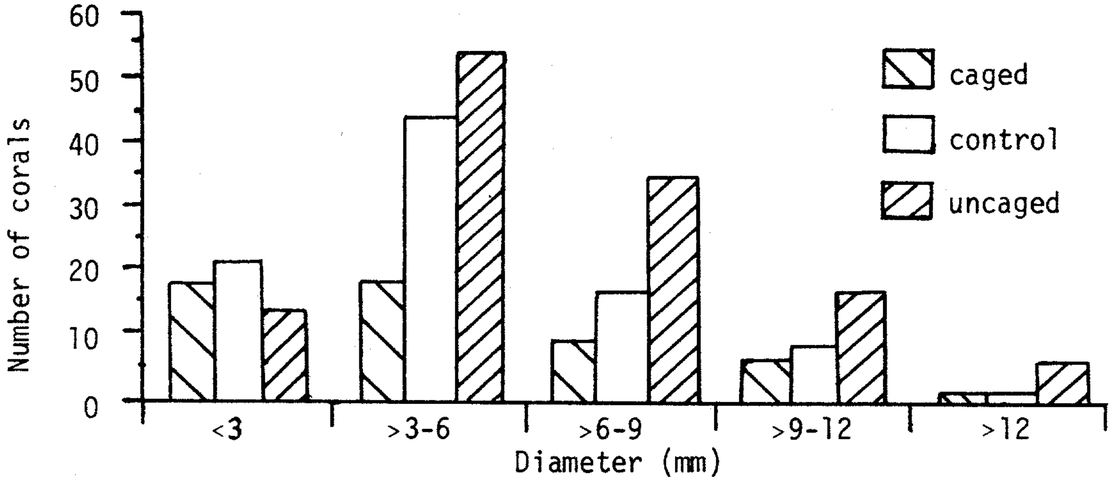
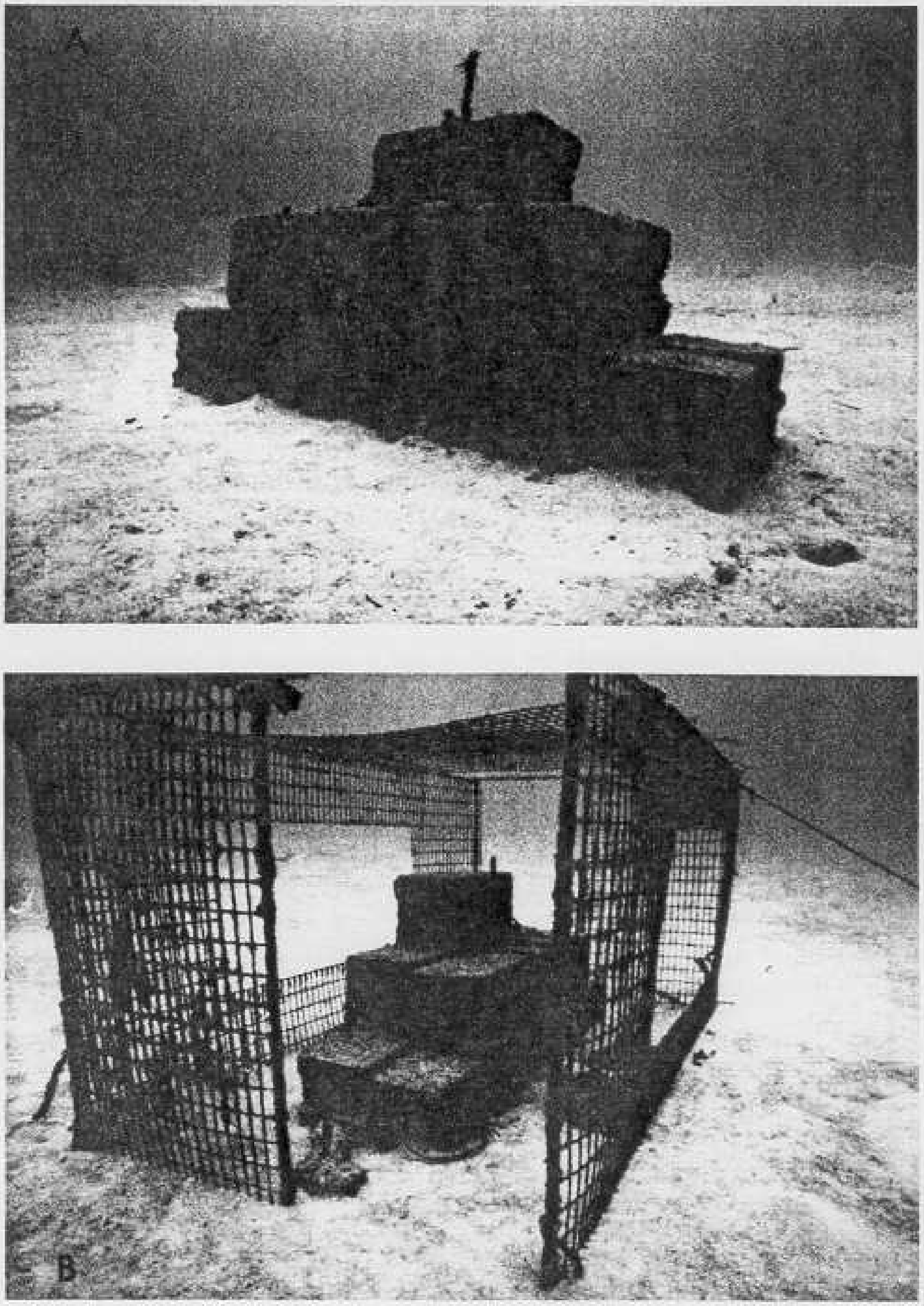
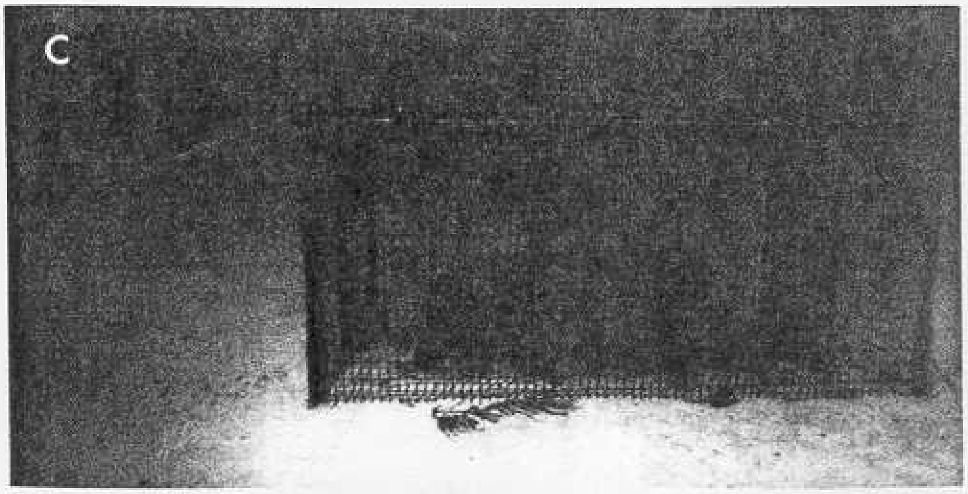


Figure 1. Total number of corals in each size class for each treatment type.

Figure 2. A. Open artificial reefs built of cinder blocks as described in the text. B. Cage control. C. Caged artificial reef. D. Closer view of caged artificial reef, showing extensive algal growth about 3 months after initiation of the experiment. E. Close-up view of fleshy algal growth on the edge of a cinder block in a caged reef.

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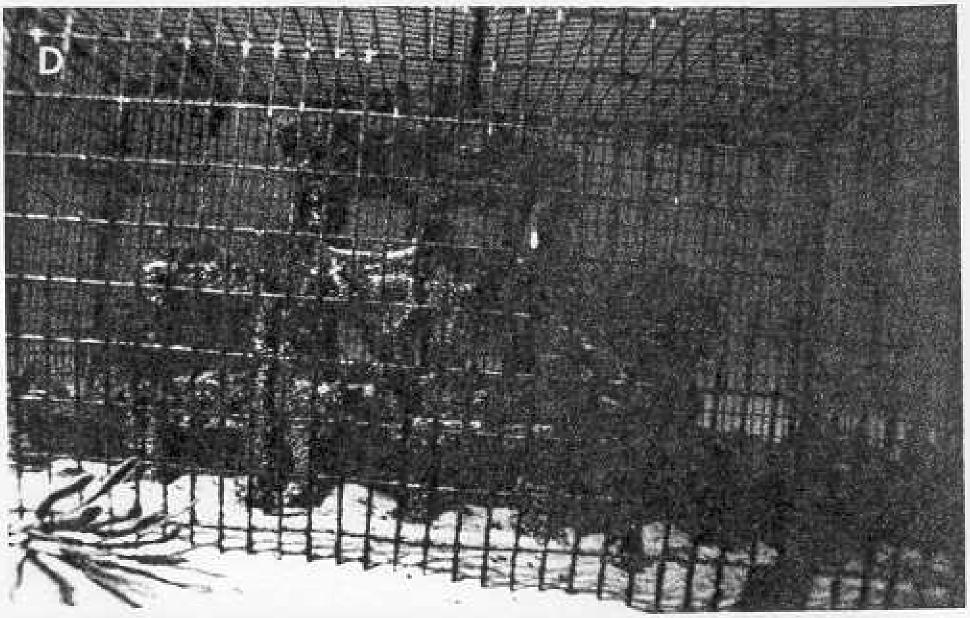
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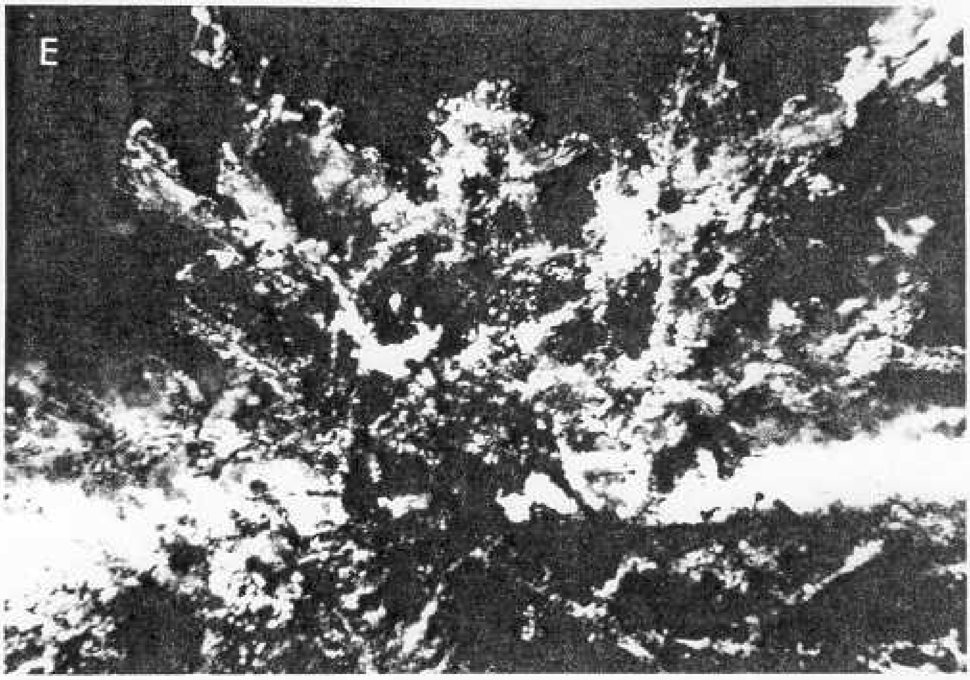
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Though no overall differences in numbers of corals existed between types of reefs, the size (age) structure of corals on the reef types was dissimilar. Corals on each type of reef were divided into five size classes at 3mm intervals. The total number of corals in each size class for the combined five reefs of each type are depicted in Figure 1; the general trend of similar numbers of newest (≤3mm) recruits and differing numbers of older corals between types of reefs is evident.

A two-way ANOVA indicated a significant effect of type of reef treatment (blocked over size classes) on the mean number of corals per reef. With this knowlege, a one-way ANOVA on each size class was used to determine which size class(es) had different mean numbers of corals between the reef types. The only significant difference was found in the >6-9mm class, with a Tukey's Studentized Range Test indicating that the caged reefs had significantly fewer corals than the uncaged reefs (Table 2). Shading by cages was insignificant, as the cage control did not differ from the uncaged reefs.

Table 2. Mean number of corals in each size class for each treatment type. Five replicates in each cell, numbers in parentheses are standard deviations, asterisk indicates significant difference ($p<0.05$).

	Caged		Uncaged	Cage control
≤3mm	3.8(±2.6)		2.6(±2.0)	4.4(±4.0)
>3-6mm	3.8(±2.6)		10.6(±7.2)	8.6(±4.6)
>6-9mm	1.8(±1.9)	*	7.0(±3.7)	3.2(±2.5)
>9-12mm	1.2(±1.3)		3.4(±4.0)	1.6(±1.1)
>12mm	0.0(±0.5)		1.0(±1.2)	0.0(±0.5)

Grazing fishes and invertebrates

Diadema antillarum was an uncommon echinoid on these reefs, well removed from the hard substratum of the East Wall of the canyon. One complete census showed an occasional *Diadema* on the ten uncaged and cage control reefs for a mean of 0.4 per reef. Total available surface area (including 12X12cm holes uncensused for corals) was $3.4m^2$.

The herbivorous fishes around the reefs were acanthurids, scarids and pomacentrids. Bicolor damselfish (*Eupomacentrus partitus*) were common residents on the reefs, along with occasional juvenile blue tangs (*Acanthurus coeruleus*). Schools of roaming doctorfish (*A. chirurgus*) and ocean surgeons (*A. banianus*) were common but, due to their transient nature, difficult to quantify (see Wolf *et al*. 1983 for the results of the fish censuses). Princess parrotfish (*Scarus taeniopterus*) were seen occasionally, again roaming about between different reefs.

The cages effectively excluded these larger macrograzers, as evidenced by the very noticable difference in cover of filamentous algae. The algal 'turf' on the exposed reefs was cropped extremely short, whereas thick, long tufts of filamentous algae and some fleshy algae were present on the completely caged reefs (see Figure 2).

DISCUSSION

Recruitment to these reefs, as evidenced by numbers of the smallest corals, was similar in both ungrazed and grazed situations. Though algal biomass was visibly greater on ungrazed reefs, space for coral settlement was apparently adequate in either type of habitat.

Large differences in numbers of >6-9mm corals between caged and uncaged reefs indicate that coral survivorship had been greater in areas subject to some grazing pressure. Thus, any incidental predation on corals by the fishes (and echinoids) was more than offset by the reduction in competition with the algae. Though differences between the types of reefs are suggestive in the >3-6mm class, the lack of statistical significance is indicative of the time required for competitive effects to become evident and of the patchy nature of recruitment. The very small sample sizes of corals larger than 9mm prevents thorough statistical treatment of differences in corals of this size. It seems unlikely that the trends toward greater survival in the corals of intermediate size on the exposed reefs would cease to be significant statistically as the community matures. For Agaricia spp. and Porites astreoides, Fitz (unpublished data) measured mean linear growth rates of 0.6 (±0.2)mm/mo for corals 5-10mm diameter, 0.9 (±0.3)mm/mo for corals 10-15mm diameter, and 1.3 (±0.3)mm/mo for corals 15-20mm diameter (n=45, 41 and 17, respectively). Few corals would be expected, therefore, to attain sizes greater than 9mm in the year-long immersion period.

Some manipulations of the coral reef community are feasible and provide insights into the processes shaping that community. This caging experiment implies that the herbivores present at moderate depths play a crucial role in the survival of juvenile corals. As has been shown in shallow water areas (e.g., Sammarco 1980), herbivory can reduce the deleterious effects of the algae on the corals by reducing the biomass of the algal competitor. Though not as abundant in deeper as in shallow waters, herbivores nevertheless appear to control the survival of coral recruits and determine the structure of this epibenthic sessile community.

ACKNOWLEDGEMENTS

Special appreciation goes to Jane Dominquez for many hours of cold saturation diving, and to the very competent surface support staff of the NOAA Hydrolab operation. We also thank Frank Pecora, Cheryl Van Zant, Hugh Reichardt, Miriam Smyth, and Joseph Dinneen, who assisted in building the reefs either as aquanauts or as part of the scientific surface support team. This work was made possible by grants from NOAA (NA81AAA01500, NA82AAA01286) and NSF (OCE-78-26605) to Marjorie L. Reaka. This is Contribution No. 110 from the West Indies Laboratory.

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BETWEEN-HABITAT DIFFERENCES IN HERBIVORE IMPACT ON CARIBBEAN CORAL REEFS

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ABSTRACT

Transplanted sections of the seagrass *Thalassia testudinum* were used as a bioassay to assess between-habitat differences in herbivory on three Caribbean reefs. Consumption of *Thalassia* by herbivorous fishes on shallow (1-10 m) reef slopes was significantly higher than on deep (30-40 m) reef slopes or on shallow reef flats. Seaweeds typical of reef flat habitats were rapidly consumed when placed on shallow reef slopes. Seaweeds typical of either deep or shallow reef slopes were relatively resistant to herbivory and a high proportion of these species are known to contain secondary chemical compounds that appear to deter herbivorous fishes. Shallow reef flats provide seaweeds with a predictable spatial escape from major reef herbivores; algae characteristic of these habitats have evolved few, if any, characteristics that significantly reduce losses to herbivory.

INTRODUCTION

Although herbivory plays a major role in determining the distribution and abundance of seaweeds on coral reefs (Stephenson and Searles 1960; Randall 1961, 1965; Ogden *et al*. 1973; Hay 1981a, b; Luchenco and Gaines 1981; Hay *et al*. 1983), few studies have addressed spatial variations in herbivory or the relative susceptibility to herbivory of seaweeds from different habitats. Recent investigations have focused on between- and within-habitat variations in herbivory on individual reefs (Hay 1981a, b; Hay *et al*. 1983) and on changes in herbivory that occur over depth gradients on several reefs scattered throughout the Caribbean (Hay 1984).

In this study we use transplanted sections of the seagrass *Thalassia testudinum* as a bioassay for herbivore activity in different habitats [reef flats, shallow (1-10 m) reef slopes, and deep (30-40 m) reef slopes] on 3 Caribbean reefs. We also transplant seaweeds from each of these habitats into areas with high herbivore activity in order to assess their relative susceptibility to herbivory.

METHODS

Thalassia was chosen as the bioassay organism because it is eaten in the field by both herbivorous fishes and urchins (Randall 1965, Ogden *et al*. 1973, Ogden 1976) and it is readily available on most reefs. Freshly collected sections of *Thalassia* were fastened in wooden clothespins; the latter were attached to small coral fragments and distributed haphazardly within the habitats where herbivory was to be measured. All *Thalassia* sections were 5 cm long and separated by a distance of 1-3 m when placed in the field. At the end of each bioassay, removal of *Thalassia* was quantified by measuring the remaining length of each blade to the nearest .5 cm. During all tests, the clothespin and coral apparatus was positioned so that it would be equally approachable by both fishes and urchins. However, on most sections of these reefs, urchins are relatively uncommon and almost all *Thalassia* removal was due to grazing by fishes (Hay 1984).

Removal of *Thalassia* on reef slopes varies with depth; portions of this pattern have been extensively analyzed elsewhere (Hay *et al*. 1983, Hay 1984). In this paper we compare herbivory on (1) reef flats that are exposed at lowest tides, (2) shallow (1-10 m) portions of reef slopes, and (3) deeper (30-40 m) portions of reef slopes.

Seaweeds from each of these habitats were exposed to herbivorous reef fishes by placing small (3-4 cm long) pieces of each seaweed in a 3-stranded rope that was fastened to the reef slope at a depth of 1-5 m. Ten to 37 individuals of each test species were used at each location (for a description of each site, see Hay 1984). Seaweeds within a length of rope were separated from one another by a distance of about 7 cm. Thus, when an herbivore encountered a rope, all species of seaweed should have been equally apparent and available. At the end of an experiment, each species on each rope was recorded as either still present or totally eaten. Ropes were only placed in the field under completely calm conditions and were shaken to be sure that all individuals were securely attached. On the reef at Becerro, Honduras, where the feeding trial was of short duration (1.75 h), we were able to directly observe the ropes for most of the test period; no individuals were lost to any source other than herbivory. For the feeding trials of longer duration (19-24 h), we cannot absolutely rule out the possibility that some individuals were lost to breakage. However, the magnitude of such loss would have to be very small given the calm conditions and our inability to observe breakage during any of the observation periods.

Assignment of seaweeds as characteristic of reef flat, shallow reef slope, or deep reef slope habitats was based on qualitative observations at each study site. For example, species that were common between 30 and 40 m deep and present but rare at 10 m deep were listed as characteristic of the deep reef slope.

RESULTS

Consumption rates for sections of *Thalassia* placed on shallow reef slopes were significantly higher than consumption rates on either reef flats or deeper sections of reef slopes ($p<.05$, ANOVA and Student Newman-Keuls Test) (fig. 1). A deep reef slope comparison could not be done at Becerro, Honduras, since the reef slope extended to a depth of only 9 m. On all 3 reefs, all daytime removal of *Thalassia* was attributable to fishes, as evidenced by their crescent shaped feeding scars (see Hay *et al*. 1983, Hay 1984). On the two reefs where comparisons were made, removal of *Thalassia* on the deep reef slope was significantly higher than removal on the reef flat (fig. 1). However, the magnitude of this difference was small when compared to differences between the shallow reef slope and either of the other habitats.

When seaweeds were transplanted onto shallow reef slopes, those from reef flats were consumed rapidly while those from either deep or shallow reef slopes were consumed slowly if at all (fig. 2). The one exception to this pattern was *Padina* sp. at Becerro, Honduras (fig. 2C). This reef flat species was not eaten when placed on the shallow reef slope, although *Padina sanctae-crucis* was rapidly consumed at Carrie Bow and Lighthouse reefs (figs. 2A, 2B).

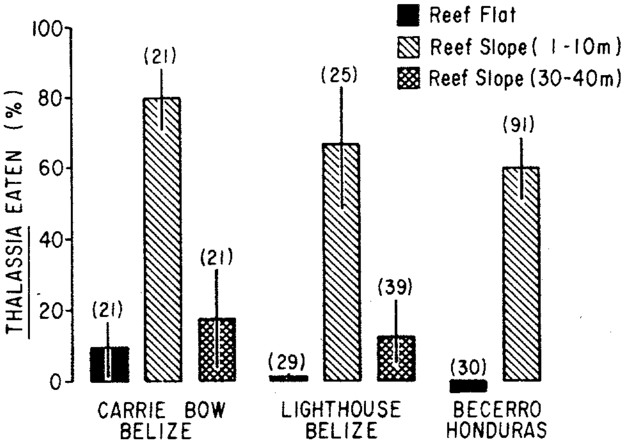

Fig. 1. The mean % of *Thalassia* eaten in different habitats on the 3 study reefs. Vertical lines represent ± 2 standard errors. Numbers in parentheses = N. At each reef, all differences are significant (p < .05, ANOVA and Newman-Keuls Test).

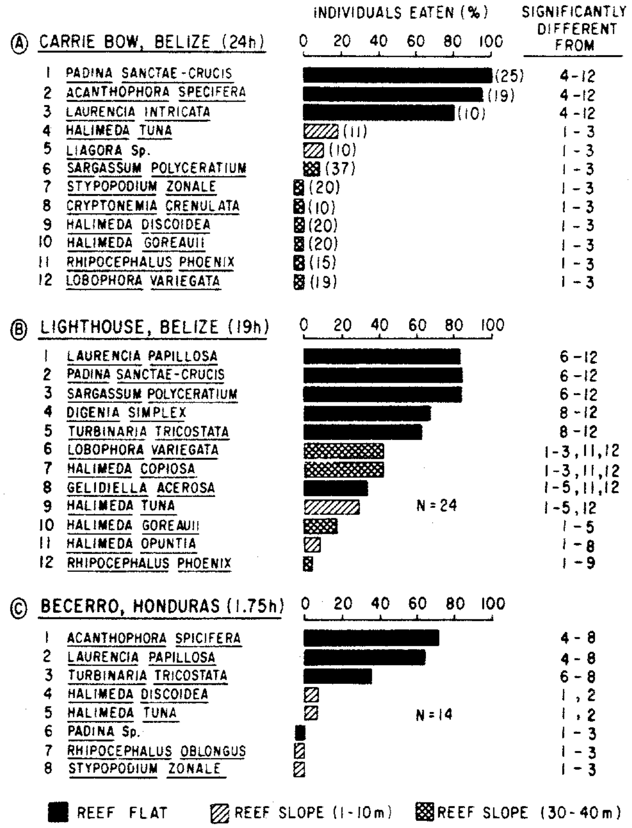

Fig. 2. Percentage of individuals eaten when placed on the shallow reef slope. For Carrie Bow, numbers in parentheses = N. Significant differences (p < .05) were evaluated using Contingency Table Analysis or Fishers Exact Test (if cell sizes were small).

Susceptibility to herbivory of seaweeds from the shallow versus the deep reef slopes showed no consistent pattern. At Carrie Bow (fig. 2A), there were no significant differences between seaweeds from deep and shallow areas of the reef slope (p < .05, Fishers Exact Test). At Lighthouse (fig. 2B), there were some differences between species but these revealed no consistent between-habitat patterns.

For a given algal species, susceptibility to herbivory showed similar patterns on different reefs (fig. 2). There were, however, a few interesting exceptions. *Acanthophora specifera*, *Laurencia papillosa*, and *Padina sanctae-crucis* were consumed rapidly on each reef where they were tested. Species of *Halimeda* and *Rhipocephalus* were consistently resistant to herbivory, as was *Stypopodium zonale*. *Turbinaria tricostata* was of intermediate preference. *Sargassum polyceratium* from the reef flat on Lighthouse was very susceptible to herbivory (fig. 2B); *S. polyceratium* from the deep reef slope on Carrie Bow was very resistant (fig. 2A).

DISCUSSION

On the scale used in this study, between-habitat differences in herbivory are shown to be consistent on 3 different reefs (fig. 1). Rates of macrophyte removal on reef flats or on deep reef slopes are significantly reduced relative to removal rates on shallow reef slopes. In addition to the reefs studied here, shallow reef flats also have been shown to function as spatial escapes from herbivory in the Virgin Islands (Adey and Vassar 1975, Steneck and Adey 1976), the Netherlands Antilles (van den Hoek *et al*. 1978), and Panama (Hay 1981c, Hay *et al*. 1983). Decreased herbivory on deep reef slopes has been hypothesized to provide an explanation for the increased algal abundance that occurs at depth on some reefs (van den Hoek *et al*. 1978), and the rate of macrophyte removal recently has been shown to decrease with depth on a wide variety of undisturbed Caribbean reefs (Hay 1984).

Reef flats and deep reef slopes usually are characterized by reduced topographic complexity; in areas where predatory fishes are abundant, these more simplified habitats may be avoided by herviborous fishes because they offer few places to hide when attacked by predators. On shallow reef slopes, herbivorous fishes concentrate their grazing in areas of greater topographic complexity (Hay *et al*. 1983) and, on heavily fished reefs where predatory fishes are relatively rare, herbivorous fishes make increased use of deeper reef slopes (Hay 1984). All of these patterns suggest that the probability of being preyed upon may play a significant role in determining the spatial pattern of foraging by herbivorous fishes.

Previous studies have suggested that the evolution of herbivore resistance in seaweeds involves costs that result in decreased growth rates and decreased competitive ability in the absence of herbivores (Lubchenco 1980; Lubchenco and Gaines 1981; Hay 1981a, c; Hay *et al*. 1983). The data presented in figure 2 provide a partial test of this hypothesis; if characteristics that promote herbivore resistance mandate costly tradeoffs, then herbivore resistance should not evolve in species that occur primarily in habitats subject to low rates of herbivory. Patterns exhibited by reef flat seaweeds support the hypothesis; they are subject to low rates of herbivory (fig. 1) and exhibit little resistance when exposure to herbivores is increased (fig. 2).

Rates of *Thalassia* removal on deep (30-40 m) reef slopes were significantly higher than on reef flats, but the magnitude of difference was not large--17.5% versus 9.3% at Carrie Bow, and 12.8% versus 1% on Ligvhthouse (fig. 1). However, differences in herbivore resistance of species from these habitats were striking (fig. 2). Despite the low rate of removal of *Thalassia* that was documented on deeper sections of the reef slope, seaweeds from these deeper areas were very resistant to herbivory. Even though the *Thalassia* bioassay shows herbivory to be relatively low in both reef-flat and deep reef-slope habitats, herbivore resistance appears to have been selected for on the deep reef slope and selected against on the shallow reef flat. This apparent paradox can be explained if one considers rate of biomass removal by herbivores (i.e., the *Thalassia* bioassay) relative to rate of production through photosynthesis. Seaweeds in shallow waters may grow many times faster than seaweeds in deeper waters (Hay 1981a, b). The low rate of biomass removal that occurs on reef flats can rapidly be replaced by photosynthesis since light is plentiful and turbulence prohibits the formation of large diffusion gradients that would slow nutrient acquisition (Doty 1971). Since production of seaweed biomass is very slow on deeper reef areas, even small losses to herbivores may exceed gains and thus select for increased herbivore resistance. As an example, if herbivores removed equivalent amounts of plant material from deep and shallow sites, selective pressure for the evolution of grazer deterrents would be much greater in the deeper habitats since losses would be a larger proportion of net growth and take longer to replace. Future studies on spatial patterns in herbivory should attempt to quantify herbivore impact as a proportion of plant production within each habitat studied.

Most of the reef slope seaweeds are known to have naturally occurring chemical substances that appear to serve as defenses against herbivory (Fenical 1975, Norris and Fenical 1982). Many species in the genus Halimeda produce diterpenoid trialdehydes (Paul and Fenical 1983), Rhipocephalus contains similar compounds (Norris and Fenical 1982), Stypopodium zonale contains several related C_{27} compounds derived from a mixed biosynthesis of diterpenoid and acetate precursors (Gerwick and Fenical 1981), and Liagora produces an unusual acetylene containing lipid (Norris and Fenical 1982). These compounds are toxic to or deter feeding in reef fishes, and some even stop cell division in fertilized sea urchin eggs or motility in sea urchin sperm (Norris and Fenical 1982, Paul and Fenical 1983). The polyphenolic compounds produced by Turginaria and Sargassum (Norris and Fenical 1982) do not appear to be especially effective, as evidenced by the feeding data in figure 2. The difference in susceptibility of Sargassum polyceratium from the deep reef slope at Carrie Bow and the reef flat at Lighthouse could result from population differences in defensive compounds or from between-reef differences in herbivorous fishes.

In general, it appears that herbivores consume a significant proportion of reef slope production and that this has resulted in strong selection for herbivore deterrents in seaweeds from this habitat. Reef flats provide predictable escapes from herbivory, and seaweeds from these habitats are characterized by very little resistance to herbivory.

ACKNOWLEDGMENTS

This study was supported by a post-doctoral fellowship from the Smithsonian Institution and by the Marine Systems Lab of the Smithsonian Institution.

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QUANTIFYING HERBIVORY ON CORAL REEFS:
JUST SCRATCHING THE SURFACE AND STILL BITING OFF MORE THAN WE CAN CHEW

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ABSTRACT

Herbivory was quantified using six different techniques simultaneously at nine discrete sites along a coral reef system on the Caribbean island of St. Croix. In order to study diverse assemblages of herbivores and algae, functional groups were used for both. The groups are based on shapes and structural properties of the algae and feeding capabilities of the herbivores.

Herbivory was most frequent and intense in the shallow forereef sites where an average of over 5,000 herbivorous fish bites per meter square per hour was recorded. Although most of these were from herbivorous fishes that do not denude primary subtratum (i.e., small damselfishes), this site also had the highest frequency of grazing from herbivores capable of denuding (i.e., yellowtail damselfish and tangs) and excavating the calcareous substratum (parrotfishes, urchins and limpets). Herbivory from all sources decreased in backreef, shallow algal ridge, and deep wall-reef habitats. The latter sites had the lowest levels of grazing.

Herbivory on macrophytes was assessed using a _Thalassia_ bioassay technique but the results at the forereef sites contradicted those of all other techniques. Caution is suggested in applying this technique as a single measure of herbivory.

INTRODUCTION

The process of herbivory is generally thought to be of primary importance to the distribution and abundance of benthic algae on coral reefs (reviewed by Lubchenco and Gaines 1981). While the units of measure and methods for determining the abundance of algal prey are well established, no such convention exists for determining the impact of their herbivorous predators. Measurements of percent cover, biomass, or number of individuals when applied to assemblages of reef dwelling herbivores are of dubious meaning for quantifying herbivory. For instance, how many foraging urchins equal the impact of a 20 kg parrotfish? The "apples and oranges" involved here result from trying to force units and techniques which are designed to determine _patterns_ in herbivore abundance on the _process_ of herbivory.

Ecological processes are factors that result in observed patterns. It is generally assumed that the abundance of herbivores corresponds with their impact on algae. This assumption has never been tested. In this paper, I will report on several techniques used simultaneously on a single reef system in order to measure the impact of a diverse assemblage of herbivores on an assemblage of reef-dwelling algae. I will also provide an argument for considering this topic at a "functional group" level so that herbivores with similar effects and algae with similar ecological properties are treated together.

ORGANISMS, STUDY SITES, AND METHODS

Functional Groups

Since herbivory involves the interaction of two diverse groups of organisms, "functional group" subdivisions will be used. Algae have been subdivided into such groups based on shared anatomical and morphological characteristics (see Littler and Littler 1980, Steneck and Watling 1982). For the purposes of this paper, I will simplify these subdivisions to three groups: 1) ALGAL TURFS (diverse, microscopic filaments; e.g., *Polysiphonia*, *Spacelaria*, and *Taenioma*), 2) MACROPHYTES (larger, more ridged forms; e.g., *Laurencia*, *Dictyota*, *Jania*, and *Asperogopsis*), and 3) ENCRUSTING CORALLINES (calcareous algal crusts; *Porolithon*, *Neogoniolithon* and *Paragoniolithon*). Note that the "turfs" referred to here follow Neushul 1967, Randall 1967, Dahl 1972, John and Pople 1973, Van den Hoek *et al.* 1975, Adey *et al.* 1977, Benayahu and Loya 1977, Pichon and Morrisey 1981, but not Hay 1981a). Among the ecological properties correlated with algal functional groups (and this simplified scheme) is toughness of the thallus. From an herbivore's perspective turfs are easiest to consume, macrophytes intermediate and coralline crusts most difficult (Littler and Littler 1980, Steneck and Watling 1982, Littler *et al.* 1983).

Herbivores fall into three categories with respect to grazing (Steneck 1983, see Table 1 for species): 1) NON-DENUDING (those incapable of, or unlikely to, denude the substratum of algae; e.g., some damselfishes [*Eupomacentrus*], amphipods and polychaetes; Brawley and Adey 1977, Kaufman 1977), 2) DENUDING (those that denude the substratum of turfs and smaller macroalgae but are incapable of excavating corallines and large leathery macrophytes; e.g., yellowtail damselfish [*Microspathodon*], tangs [*Acanthurus*] several non-limpet archaeogastropods and mesogastropods; Randall 1967, Jones 1968), and 3) EXCAVATING (those capable of consuming even the toughest forms of algae, such as encrusting corallines e.g., limpets [*Acmaea*], chitons, some regular echinoids [*Diadema*] and parrotfishes [*Scarus* and *Sparisoma*]; Randall 1967). For a more complete discussion of these categories see Steneck 1983.

Study Sites

This study was conducted at nine sites in three locations along the north shore of St. Croix (Fig. 1). The locations were selected as representative of three common reef types in the Caribbean 1) Algal Ridge (Boiler Bay), 2) Bank barrier-reef (Tague Bay), and 3) Deep wall-reef (Salt River Canyon). All three are geographically close to one another, thus giving them about the same exposure to light, destructive storms and recruitment events.

The predominant algal growth form at the bank-barrier and deep wall-reef sites are turfs with an average canopy height of 2mm. Turfs are highly diverse with about 30 to 50 species found in an average four square centimeter area (Adey and Steneck in ms.). Species composition is temporally variable with up to an 80% change in community dominance every 3-4 months (Steneck in prep.). Patches of encrusting coralline algae are also scattered throughout. Macroalgae are only abundant in places at the algal ridge site (see Connor and Adey 1977).

At each site, circular slabs of coral (1 cm thick, and 10 cm diameter) were placed on racks and affixed to the reef (locations and depths in Fig. 1). The plates were placed in December of 1979, and most of the experiments were conducted more than three years later from March to May 1982. At the time of the experiments, the coral plates had the same algal community structure, canopy height, and biomass as the surrounding substrata. All the plates at the nine stations were covered with the same (algal turf) functional group. Details of specific experiments are described below where appropriate.

RESULTS AND DISCUSSION

To reduce some of the variables related to herbivory, the study was conducted at one spot and at one time at each of the nine sites. Several of the experiments ran simultaneously, focusing on the same six (100 to 200 cm sq.) planar coral plate surfaces or their surrounding areas.

TABLE 1
HERBIVORES OBSERVED IN THIS STUDY

NON-DENUDING HERBIVORES

FISHES:	REFERENCES
Eupomacentrus dorsopunicans (dusky damselfish)	Randall 1967, Pers. Obs.
Eupomacentrus planifrons (threespot damselfish)	Brawley and Adey 1977, Kaufman 1977
Eupomacentrus variablis (cocoa damselfish)	Randall 1967, Pers. Obs.
Eupomacentrus leucostictus (beaugregory)	Randall 1967, Pers. Obs.
GASTROPODS:	
Fissurella angusta (keyhole limpet)	Steneck and Adey 1982

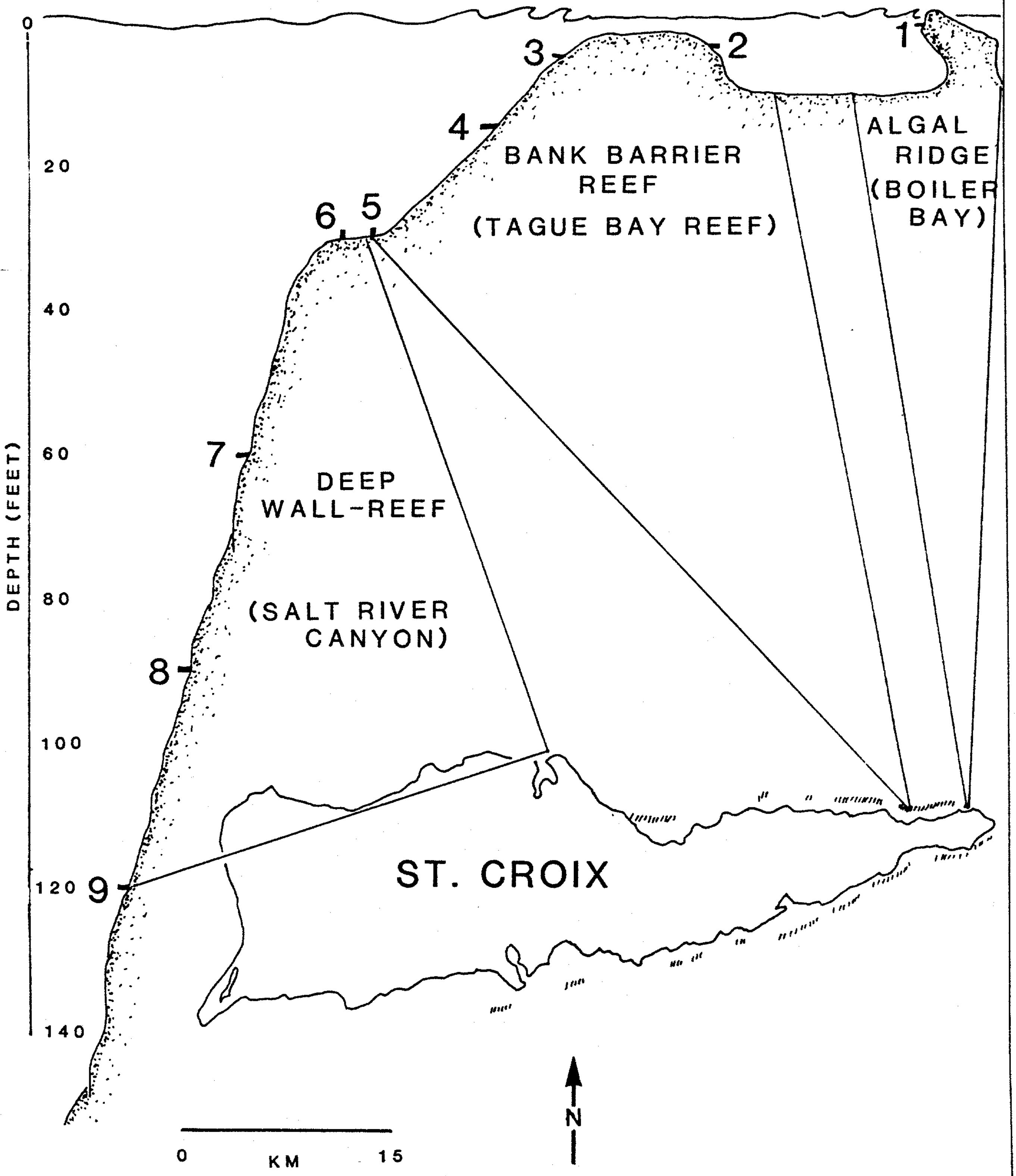
DENUDING HERBIVORES

FISHES:	REFERENCES
Microspathodon chrysurus (yellowtail damselfish)	Randall 1967, Steneck 1983
Ophioblennius atlanticus (redlip blenny)	Randall 1967, Steneck 1983
Acanthurus bahianus (ocean surgeon)	Randall 1967, Steneck 1983
Acanthurus coeruleus (blue tang)	Randall 1967, Steneck 1983

EXCAVATING HERBIVORES

FISHES:	REFERENCES
Scarus croicensis (striped parrotfish)	Randall 1967, Steneck 1983
Sparisoma chrysopterum (redtail parrotfish)	Randall 1967, Steneck 1983
Sparisoma viride (stoplight parrotfish)	Randall 1967, Steneck 1983
ECHINOIDS:	
Diadema antillarum (long-spined sea urchin)	Steneck 1983
GASTROPODS:	
Acmaea pustulata (limpet)	Steneck and Watling 1982, Steneck 1983

FIGURE 1. Diagrammatic composite representation of reef transects along the north of St. Croix. Numbers correspond to study sites in Table 2.



Observing Herbivory

Quantifying fish grazing employed two methods. The first involved watching each rack of six coral plates at each station for five-minute intervals several times a day and recording which species fed on them. The second method is identical to the first except that an underwater time-lapse movie camera takes the place of a diver. Each movie lapses between 10 and 12 hours and generates 3600 observations (frames). During the movies, divers avoided the area except to simultaneously count fish bites over a few five minute intervals. Since the plate areas are known, the number of bites per square meter per hour can be determined for both techniques.

Fish grazing was greatest in shallow forereef habitats and least at depth (Table 2). Mean grazing frequencies of over 5,000 bites per meter square per hour were recorded using visual and time-lapse techniques in 1982 and visually in 1981. At the algal ridge and bank barrier-reef sites grazing was predominantly from non-denuding herbivores (i.e., *Eupomacentrus*). This group of damselfishes (four species) accounted for 72% (± 30) and 50% (± 22) of the bites observed at this site visually and on film, respectively. Pomacentrid grazing on the deep wall-reef was relatively low (6 % ± 12). Denuding herbivores (particularly *Microspathodon*) were most abundant at the mid-depth forereef site. Excavating herbivores (*Scarus* and *Sparisoma*) were most abundant at the shallow forereef site. Juveniles of this group were the primary herbivores at the deep wall-reef sites.

It is difficult to determine why a better correspondence between visual and time-lapse movie techniques does not exist, since both were conducted at the same time (Table 2). Time-lapse, of course, gives high resolution data over an entire day whereas visual techniques give high resolution over only short intervals spread over several days. The latter technique also requires the presence of a human observer which may suppress normal grazing frequencies during the observation period.

Invertebrate herbivores are easier to count, but more troublesome to actually observe feeding since their mouths are under their bodies. Since they have reduced mobility, their range of grazing influence is relatively restricted. Thus, some indication of their impact can be assessed by determining their population density in a given area.

Excavating invertebrate herbivores (i.e., echinoid *Diadema* and limpet *Acmaea*), are most abundant in shallow forereef environments (Table 2). In fact, the two shallowest forereef stations have more echinoids per area than all seven other stations combined. Limpets were only found at the shallowest station.

Impact of Herbivory:

The impact of herbivory requires studying the plants being eaten. Because different functional groups of algae have different structural and morphological properties that contribute to the rate at which they are consumed (discussed above), I will treat three functional groups of algae differently.

In terms of areal coverage, minute turfs are the most abundant algal form on coral reefs. They are impossible to handle without damage so all turf experiments and observations were confined to the coral plates.

To determine herbivore impact on turfs, the rate of biomass loss to herbivores was studied. For this, a set of six plates at each depth (at the deep wall-reef site) was suspended in the water column at the depth they had been growing in for the past three years. An identical set of plates remained on the benthos. No herbivores were observed grazing the suspended plates (nor was there any evidence of grazing using other techniques (i.e., *Thalassia* bioassay technique, described below). Table 2 shows that there is a steady (nearly linear) decline in the rate of turf algae biomass loss to herbivores with depth. Assuming that the productivity of suspended plates equals that of the benthic plates, the difference in algal biomass after a period of 6 days should indicate the amount of algal biomass that is eaten during that period. Negative numbers indicate that algal growth rate exceeds the

TABLE 2
COMPARISON OF RESULTS IN MEASURING HERBIVORY

STATION NUMBERS	1	2	3	4	5	6	7	8	9
DEPTHS (FEET)	0.5	3.5	5	15	30	30	60	90	120
HERBIVORY (BITES/M^2/H) FROM:									
Non-Denuding Fishes									
Visual Obs. 1981	0	0	3,269	170	28				
Visual Obs. 1982	448	273	518	147	230	0	94	0	0
Time-lapse 1982	7,061	1,567	3,325	1,630	1,151				
MEAN	2,503	613	2,371	649	470	0	94	0	0
Denuding Fishes									
Visual Obs. 1981	3	0	2,774	170	28				
Visual Obs. 1982	0	0	532	193	48	39	12	0	0
Time-lapse 1982	936	2,687	0	4,326	1,151				
MEAN	313	896	1,102	1,563	409	39	12	0	0
Excavating Fishes									
Visual Obs. 1981	0	0	2,476	0	0				
Visual Obs. 1982	0	0	27	0	0	79	282	235	0
Time-lapse 1982	0	0	2,660	0	0				
MEAN	0	0	1,721	0	0	70	282	235	0
Total Herbivory From Fishes									
Benthic Plates	2,816	1,509	5,194	2,212	879	118	338	235	0
Suspended Plates						0	0	0	0
Excavating Invertebrates (No/m^2)									
Diadema	0.8	3.8	14.3	17.5	3.9	0.2	0.3	0.5	0
Acmaea	0	0	2	0.3	0	0	0	0	0
GRAZING IMPACT ON:									
Algal Turfs (g dry/m^2/day)									
Rate of Turf Biomass Loss						2.8	1.35	0.933	-0.79
Macrophytes (% *Thalassia* eaten/day)									
On benthos	2.04	14.9	1.45	0.74	49.8	25.2	10.1	3.0	0.69
On Plates	4.8	0.004	1.6	0.79	37.4	16.0	2.2	3.4	1.5
Suspended Plates						0	0	0	0
% Grazed by Fish	100	95	50	50	96	98	100	100	90
Corallines									
% Coralline Grazed	0.6	54.2	82.7	48.0	44.6				
% Grazed by Urchins	0	26.6	57.9	42.0	28.0				

NOTE: Blanks indicate no data

herbivore grazing rate.

Macrophytes are not usually abundant on reefs. In the study areas, macrophytes were most abundant in the intertidal zone of the algal ridges at Boiler Bay (e.g., Gracilaria, Laurencia, Gelidiella, Dictyota and Acanthophora) and to a lesser extent on the Acropora cervicornis in the sand plain in front of the forereef sites (e.g., Asparagopsis, Dictyota and Laurencia). A scattering of macroalgae can also be found at the backreef site (e.g., Acanthophora, Laurencia and Dictyota).

To determine grazing pressure on macrophytes, a Thalassia bioassay technique of Hay (1981b, and Hay et al. 1983) was used. For this, five centimeter long blades of Thalassia were placed in clothes pins. The blades were checked every several hours to determine the amount grazed by herbivores. Bite marks were interpreted as to whether they were from parrotfishes (semicircular bites) or urchins (a shredded appearance) (See Fig. 2 in Hay et al., 1983). At each station, eight blades of Thalassia were affixed to the rack of coral plates and an additional 20 were scattered nearby on the bottom.

The rate of Thalassia loss was greatest at the deepest forereef station (for both those scattered on the bottom and attached to the rack; Table 2). The next highest rate of loss at the Tague Bay stations was in the backreef. In this case however, only those scattered on the bottom were heavily grazed. The deep wall-reef sites showed a consistent decrease in Thalassia grazing with depth. None of the suspended Thalassia blades were grazed.

Nearly all grazing marks were attributable to parrotfishes. No urchin marks were identified on Thalassia blades attached to the racks of coral plates. At benthic stations, however, a few urchin marks were observed. The highest proportion of urchin marks occurred in the shallow forereef stations of the Tague Bay locations (where urchin densities were highest). The 10% urchin bites recorded for the 120' station represents only one urchin-looking bite out of 10 recognizable bites. It is probably an error since no urchins were found below 90'. Other shredding herbivores such as crabs could have been responsible for the marks.

The pattern of Thalassia loss across the Tague Bay reef is opposite that of all other measurements of herbivory. There is no indication from other measures (Table 2) that the deep forereef, and to a lesser extent the backreef, receive as high a rate of predation as the Thalassia bioassay suggests. Conversely, all other techniques indicate that the two shallow forereef stations are most heavily grazed by all herbivore groups rather than minimally grazed as the Thalassia bioassay indicates. There is no question, however, that whatever the Thalassia bioassay measures, it does so consistently and repeatably. It is possible that fishes with a search image for Thalassia, or other conspicuous macrophytes of sand flats or lagoons, are attracted to the Thalassia of this experiment and consume it at a rate unrepresentative of overall grazing rates on the reef.

Relatively few herbivores are capable of excavating crustose coralline crusts (discussed in detail in Steneck 1983). Since crusts can "erase" most graze marks as they grow undisturbed for 10 to 30 days (depending on the depth of the injury and the growth rate of the coralline), marks on corallines are a rough indication of the rate of grazing by excavating herbivores. In addition, the bite marks of the major groups of excavating herbivores (i.e., parrotfishes, urchins, limpets and chitons) are readily identifiable. The pattern of graze marks among excavating herbivores indicates that the greatest grazing pressure occurs in the shallow forereef. Data were not collected for the deep wall-reef site. Overall urchin grazing was most conspicuous on the crusts, with the proportion of graze marks generally corresponding with the abundance of urchins in the area (Table 2).

Patterns of Herbivory on Reefs

Herbivory is greatest in shallow forereef habitats and reduced in shallow algal ridge and backreef habitats. The reduced herbivory around massive algal ridges is likely due to the absence of habitat and refuge space in those environments coupled with the characteristic turbulence (discussed in Steneck and Adey 1976). Backreef habitats are an enigma. They consistently indicate lower levels of grazing (both intensity and frequency) but no simple explanation can be offered. The decrease in herbivory with depth is not surprising since the trophic carrying capacity for herbivores probably diminishes with depth as a function of reduced benthic productivity (Steneck in prep.).

Ecologists are far from agreeing on a method (or methods) for measuring herbivory on reefs. While this does not seem to inhibit publications on the subject, comparisons between reefs are impossible. The simplest and most easily replicated technique, the *Thalassia* bioassay, is of dubious meaning and must be examined critically in other comparative studies before its general application can be accepted (see Hay 1983 for caveat). The only clear message revealed in this study is that quantifying a process is infinitely more difficult than quantifying patterns in the abundance of herbivores. So far we have only scratched the surface and still we are biting off more than we can chew.

ACKNOWLEDGEMENTS:

This project was funded by a grant from NOAA NA82AAA01460 for Hydrolab mission 82-6. D. Blanchard, S. Brusila, R. Carpenter, D. Cancilla, D. Estler, E. Fleishmann, M. Hay, L. Mayer, B. Milliken, D. Morrison, J. W. Porter, and L. Schick assisted in various phases of the study.

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DIFFERENTIAL EFFECTS OF CORAL REEF HERBIVORES ON ALGAL COMMUNITY STRUCTURE AND FUNCTION

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ABSTRACT

Functional herbivore groups were categorized according to the intensity and frequency of disturbance resulting from feeding. Biomass removal, species composition and primary productivity of experimental algal communities subjected to herbivory by each functional group revealed differences among groups. Combined removal of biomass by all herbivores ranged from 32 to 84% of daily algal production. Algal species composition varied according to grazing regime, with crustose forms dominating the most intensely grazed treatments. Specific rates of primary production of urchin grazed treatments were 2 to 4 times those in non-urchin grazed treatments. Species composition of reef algal communities is affected differentially by herbivores, which leads to subsequent changes in community metabolism.

INTRODUCTION

Coral reef communities are characterized by a high level of primary production that supports an abundant and diverse assemblage of organisms. The majority of this production is accomplished by the free-living algal component (Marsh, 1976); however, this component is notably inconspicuous when compared to other highly productive marine algal communities such as kelp forests. Intense grazing pressure by herbivores has been repeatedly shown to limit the standing crop of reef algae (Stephenson and Searles, 1960; Sammarco, _et al_., 1974; Carpenter, 1981). The predominance of such herbivores in reef communities invites speculation on how such biomass can be achieved and supported by the apparently sparse algal community. In addition, such intense disturbance (herbivory) may have significant effects on the structure of the algal community. Because herbivores differ in their magnitude and mode of biomass removal and the frequency with which such removal takes place, the effects may not be the same for different groups of herbivores.

This paper reports some preliminary results of a study to quantify the effects of different functional groups of herbivores on shallow reef algal community structure and function. A more detailed description of methods and results will be presented elsewhere.

MATERIALS AND METHODS

Functional herbivore groups were categorized using two criteria: the size of patch (disturbance) created per feeding bout, and the probability (frequency) of regrazing the same patch on a subsequent feeding bout. The former is mainly dependent on the size of the feeding apparatus and foraging behaviors such as the number of bites in a particular feeding bout. The second criterion depends on the mobility of the organism as well as on behaviors which determine the size of the foraging range (i.e., homing). These groups cross phylogenetic boundaries (Figure 1) and are depicted as non-overlapping only for illustration. The organisms listed are potential Caribbean members of each group; the actual composition at a given locality, even on a micro-habitat level, will depend on patterns of species distribution and abundance. For the present study site, Group 1 consists of several fish species in the families Scaridae and Acanthuridae and hereafter will be referred to as the herbivorous fish category. The most important herbivore in Group 2 at this locality is the echinoid *Diadema antillarum*. Members of Group 3 include several amphipods, tanaids, syllid polychaetes and small gastropods.

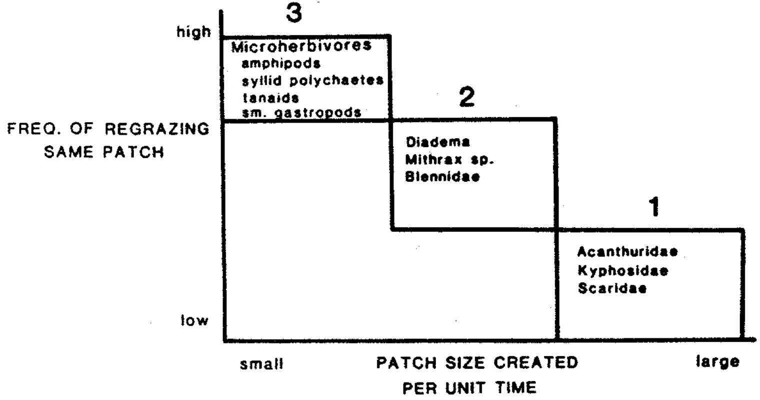

Figure 1. Diagramatic representation of herbivore functional groups. Group members are potential Caribbean herbivores.

Algal communities were allowed to develop under ambient backreef conditions (depth, 2 m) in St. Croix, U.S.Virgin Islands on experimental substrata consisting of 8 cm x 8 cm x 1 cm cross-sections of the coral *Acropora palmata*. These experimental plates were randomly placed in one of the following treatments: grazing by groups 1 and 3, grazing by groups 2 and 3, grazing by group 3 only, no grazing and control. The accessibility of plates to functional groups was controlled using a combination of cages and suspended platforms at the same depth. Each treatment was replicated once. A detailed description of the experimental design and methods is forthcoming (Carpenter, ms. in prep.). Algal community primary productivity was estimated monthly from changes in dissolved oxygen in well-stirred light and dark plexiglass chambers on randomly chosen plates from each treatment. From the same plates samples were taken to estimate algal biomass (decalcified dry wt.), species composition and chlorophyll *a* content.

The amount of algal biomass removed by each functional group was estimated in two ways. The difference in algal standing crop between plates not grazed and those grazed by a given group gave one estimate. The second, more accurate method converted the areal production rate (corrected for a constant percent of dissolved organic matter excretion (Fogg, 1976)) for a treatment to carbon equivalents, and assuming a constant carbon content, this was translated into the expected dry, decalcified biomass accumulation over a time period. The difference between this expected amount and the actual algal standing crop was assumed to be removed by herbivores.

All data reported here were obtained at least one year after the initiation of the described treatments.

RESULTS

Removal of Algal Biomass

Herbivores removed between 0.88 and 2.10 g dry wt. m^{-2} day^{-1}, which represents between 32 and 84% of the daily production of algal biomass (Table 1). The temporal variation in the total biomass removed was mainly the result of variation in the amount removed by the herbivorous fish component. The percent of the total biomass removed by all herbivores that was taken by fishes varied between 3 and 39%. The percent removed by Diadema only varied from 41 to 68%, and micro-herbivores removed from 11 to 28% of the biomass.

Table 1. Mean decalcified dry wt. removed (g $m^{-2}d^{-1}$) ± S.D. by each functional herbivore group; the % of daily algal production that this represents; and, in parentheses, the % of the total amount removed (N=4). Note that the biomass removed by all herbivore groups is an independent estimate, not the sum of the removals by the three separate groups.

GROUP	JUNE		JULY		AUGUST	
	wt.	%	wt.	%	wt.	%
1	0.45±0.12	19(38)	0.78±0.18	33(39)	0.03±0.05	1(3)
2	0.65±0.05	26(51)	0.85±0.14	35(41)	0.59±0.11	22(68)
3	0.09±0.07	6(11)	0.31±0.20	16(20)	0.25±0.17	9(28)
ALL	1.27±0.28	51	2.10±0.61	84	0.88±0.26	32

Based on herbivore densities in the study area, Diadema is responsible for approximately 50% of the herbivory, fishes 20-30%, and micro-herbivores the remaining 20-30% of the biomass removed.

Algal Species Composition

Algal species composition differed both in terms of what species were present, and their relative abundance. Analyses are not yet complete, so percent relative abundance can not be given; however, presence/absence and dominance data show a pattern related to grazing regime. Plates grazed by all herbivore groups and those grazed by Diadema show similar patterns of algal community structure. Each is dominated by crustose forms (Ulvella lens and crustose corallines) with minute (10-50 um diameter) filamentous representatives of the Chlorophyta, Phaeophyta and Rhodophyta. Cyano-bacteria were also well represented. No large corticated algal species were found on any of these plates. Plates from the fish grazing treatment were dominated by a single species of filamentous brown algae (Sphacelaria tribuloides) that formed patches of varying size. Observations suggest that this species is actively avoided by herbivorous fishes. Crusts and other filaments were also of primary importance on these plates.

In contrast, plates grazed only by micro-herbivores fluctuated from a community dominated by larger algae (Coelothrix irregularis, species of the family Gelidiaceae, the upright corallines Jania adherens and Amphiroa fragilissima) to one comprised primarily of crusts and benthic foraminifera. This shift in community structure coincided with the recruitment of the gastropod *Cerithium litteratum* onto the plates. This was also accompanied by an increase in the amount of algal biomass removed by micro-herbivores (Table 1). Small filaments also occurred on these plates.

The filamentous species *Herposiphonia secunda*, *Giffordia rallsiae* and several blue-greens dominated plates where herbivory was absent or minimal. Pennate diatoms were also abundant. Several larger algal species (*Champia parvula*, *Ceramium nitens* and *Laurencia obtusa*) were present only on these plates.

At this time there appears to be no clear pattern in the number of algal species occurring under each type of grazing regime.

Algal Primary Production

Production per unit area was not significantly different between treatments (Figure 2). When expressed per unit algal weight or per chlorophyll *a* weight, productivity rates varied widely between grazing regimes. A consistent pattern of higher specific production rates in urchin grazed treatments (all herbivore treatment and urchin only treatment) than in fish grazed, micro-herbivore grazed and non-grazed treatments, was maintained. Net specific community primary production rates (ug O_2 ug chl. *a*$^{-1}$ hr.$^{-1}$) differed by a factor of two to four among the treatments, The micro-herbivore grazed and ungrazed treatments had the lowest specific rates of algal production. Specific rates were inversely related to algal standing crop.

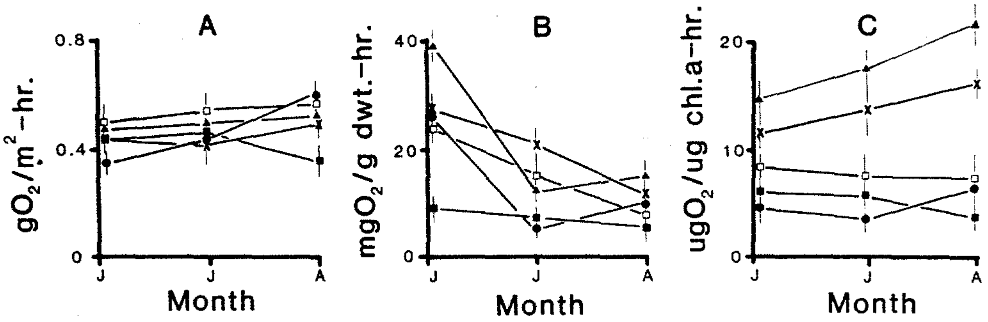

Figure 2. Mean net community primary production ± 95% confidence limits; A) per area, B) per unit algal weight, and C) per unit chl. *a* weight. (**X**)- all herbivore treatment. (□)- group 1 and 3 treatment. (▲)- group 2 and 3 treatment. (■)- group 3 only treatment. (●)- no grazing treatment. J, J, and A on the x axis indicate June, July, and August. Plates were submerged initially in December, 1981, and these data were collected during the summer of 1983.

DISCUSSION

These data provide evidence that different herbivores have variable effects on the benthic algal community. Data on algal species composition and specific primary productivity between treatments demonstrate that functionally different herbivores have qualitatively and quantitatively different effects on these parameters. Algal communities grazed by *Diadema* apparently consist of algal species with much higher specific rates of production. Such low biomass communities are maintained in a high turnover state by intense herbivory. Without urchin grazing, specific production rates decrease by a factor of approximately two, and it appears that different algal species become dominant. This difference may be the result of the visual nature of fish grazing, allowing discrimination and preferences for certain algal species (Ogden and Lobel, 1978). Differential effects on algal specific productivity are in part due to differences in grazing intensity between treatments (amount of biomass removed). In this locality, the abundance of Diadema (and grazing intensity) is sufficiently great to maintain a very productive, low biomass algal community. In other localities, the abundance of herbivorous fishes may be high enough to maintain a similar algal community. However, if fishes avoid some algal species, biomass would be higher (and specific production lower) than if truly generalized grazing occurs.

The rates of algal biomass removal reported here are very close to those found for herbivores on the Great Barrier Reef (Hatcher, 1981) and, though temporally variable, represent between 50 and 60% of net daily algal production. Variations in the percent of daily production removed can result from changes in the absolute amount of biomass taken by herbivores, variations in rates of production, or a combinaation of both these factors. For the data presented here, variations in the percent biomass removed did not consistently correlate with variations in algal production and represent changes in the absolute amount of biomass removed. This estimate of the percent production taken by herbivores may be an underestimation due to the assumption that all the net primary production (less excretion) is going into biomass accumulation that is available for consumption by herbivores. However, a larger proportion of material goes to herbivores in this than in most ecosystems (Wiegert and Owen, 1971). An interesting contrast between these results and those obtained in Australian reefs is that Hatcher (1981) found that herbivorous fishes were responsible for all of the algal consumption. In this study, the amount removed by fishes was less than 50%, with urchins consuming 40-70%. This probably reflects the relative abundances of these herbivores at each site.

For algal communities accessible to all herbivore groups, the differential effects of various herbivores may be masked. Spatially complex reefs, however, preclude access by all groups, at least in some areas, which may lead to mosaics of algal communities with different structure and function. Patterns of herbivore distribution and abundance between and within reef zones would introduce additional variability in these parameters. This suggests that shallow reef algal communities are not only structured by a complex of environmental factors (water movement, nutrient availability, substrate type, etc.), but also by biologically, possibly species-specific, mediated processes which in turn affect functional aspects of the community.

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NEARSHORE AND SHELF-EDGE *OCULINA* CORAL REEFS: THE EFFECTS OF UPWELLING ON CORAL GROWTH AND ON THE ASSOCIATED FAUNAL COMMUNITIES

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ABSTRACT

Colonies of *Oculina varicosa* were collected from nearshore, mid-shelf, and shelf-edge reefs off central eastern Florida. The shelf-edge reefs are inundated episodically throughout the year by upwelling of cool, nutrient rich water. On the inner shelf, cyclic seasonal factors predominate and upwelling intrudes only for a few weeks during the summer. Growth rates of the coral are significantly greater on the shelf-edge reefs than nearshore, even though at the shelf-edge temperatures are cooler and the coral lacks zooxanthellae. Species diversities of assemblages of decapods and mollusks associated with the coral are greater at the shelf-edge reef than at the mid- and inner-shelf reefs. It is suggested that the upwelling of nutrient rich water onto the shelf-edge *Oculina* reefs enhances the growth rate of the coral and facilitates the greater species diversity of the associated faunal communities compared to the inner-shelf reefs.

INTRODUCTION

High latitude coral reefs in the western Atlantic off central Florida are comprised of a single species of branching coral, *Oculina varicosa* Lesueur 1820. Disjunct populations of the coral are present on the shelf, ranging from nearshore shallow reefs to shelf-edge deep-water reefs (Reed, 1980). The shelf-edge reefs are subject to episodic upwelling of cold and nutrient rich water throughout the year, whereas the nearshore reefs are affected by upwelling only a few weeks during the summer. Yoder, *et al*. (1983) reported that upwelling occurred along the southeast U.S. over 50% of the time from November to April, and Smith (1981) documented summer upwelling events off central Florida. Upwelling is known to cause increased primary production with a concommitant increase in zooplankton and fish populations (Atkinson, *et al*., 1978; Paffenhöfer, 1980; Atkinson and Targett, 1983). Upwelling and downwelling events have been targeted as the primary determinant of the benthic community structure on kelp beds off S. Africa (Wulff and Field, 1983) and as a primary source of nutrients for the Great Barrier Reef (Andrews and Gentien, 1982).

This paper compares the growth and community structure of *Oculina* reefs on the inner shelf where cyclic and seasonal environmental parameters predominate, to reefs on the outer shelf where episodic upwelling occurs year round.

METHODS AND MATERIALS

Colonies of *Oculina varicosa* were sampled with SCUBA at the 6 m reef (27°30'N, 80°17'W) and with the Johnson-Sea-Link submersibles at the offshore reefs at 27, 42 and 80 m. Colonies were randomly selected at each site, but noticeably damaged colonies were rejected. Sediment traps, thermographs, current meters, and light meters were deployed at the 6 and 80 m sites for one year.

Various measurements of coral morphology were determined from a total of 37 colonies. For each colony (corallum), maximum width and height were measured and an average for each of the following was determined: tip length (distance from the apex of a branch to the first bifurcation), tip diameter (diameter of a branch tip at its midpoint), branch diameter (measured at 1-2 cm increments throughout a colony), calical diameter (maximum width from rim to rim of a polyp's cup, i.e., corallite), intercalical distance (measured between the cup rim of a corallite and the rim of the nearest neighboring corallite). Relative branch size was the ratio of mean branch diameter to corallum width, and relative tip length was the ratio of mean tip length to tip diameter.

Growth rates of 44 colonies were compared and described by Reed (1981). Linear growth rates of branch tips were measured by use of plastic bands and Alizarin dye. Calification rates were determined by periodically weighing the coral _in situ_.

The faunal community was sampled by a collection of a total of 42 colonies; 2-4 colonies were collected every 2-3 months at the study sites. All the motile, epilithic, and endolithic fauna were captured by placing a 0.5 mm mesh Nytex bag over each colony during collection. The decapod community is described by Reed, _et al_. (1982).

RESULTS

Habitat and hydrology

The inner-shelf (6m) and mid-shelf (27m) reefs are disjunct and consist of coquinoid limestone pavement and ledges (1-5 m relief) which parallel the coast. Colonies of _Oculina_ are interspersed among a cover of algae, sponge and octocoral. At the 42 m site, a sand veneer over a rock pavement inhibits algal and sponge attachment; however, _Oculina_ occurs in dense populations on isolated patch reefs. At the shelf edge (80 m), discontinuous pinnacles form a ridge (Avent, _et al_., 1977) with 5-25m relief and are covered with colonies of aposymbiotic _Oculina_. The coral grows to 1.5 m in height and forms extensive living thickets and dead rubble areas.

The nearshore reef is influenced by strong wave surge which causes sedimentation rates to be 10 times greater than those at the shelf-edge reef (Reed, 1982). Transmittance of light is variable nearshore (0-31%), depending on surge. Light levels are too low to support algal (including zooxanthellae) growth at the 80 m site which often is inundated with a turbid, bottom nepheloid layer.

Temperatures are significantly colder at the shelf-edge reef than nearshore ($\bar{x}$ = 16.2 and 24.6°C, respectively; Reed, 1981). Cold-water upwelling which produces a 3-7°C drop in temperature (Smith, 1981) apparently intrudes onto the nearshore reefs only during the summer. Between 1977 and 1979, thermographs at the nearshore reef recorded one major intrusion a year, lasting 2-3 weeks. Temperatures at the shelf-edge reef indicated episodic intrusions throughout the year which causes temperatures to drop below 10°C. Unpublished research (R. Gibson, pers. comm.) on upwelling on the outer shelf near this study area shows that levels of nutrients and chlorophyll increased nearly an order of magnitude during these intrusions of cold bottom water (nitrates- <2 μM during non-upwelling to 9-18 during upwelling, phosphate- from < 0.25 to 0.5-2 μM, chlorophyll a- from <1 to 1-9 mg/m^3).

Table 1. Comparison of temperatures (mean and range) and various measurements of *Oculina varicosa* colonies collected from inner- (6m), mid- (27m), outer-shelf (42m), and shelf-edge (80m) reefs off central eastern Florida. RTL= relative tip length, CD= intercalical distance, and RBS= relative branch size.

Site	Temperature (°C)	$\bar{x}$ Colony Size (g)	RTL	CD (mm)	RBS	$\bar{x}$ Growth cm/yr	$g/cm^2/yr$
6m	24.6(13.7-31.0)	175	2.29	1.48	.092	1.13	.508
27m	-	115	3.23	1.67	.070	-	-
42m	18.4(8.0-27.8)	1049	4.04	2.24	.039	-	-
80m	16.2(7.4-26.7)	3173	4.84	2.66	.018	1.61	.651

Corallum morphology

Colony size, relative tip length and intercalical distance generally showed a progressive increase with depth, whereas relative branch diameter decreased with depth (Table 1). The increase in branch diameter from the top to the base of a colony also became less pronounced as depth increased. Mean corallite height was greatest for the nearshore population. These results suggest that the coralla of the inner-shelf colonies are wave-resistant; the branch tips are significantly shorter and the corallum is seldom greater than 15 cm in height and has a wide encrusting base. Colonies of *Oculina* from the shelf edge have significantly thinner branches and grow to heights of 1.5 m.

Calical diameter was the only conservative feature and showed no significant change between depths (t-test, $p < .05$). The other morphological characters generally showed a clinal progression over the depth range of the 4 disjunct populations (Table 1).

Coral growth

The mean growth rate of *Oculina* was significantly greater at the shelf-edge reef than nearshore (Reed, 1981). At the nearshore site, growth was positively correlated with water temperature and insolation but negatively correlated with sedimentation and current. At the shelf-edge reef, temperature, current and light accounted for 84% of the variance of growth. Initial studies showed calcification rates to be slightly greater at the 80 m site than at 6 m (Table 1).

Faunal associations with *Oculina*

For the 42 coral samples, the mollusks were considerably richer in numbers of individuals (N=5132) and taxa (S=230) than the decapods (N=2300, S=50; Reed, *et al.*, 1982). Community structure, however, was similar for these two assemblages in terms of dominance-diversity, areal relationships with the coral, and between-station similarity. Both the mollusks and decapods were numerically dominated (65-70% of N) by a few abundant species (5-12% of S). Over 50% of the decapod and molluscan taxa were rare (N < 10); these species comprised only 10-11% of the total individuals collected.

Both assemblages have few species that are obligate symbionts with the coral, requiring live coral tissue and mucus. Most of the taxa are facultative associates that are more dependent on the size of the dead than the live portions of the coral. For the decapods, 43 and 49% of the variance of N and S, respectively, was attributed to the amount of dead coral present (Reed, et al., 1982). The mollusks also had a strong relationship, with 52 and 79% of the variance of N and S due to dead coral size. The live coral, however, forms an expanding volume of living space for the associated fauna as the coral grows and the central portions die.

The assemblages of both the mollusks and decapods were strikingly different at the inner-shelf and shelf-edge reefs. Although the nearshore reef and shelf-edge reefs were both species rich, the shelf-edge site had greater species diversity (Brillouin's H). The percent faunal similarity between the 6 and 80 m sites was only 5.7% for the decapods and 3.2% for the mollusks. The ordination technique of Reciprocal Averaging also showed strong site separation (Reed, et al., 1982). These two reefs showed distinct trophic partitioning. For the decapods, the nearshore reef was dominated by filter feeders such as the porcellanid crab Megalobrachium soriatum; these may be responding to the high turbidity and wave surge which keep food in suspension. In contrast, the shelf-edge reefs were dominated by detritus and deposit feeders such as the pagurid crabs. These species were more dependent on the size of the dead coral which were used for detrital collection sites. For the mollusks, percentages of filter feeding taxa were similar at 6 and 80 m, but the 80 m site had more specialized feeding types such as corallivores, parasites and carnivores than the 6 m site. The densities of the carnivores were significantly correlated with the amount of dead coral; these possibly were responding to the greater abundance of food items that were available with dead coral rather than live coral.

DISCUSSION

The episodic upwelling of cool, nutrient rich water from the Florida Straits inundates the shelf-edge region frequently throughout the year, but apparently further onshore movement of upwelled water only occurs during the summer (Atkinson, et al., 1978). The sampling periods in this report were too long to distinguish any immediate responses, if any, of the coral or faunal communities to individual upwelling events. However, general trends may be inferred. Seasonal cycles of temperature, light and turbidity predominate at the nearshore reefs whereas on the shelf-edge reefs seasonal cycles are partially negated by episodic upwelling.

The clinal change in corallum morphology (i.e., branch diameter, tip length, and intercalical distance) of Oculina most likely is due to differences in wave energy and light levels but is not a result of upwelling. For example, many corals become more spindly and fragile in calm (deep or sheltered) environments (Stoddard, 1969), high calical relief is more efficient in removing sediment in nearshore areas of high turbidity (Hubbard and Pocock, 1972), and density of calices appears to be related to efficiency of light gathering and excretion of metabolites (Yonge, 1973; Wijsman-Best, 1974). However, the structure of the shelf-edge Oculina reefs, which are similar to deep-water Lophelia coral banks, may be a result of upwelling; both Lophelia and Oculina occur at crests of escarpments or at edges of continental shelves where water wells up and around promontories (Teichert, 1958; Reed, 1980).

The aposymbiotic populations of Oculina at the shelf-edge reefs, where temperatures average 8.4°C cooler than the nearshore reefs, theoretically should have lower growth rates than the shallow population which possesses zooxanthellae. Upwelling of nutrient rich water onto the shelf edge of the study area (Gibson, pers. comm.) and subsequent increases of phytoplankton and zooplankton (Atkinson, et al., 1978; Paffenhöfer, 1980) may enhance growth rates of the shelf-edge Oculina. The shelf-edge coral must rely on dissolved and particulate organic material and plankton for nutrition. Even though growth at 80 m shows a positive response to temperature, growth may be pulsed, occurring during warmer non-upwelling periods after the coral has stored up the nutrition gained during the upwelling. Of course other factors such as greater sedimentation rates on the nearshore reefs also could be important. Short term growth studies under controlled environmental conditions are necessary to resolve this question.

Distinct assemblages of both decapods and mollusks occur on the nearshore and shelf-edge reefs. These two reefs have more species than the mid-shelf reefs and diversity is greatest at the shelf-edge reef. The high species richness at the nearshore reef may be due to a more stable thermal environment. Also the nearshore reef has greater surrounding habitat heterogeneity; thus, the species pool may be drawn from algal-sponge, rock, and sabellariid worm reef biotopes. The 80 m Oculina reef site, however, is an isolated pinnacle surrounded by miles of sand, and temperature fluctuations from upwelling are extreme; in fact, a 13.4°C variation was recorded within a 24 h period. I suggest that the high species diversity on the shelf-edge Oculina reefs is a result of the upwelling which induces increased productivity of that region. The specific pathways of energy transfer from the nutrients of upwelled water to the coral and faunal communities remain unknown.

ACKNOWLEDGEMENTS

R.M. Avent is gratefully acknowledged for initiating these studies on Oculina. H.L. Edmiston did much of the research on the morphology of the Oculina corallum. P.M. Mikkelsen assisted with the molluscan research. C.M. Hoskin, R.W. Virnstein, and K.J. Eckelbarger are thanked for their critical reviews of the manuscript. This is Contribution No. 355 from Harbor Branch Foundation, Inc.

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CHAPTER V: THE ORGANIZATION OF CORAL REEF ECOSYSTEMS

NET PRODUCTION OF CORAL REEF ECOSYSTEMS

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INTRODUCTION

How do coral reefs survive as rich and diverse ecosystems generally found in nutrient-deficient water? This fundamental question has directed much research on the community metabolism of coral reefs towards two ancillary questions:

1. Does the high biomass of coral reef communities indicate high gross organic carbon production?
2. Are coral reef communities net importers or exporters of organic material?

If coral reefs were found to produce organic carbon very slowly, then their survival in nutrient-deficient waters would be more easily understood; their nutritional requirements would be minimal. However, early work (Sargent and Austin, 1949, 1954; Odum and Odum, 1955) through to recent research (see references in Kinsey, 1979; Smith, 1981) has consistently demonstrated that the gross production rate of these reef communities is relatively high. The best estimate for the average gross production rate of these communities is 7 gC m^{-2} d^{-1}, not an entry to the Guinness Book of Records, but impressive nevertheless.

The organic and inorganic nutritional requirements of any biological system are determined by the difference between the amount of organic material produced and that which it consumes. We therefore turn to the second question. Can we learn something about the survival mechanisms and ecosystem requirements of coral reefs by considering their net trophic status?

The flow respirometry model advanced by Sargent and Austin (1949) and popularized by Odum and Odum (1955) to study the community metabolism of coral reef flats was an elegant approach to community metabolism. Much has been done to refine the model and to adapt it to communities besides reef flats. Probably to the detriment of the original question about the survival of reefs in nutrient-deficient waters, the flow respirometry model and its extensions have focused attention on the metabolic performance of coral reef communities, not coral reef ecosystems.

By now we know that individual coral reef communities can be net producers or consumers of organic material, by substantial margins in either direction (Smith and Marsh, 1973; Kinsey, 1979). However, net community production is not directly relevant to the question of net ecosystem performance, because we know that the transfer of particulate and dissolved materials across boundaries between adjacent autotrophic and heterotrophic communities tends towards an intercommunity trophic balance. Such a tendency towards trophic balance has been demonstrated by examining groups of distinct communities (or zones) on coral reefs (Smith and Marsh, 1973; Kinsey, 1979) and is discussed in some detail for a non-reef ecosystem that is metabolically dominated by seagrass and soft bottom communities (Smith and Atkinson, 1983). This characteristic also has been noted as a general characteristic of adjacent communities in flowing water (Odum, 1956).

But do we really have a firm notion about the metabolic balance among the entire consortium of biotic communities which form a coral-reef ecosystem? I believe that the answer to this question in any explicit fashion must be "No!" We simply cannot expect to weight and sum the component estimates for individual communities in most ecosystems to a quantitatively satisfying estimate of net ecosystem production. Neither the sizes of communities within the ecosystems nor the community production rates can be measured with sufficient accuracy or precision to accomplish such a summation to within a few percent. At least such precision is required.

RESULTS

I have recently revisited a subset of my own research papers (and have literally revisited one site and added another) in an attempt to derive an explicit answer about the net production rate of entire coral reef ecosystems. This subset deals with coral atoll lagoons. The lagoons in question are a special case of atoll lagoons: I have examined lagoons virtually surrounded by land (rather than by the more usual oceanic reef rim). Within the lagoons are reef flats, slopes, and inter-reef communities--all of the essential units of more classical "open" coral reefs. The advantage of these confined lagoonal reef ecosystems over more open reef ecosystems is the clear definition of ecosystem boundaries and fluxes. These lagoonal reef systems apparently function as self-contained entities with little communication (with respect to carbon flow, at least) with the oceanic reefs beyond the enclosing islands.

The sites being considered are Fanning (Smith and Pesret, 1974, plus new data), Canton (Smith and Jokiel, 1978), and Christmas (Smith, et al., 1983), all in the central Pacific Ocean. I will also include some relevant discussion with respect to a more open atoll lagoonal system in the Indian Ocean (the Abrolhos Islands; Crossland, et al., 1983) and a seagrass-dominated coastal lagoon in Western Australia (Shark Bay; Smith and Atkinson, 1983). These last two systems provide additional insight into material processing at the scale of entire ecosystems.

I have used water, salt, and CO_2 budgets to examine the net metabolism of these confined lagoonal systems for clues about the total system metabolism of coral reef ecosystems. Shark Bay provides the clue that my suggestions about the metabolism of coral-reef ecosystems may be generalized to other well-defined ecosystems with little input from the surroundings, and the Abrolhos lagoon is an anomaly which strengthens our understanding of the mechanisms controlling these systems.

The initial work at Fanning and Canton resulted in values for $CaCO_3$ production and total CO_2 flux, but failed to separate organic metabolism from gas flux across the air-water interface. In that early work, we were initially very conservative about the gas transfer coefficient. Expressing this coefficient in terms of "piston coefficients," we assumed a possible range between 0 and 20 $m\ d^{-1}$. More recent assessment of available data suggests that at wind speeds below 7 $m\ s^{-1}$ (i.e., about the median wind speed on most coral reefs), the piston coefficient lies in the much narrower range of 0.3 to 3 $m\ d^{-1}$ (Smith and Atkinson, 1983). If the average piston coefficient is applied to the data set previously mentioned, we derive the following organic carbon production rates (Table 1):

Table 1. Organic carbon production (+) or consumption (-) rates for atoll lagoon reef ecosystems. Note that the calculated rates reflect the budgets adjusted to the presently estimated piston coefficient based on other budgetary data presented in the original reference citations.

Location	Rate mgC m^{-2} d^{-1}	Reference
Canton 1973	170	Smith and Jokiel (1978)
Christmas 1983	70	Smith, et al. (1983)
Fanning 1983	0	Smith (unpublished data)
Fanning 1972	-10	Smith and Pesret (1974)

It should be noted that Canton, by its proximity to equatorial upwelling and because of its ocean/lagoon exchange characteristics, has the highest nutrient concentration and loading of these sites. Moreover, it is clearly demonstrated in Table 1 that this site exhibits the highest net ecosystem production observed according to this model.

Shark Bay, although not a coral reef, is another confined ecosystem showing a very low net production rate (15 mgC m^{-2} d^{-1}; Smith and Atkinson, 1983). The Abrolhos lagoon is an open atoll lagoon surrounded by oceanic reefs. The slopes of these oceanic reefs have a very large standing crop of typically temperate-water macroalgae (kelp), much of which gets swept into the lagoon during storms (Crossland, et al., 1983). Based on dissolved nutrient export from that lagoonal reef system, we concluded that that system is marginally heterotrophic. We could not quantify the degree of heterotrophy there, although research on that question continues (B. Hatcher, personal communication).

DISCUSSION

Based on this very limited set of data from a particular subset of coral reefs, I suggest that the net organic carbon metabolism of coral reefs and related ecosystems in low-nutrient waters is very low, probably generally averaging well less than 100 mgC m^{-2} d^{-1}. The available data show a slight bias towards net autotrophy, but it seems likely that individual systems can be influenced to swing one way or the other. This swing will reflect variations in availability (and lability) of inorganic and organic materials used for metabolism.

The important conclusion to be drawn from these calculations does not ultimately concern the trophic status of coral reefs and related systems. Rather, note the very low absolute values of net organic carbon flux in these ecosystems. Let us compare, for example, the net nutritional requirements of coral reefs with the requirements of the surrounding ocean.

Eppley and Peterson (1979) defined "new production" of plankton to be that production in the surface waters supported by external nutrient inputs, mostly from upward nutrient flux out of the aphotic zone. Those authors estimated an ocean-averaged new production rate of about 30 mgC m^{-2} d^{-1}, within the range for net coral-reef production (Table 1).

Coral reefs and other ecosystems dominated by benthic plant production apparently have a nutritional advantage over plankton. Rather than approximating the Redfield C:N:P ratio of 106:16:1, benthic plants have a C:N:P ratio of about 550:30:1 (Atkinson and Smith, 1983). The nutritional implication of this observation is that reefs and other benthos-dominated ecosystems can produce more net C per unit of P and N availability than can plankton systems. Moreover, it is well established (e.g., Webb, et al., 1975; Wiebe, et al., 1975) that coral reef communities can fix large amounts of N. Recent work suggests that entire reef ecosystems, as well as other confined aquatic ecosystems, can provide most of their N requirements via N fixation (Smith, et al., 1983; Smith and Atkinson, submitted).

Thus, in any net sense, the nutritional requirements of coral reefs do not differ greatly from the requirements of the plankton in the surrounding ocean. We need not look for upwelling or other exogenous nutrient sources to explain the survival of coral reefs. This conclusion does not imply that coral reef metabolism will not respond to increased subsidy of inorganic or organic nutrients. To the contrary, Canton and the Abrolhos appear metabolically responsive to inorganic and organic subsidies, respectively. Direct evidence of reef metabolism response to increased nutrient loading has been documented (Kinsey and Domm, 1974), and both community metabolism and community structure of a reef system have been demonstrably altered by long-term elevation of the supply of inorganic and organic nutrients (Smith, et al., 1981; Brock and Smith, 1983).

We can therefore return to the original question about reef survival in nutrient-poor waters. Despite the rapid metabolic activity of components within coral reefs, the net nutritional demands of entire coral-reef ecosystems are low. The key to the success of coral reefs as biologically rich and diverse entities would appear to be the accumulation of a large biomass into a network of biotic communities which are effective at preventing leaks to the surrounding ocean.

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FUNCTIONAL ASPECTS OF NUTRIENT CYCLING ON CORAL REEFS

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ABSTRACT

Coral reef waters are generally very low in nutrients, yet benthic productivity is among the highest in the world. A general concern of reef ecologists has been to identify the sources of nutrients for reef productivity and the processes responsible for nutrient recycling on reefs. One potentially important process that has been poorly studied is the recycling of regenerated nutrients from sediments and feces trapped in reef holes and crevices. These nutrients, if available to the benthos in concentrated form, could have a major influence on reef productivity.

INTRODUCTION

Coral reef communities are extremely diverse and variable, and we should not expect that the relationships between reef organisms or the dynamics of the system to be simple to understand. On the other hand, by analyzing these complex systems in terms of functional groups, we may gain a better understanding of important processes, and identify research areas that need our attention. In this paper, I will try to identify processes and functional groups involved in nutrient dynamics on coral reefs.

Understanding nutrient dynamics on coral reefs is important because, as in any other ecosystem, primary production is controlled by the availability of nutrients, and primary production is one of the main factors that determines community biomass and secondary production.

Coral reefs occur in tropical areas, where oceanic waters are generally very low in nutrients, yet these complex ecosystems have some of the highest biomasses and productivity that have been reported (Lewis, 1977). This dilemma can been termed the 'paradox of the coral reef'. There has been a great interest in identifying mechanisms that could explain this paradox. Two important ones that have been well studied are the recycling of nutrients between algal/invertebrate symbionts and the fixation of N_2 by blue-green algae and bacteria. Another approach has been to identify additional sources of dissolved nutrients, such as from ground water seepage or upwelling of nutrient enriched deepwater. A final approach has been to examine the reef ecosystem for structural and functional properties that lead to enhanced conservation of nutrients. This is the approach that will be emphasized here.

SOURCES OF NUTRIENTS

There are two general sources of nutrients for primary production: New nutrients and regenerated (recycled) nutrients. If only regenerated nutrients were available, gross photosynthesis could not excede respiration (i.e., P/R ratios could not excede 1.0) unless there was a change in elemental ratios (e.g., an increase in the C/N and C/P ratios). Net production (growth) requires the input of new nutrients into the system, as does net export from the system. It is important to point out that nutrient recycling mechanisms, even when 100% efficient, cannot supply nutrients for a positive net production. Furthermore, if recycling mechanisms are inefficient it will take an input of new nutrients to maintain a steady state biomass.

New Nutrients:

New nutrients can enter reef systems from both terrestrial and oceanic sources and, in the case of nitrogen, by *in situ* N_2 fixation. Nutrient input to reefs from terrestrial sources remain poorly studied. However, we can make several general statements. Coral reefs located off the coasts of high volcanic islands or on continental shelves may receive a considerable supply of nutrients via terrestrial runoff (Marsh, 1977). However, coastal areas with high runoff are usually devoid of coral reefs unless estuarine systems, such as mangrove forests, trap the nutrients near shore. It is not clear at this time whether the negative effect of runoff on reef development is due to siltation stress, salinity stress or nutrient stress (in the latter case, high nutrient concentrations can promote high phytoplankton and macroalgal growth rates, which in turn can result in unfavorable environmental conditions for reef-building corals). Most likely, all three stresses contribute to the effect. In any case, the on-shore current patterns that generally dominate coral reef circulation should limit the amount of terrestrial runoff that reaches most offshore reefs. One interesting phenomenon that has been reported recently is the submarine seepage of NO_3 enriched fresh water inshore of a fringing reef (D'Elia, *et al.*, 1981; Johannes, 1980). It is unlikely that this kind of seepage will reach offshore reefs, and there is little or no information on how frequently this phenomenon occurs. Reefs located offshore of low carbonate islands should receive little input of terrestrial nutrients because runoff from these terrains are usually low in nutrients unless fertilizer has been applied for agricultural purposes. Atoll reefs generally have no significant land masses nearby from which to receive terrestrial runoff.

Oceanic sources of nutrients will be dependent on the concentration of nutrients in the source water, the rate of flow of water over the reef, and the ability of primary producers to take up the nutrients at the given concentration. Nutrient concentrations in tropical oceanic waters are generally near limits of detection, but there are reports that upwelling may occasionally result in higher concentrations (Thompson and Golding, 1981; Andrews and Gentien, 1982). The rates of water flow over the reef are high,and several species of reef coral have been found to be able to take up nutrients from these low concentrations (Franzisket, 1974; D'Elia, 1977; D'Elia and Webb, 1977; Webb and Wiebe, 1978). Atkinson (1981) has estimated that there was a sufficient uptake of dissolved phosphorus from water crossing the reef flat to account for the measured primary production (ΔO_2) if a Redfield ratio (C:P) of 490 was assumed (the oceanic C:P ratio is 106). He also found that marine algae from a variety of sources had C:N:P ratios much higher than the Redfield ratio (Atkinson and Smith, 1983), a possible indication of an evolutionary adaptation to low nutrient conditions. An alternative explanation is that macroalgae need a greater amount of C-rich structural material than phytoplankton, which results in higher C:N:P ratios for the former. It should be instructive to measure the C:N:P ratio of other reef organisms, especially the microcrustaceans, which have body structures similar to planktonic organisms.

In any case, a quick calculation shows that for the following average conditions: dissolved inorganic nitrogen (DIN) concentrations in the range of 0.5 to 1.0 μM, currrent velocities in the order of 0.06 to 0.50 cm/s, annual gross productivity of 3,220 $gC \cdot m^{-2} \cdot y^{-1}$, P/R ratio of 1.4 and net productivity of 950 $gC \cdot m^{-2} \cdot y^{-1}$, the first m^2 of reef substrate to make contact with oceanic water would need to strip out 0.08 to 1.3% of the DIN to support net production and maintain a C:N of 6.6. This assumes a mixed layer 1 m deep; twice that percentage would have to be taken up if the organisms can only strip nutrients from the bottom-most 0.5 m of water. Uptake of nutrients to support all of gross production (i.e., if no recycling occurred) would require stripping somewhere between 0.25 to 8.5% of DIN. This means that for many reef flats, where the water column is usually less than a meter deep, waters flowing over downstream areas may be significantly depleted in nutrients. In fore-reef zones, vertical mixing should prevent this type of depletion from being as important, but it is still apparent that at low concentrations and at slow current velocities it is unlikely that uptake of new oceanic nutrients could account for much more than net productivity. Otherwise, we should see a much greater drop in DIN and dissolved inorganic P concentrations during upstream-downstream experiments (Pilson and Betzer, 1973). In fact, DIN and dissolved organic N (DON) concentrations generally increase as oceanic waters cross the reef, and a net export of N has been found for some reefs (Johannes, et al., 1972; Webb, et al., 1975). This implies a source of fixed N from within the reef community, which can be attributed to N_2 fixation by benthic blue-green algae and N_2-fixing bacteria (Mague and Holm-Hansen, 1975; Burris, 1976; Capone, et al., 1977; Wiebe, et al., 1975). Rates of N_2 fixation on coral reefs have been found to exceed those of alfalfa fields, the terrestrial community with the highest reported rates of N_2 fixation. These high rates have led many investigators to conclude that fixed N is plentiful on reefs, and that concentrations of P must be controlling reef productivity. However, measurements of N_2 fixation generally have been restricted to shallow reef flats or back reef areas and denitrification rates have not been adequately measured in any reef environment. Until they are, any conclusions about N availability are premature.

Regenerated Nutrients:

It generally is believed that the main evolutionary adaptation to low nutrient conditions in reef environments has been the evolution of relationships that lead to efficient recycling of nutrients. The foremost example of this type of relationship is the endosymbiosis between algae and invertebrates. Present day coral reefs are physically dominated by a variety of orders and classes of coelenterates and virtually all of them have symbiotic dinoflagellates (zooxanthellae) in their tissues. It has been repeatedly demonstrated that these animals do not excrete waste products as do other nonsymbiotic animals (Kawaguti, 1953; Pomeroy and Kuenzler, 1969) and that there is even a measurable uptake of dissolved nutrients by them attributable to the presence of the algae (see earlier references). Other invertebrate groups, including sponges, molluscs and ascidians, also have some species with algal symbionts. This form of recycling is the most efficient possible (often 100%) as the nutrients are available to the algae in concentrated form. It should cost the algae much less energy to take up the nutrients they need from a concentrated source than to take them up once they had been excreted and diluted.

As important as this type of relationship may be, there are still many groups of algae and many more of vertebrates and invertebrates living on the reef that are not involved in endosymbiotic relationships. These plants and animals need nutrients and excrete nutrients, respectively, and depending on their biomass these fluxes may be quite large. There are few estimates of the absolute and/or relative biomasses of reef organisms. Odum and Odum (1955) found that zooxanthellae make up roughly 15% of the biomass of primary production on a Enewetak reef flat and that coral polyps make up about 50% of the biomass of consumers. However, they had very poor estimates for the biomass of reef fishes and their samples were from the reef flat, which is topographically and biologically less diverse than most forereef areas. Measurements of biomass on a Caribbean fore reef (Szmant-Froelich, 1972) show a greater percentage of the algal biomass to be made up of zooxanthellae and a smaller percentage of the consumer biomass to be made up of symbiotic coelenterates. In order for the reef as a whole to be efficient in recycling nutrients, there must be mechanisms for recycling nutrients among these free-living plants and animals. The main problem arises when one considers that the same high water flow over the reef that assures a large source of low-nutrient oceanic water also assures that any nutrients excreted into the water by animals will be rapidly diluted and carried away. Therefore, what is needed is a mechanism to prevent dilution and loss.

I would like to bring attention here to a little studied mechanism, that of particle entrapment and nutrient regeneration within the reef framework.

REGENERATIVE SPACES

Coral reefs are riddled with holes and tunnels of all sizes. From 50 to 75% of the reef volume can be made up of these voids (Ginsburg, 1983). These holes contain varying amounts of sediment which comes from a variety of sources, including carbonate sediments generated by degradation of the reef structure by borers, fecal material from fishes and invertebrates that use these holes as shelters or encrust the walls of the holes, and non-reefal material (including terrestrial and pelagic) that is trapped inside the reef as seawater percolates through the porous structure. Organic materials in these sediments are metabolized by microorganisms, and in the process, nutrients are regenerated. Elevated concentrations of nutrients have been measured in waters from reef cavities (Di Salvo, 1969; Andrews and Muller, 1983; Szmant-Froelich, 1983).

I suggest that 'burps' of nutrient enriched water exit these holes and provide benthic primary producers with short episodes of exposure to higher nutrient concentrations. During Hydrolab Mission 83-10, whose objective was to study the role of herbivorous fish in nutrient regeneration, we measured nutrient (NH_4, NO_3 and total dissolved N) concentrations of surface and bottom waters at two sites, one near shore ("Habitat" site), the other less protected and more offshore (East Slope site), as well as waters from about 400 m offshore of the reef, and from inside caves at the East Slope site (Table 1). The results of these measurements show that reef water is 3 to 4 times higher in NO_3 and slightly higher in NH_4 and organic N concentrations than oceanic waters. The most dramatic difference in nutrient concentration, however, can be seen between the offshore water and the cave water. Cave water concentrations are 13 times higher in NO_3, 2 times higher in NH_4 and 3 times higher in organic N than offshore waters. These enrichments in the caves represent a signficiant increase in nutrients for any primary producers that might have access to them. Dye injections into caves showed that there was rapid outwelling of cave waters onto the reef, and, importantly, that these cave waters flowed within 1 m of the bottom for 10-15 min or longer before mixing upwards. This indicates that there is a process that restricts vertical mixing and dilution of nutrient enriched outwelled cave waters, such that benthic primary producers would have sufficient time to strip the nutrients from these waters before they mix upwards. Corollary evidence that 'burps' of enriched water exist near the reef bottom were obtained from fish excretion experiments during which fishes were incubated inside PVC pipes. Concentrations of NO_3 were always constant during each incubation but varied considerably between incubations (Table 1). Since these were short incubations (30 min) replicated repeatedly with new fish during 4 to 5 hour periods, and conducted at various locations over the reef, the differences in NO_3 concentration reflect true spatial and temporal differences in NO_3 concentrations of reef bottom waters. The rapid outwelling of the dye from the caves further indicates that rates of nutrient regeneration in cave sediments must be fairly high in order to maintain the observed enrichments in spite of the high water flow.

Table 1. Mean nutrient concentrations at various sites in Salt River Canyon, St. Croix (Hydrolab Mission 83-10) during August 4-10, 1983 (mean ± 1 std. dev.).

Site	Depth (m)	No. Sampling periods	uM			
			NH_4	NO_3	DIN	DON
Offshore	0	2	0.40 ± 0.04	0.07 ± 0.03	7.7 ± 0.2	7.2
	15	2	0.28 ± 0.06	0.07 ± 0.04	8.2 ± 0.4	7.8
East Slope	0	8	0.49 ± 0.19	0.24 ± 0.12	7.8 ± 1.4	7.1
	15	17	0.45 ± 0.27	0.30 ± 0.13	9.2 ± 3.3	8.4
"Habitat"	0	9	0.57 ± 0.25	0.27 ± 0.05	9.0 ± 1.8	8.2
	15	16	0.53 ± 0.24	0.31 ± 0.11	8.6 ± 1.8	7.8
Caves	15-30	15	0.67 ± 0.26	0.93 ± 0.42	24.6 ± 11.0	23.0
Fish Incubation	15	49	-	range 0.14 - 0.40	-	-

Nutrient regeneration also occurs in lagoon sediments (Entch, et al., 1983) where nutrients are utilized by extensive macroalgae and turtle grass beds. These beds are heavily grazed upon by reef fish. Many of these fish exhibit diel migration patterns, whereby they graze on the backreef and in the lagoons by day but shelter in the deeper forereef by night. Material that they transport in their guts at dusk is defecated over the forereef or in their nocturnal shelters. This form of transport may be an important means of upstream nutrient recycling on coral reefs. The reverse cycle of migration (nocturnal feeding, daytime sheltering) by juvenile grunts has been shown to have measureable impact on nutrient concentrations around coral heads (Meyer, et al., 1983).

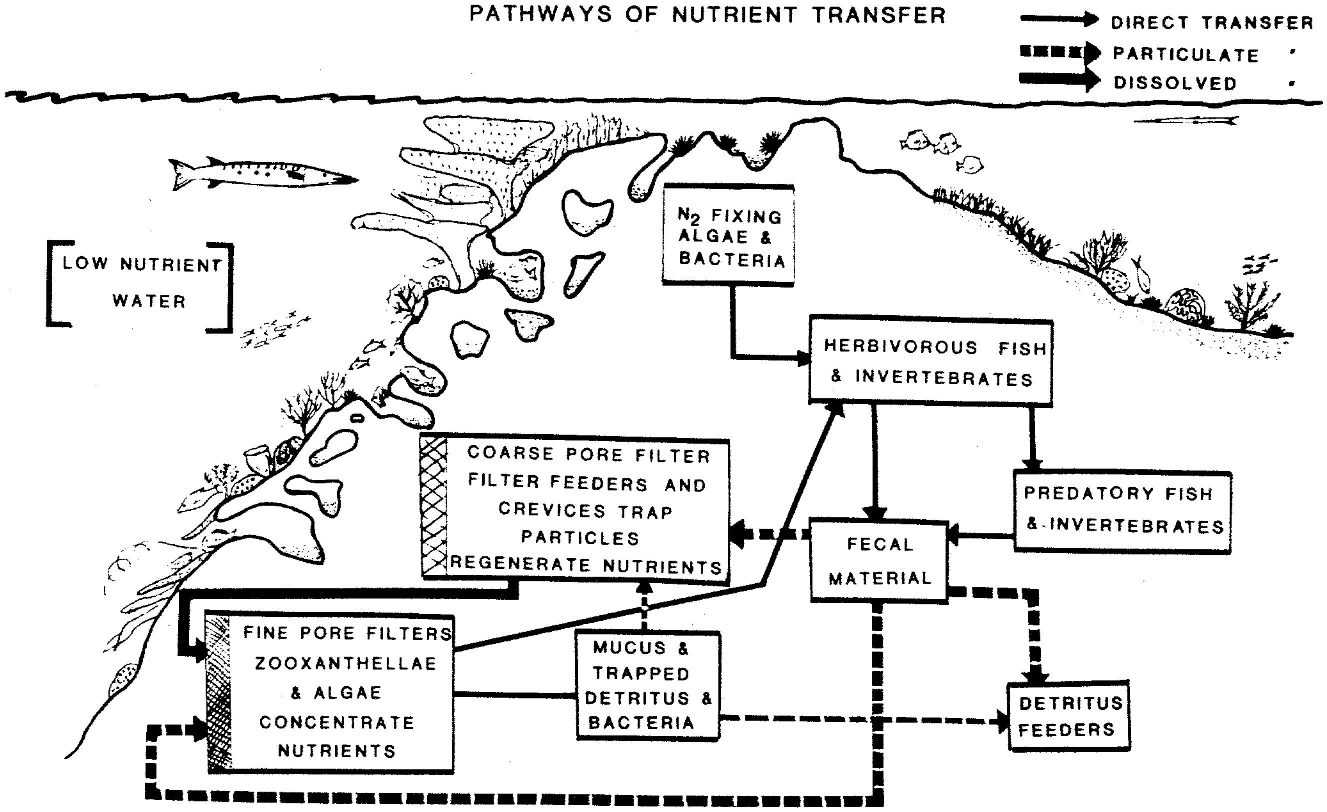

Figure 1. Diagramatic representation of nutrient pathways on a coral reef.

FUNCTIONAL GROUPS

The various processes and functional groups involved in coral reef nutrient dynamics are diagramatically represented in Figure 1.

New nutrients enter the system in both dissolved and particulate form, or are generated in situ by N_2 fixation. Dissolved nutrients and some particulates are taken up by the organisms included in the "fine-pore concentrators" group made up of algae and zooxanthellae. Other particulates are trapped by the reef framework and by filter-feeding organisms, which I call the "coarse-pore concentrators". Planktivorous fish also concentrate particulates and have been shown to excrete and defecate significant amounts of NH_4 and organic material in their nocturnal shelters (Bray, 1982). Herbivores graze on the algae and corals, and carnivores, in turn, feed on the herbivores. The fecal material from both of these groups, many of which spend about one-half of their time sheltering in reef crevices, are deposited either into reef crevices or released just above the reef surface, where it rains onto what can be viewed as a benthic wall-to-wall carpet of mouths. I have observed particles of cardinal fish feces being consumed by Agaricia agaricites and by other fish. Fish feces contain a lot of mucus, and I believe that fish fecal material is the source of much of the "organic-aggregate" material reported from reef waters. Fecal particles that are eaten form a direct link in nutrient recycling. They are an important nutritional source for corals and other sessile invertebrates that previously has not been taken into account when considering questions of food availability. Regenerated nutrients outwelling from reef interstices form an indirect link in nutrient recycling on the reef, possibly a critical one in maintaining the high rates of reef productivity.

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CONTRASTS IN BENTHIC ECOSYSTEM RESPONSE TO NUTRIENT SUBSIDY: COMMUNITY STRUCTURE AND FUNCTION AT SAND ISLAND, HAWAII

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INTRODUCTION

Controlled technological events may provide a well-defined framework for experiments that demonstrate community metabolic response to large-scale nutrient subsidies (Smith, et al., 1981). Sand Island, Oahu is an Hawaiian site where a major change in sewage discharge technology has presented an opportunity to compare response patterns of two very dissimilar benthic communities to essentially the same effluent. From 1955 to 1977 the Sand Island sewage outfall discharged approximately 2.3 x 10^5 m^3 raw effluent per day from a point source discharge at a depth of 10 meters. Prior to discharge the receiving environment was a coral reef typical of those off leeward areas of Hawaii. Two research programs were conducted at the shallow discharge site, one in 1975 while sewage was still being discharged (Grigg, 1975) and one in 1979, 1.5 years after sewage diversion (Dollar, 1979). In 1977, in response to federal mandate, the Sand Island discharge was shifted to a newly constructed multi-port deepwater outfall. The receiving environment, at a depth of approximately 70 m is a homogeneous calcium carbonate sandy substratum. For the first 5 years of operation effluent was discharged raw, while for the last two years effluent has undergone primary treatment. In 1981, an ongoing research program designed to examine the response of the benthic ecosystem to the Sand Island outfall was begun. The questions posed in this study were based on the functional metabolic approach developed by Smith, et al. (1981): can a total system response be ascertained from a description of nutrient addition, community metabolism and resultant nutrient fluxes? The purpose of this paper is to present a summary of results and a short discussion of the contrasting effects to the benthic ecosystems resulting from the nutrient subsidies from the Sand Island sewage outfalls. Of particular interest in this regard are the contrasting approaches to defining ecosystem response by community structure and community function analyses.

RESULTS

Shallow Outfall

The 1975 and 1979 benthic surveys at the shallow Sand Island Outfall consisted of series of line transect and photographic quadrats used to estimate quantitatively the effects of sewage on macrobenthos at 28 stations ranging from 3000 m east to 11,000 m west of the outfall. A clear pattern of community alteration associated with the sewage impact was distinguished by two distinct zones; an acute impact zone included approximately 4 km^2 of bottom and was characterized by a total lack of living reef coral. The epibenthos was dominated by large mounds of deposit feeding worms (Chaetopterus sp.) apparently adapted to the high organic particulate loading from the outfall. The zone of intermediate impact covered approximately 20 km^2 in an asymmetric pattern reflecting prevailing current patterns which transported the sewage laden plume to the southwest. Coral mortality was high, but not total in this area. Macrobenthic species diversity was highest in the zone of intermediate impact due to the co-occurrence of species found in normal, unstressed communities and those species directly associated with the particulate loading.

Following sewage abatement, the pattern remained essentially the same, and was reflected in the physical condition of the benthic surface, as well as in species distribution (Dollar, 1979). In the acute impact zone the reef platform was reduced to a pitted flat limestone pavement by biological/chemical erosional activity. The dense aggregations of polycheate worms were totally absent. Termination of the heavy fallout of particulate organic material emanating from the outfall resulted in a complete change in trophic community structure in the acute impact zone. Apparently qualitative alteration of the limestone surface affected the reconditioning process that is a precursor to hermatypic coral colonization.

Deep Outfall

Preliminary observations revealed that diversion of sewage to the deep water discharge resulted in none of the severe community structure alterations that were apparent at the shallow site. No changes occurred either by removal of organisms from adverse environmental conditions or additions of new species in response to increased nutritional loading. In addition, there were no apparent changes in water column productivity and nutrient characteristics in the vicinity of the outfall (Laws and Terry, 1983).

However, results of benthic nutrient flux experiments performed with the Hawaii Undersea Research Laboratory Submersible *Makali'i* showed a very distinct pattern of metabolic community response to nutrient subsidy from sewage loading.

Table 1 summarizes the results of the deep Sand Island outfall study and includes for purposes of comparison similar data from a Hawaiian estuary, Kaneohe Bay (Harrison, 1981) and a deep ocean site underlying an area of intense upwelling off the coast of California known as the Patton Escarpment (Smith, *et al*. 1979). Results of oxygen uptake experiments indicate that within a horizontal distance of 25 meters from the diffuser, metabolic oxygen uptake varies from levels of the deep ocean (3800 m) to an estuary subjected to high levels of terrigenous input from stream runoff and recycled sewage-derived nutrients.

				NUTRIENT FLUX (uM M^{-2}day^{-1})					
STATION	DEPTH (M)	DISTANCE FROM OUTFALL(M)	O_2FLUX (mM M^{-2}day^{-1})	NH_4^+	$NO_3^-NO_2^-$	PO_4	SEDIMENTATION RATE-ORGANIC C (grams M^{-2}day^{-1})	% ORGANIC C IN BOTTOM SEDIMENT	% SEDIMENTED ORG. CARBON OXIDIZED
SAND ISLAND	72	5	-16.9 s=7.4 n=13	2209.0 s=1186 n=13	196.5 s=82.9 n=13	222.4 s=139.2 n=13	1.20 s=.55 n=10	0.60 s=.06 n=6	12.9
SAND ISLAND	72	15	-13.2 s=6.1 n=8	328.2 s=111.7 n=8	347.3 s=237.6 n=8	-12.45 s=62.77 n=8	1.30 s=.26 n=8	0.57 s=.03 n=6	9.3
SAND ISLAND	72	25	-4.4 s=4.5 n=9	319.0 s=173.0 n=9	216.2 s=51.1 n=9	56.0 s=14.4 n=9	0.93 s=.52 n=9	0.76 s=.08 n=7	4.3
SAND ISLAND	72	5000	-1.3 s=4.0 n=6	90.2 s=59.2 n=6	50.4 s=8.3 n=6	-14.6 s=27.7 n=6	0.40 s=0.2 n=6	0.80 s=0.05 n=4	3.0
KANEOHE BAY (presewage diversion)	10	500	-18.3 s=4.6 n=17	1857 s=958 n=17	182 s=93 n=17	110 s=68 n=16	0.49* s=.22	3.2*	34.4
KANEOHE BAY (post sewage diversion)	10	-	-11.9 s=6.6 n=16	959 s=556 n=15	218 s=161 n=15	82 s=6.0 n=15			
PATTON ESCARPMENT	3815	-	-2.4 s=.7 n=3	283.2	640.3	-5.4		1.22	

TABLE 1. Summary of results of Sand Island nutrient flux and sedimentation rate studies. Positive fluxes indicate efflux from sediments; negative fluxes indicate uptake by sediments. Kaneohe Bay data is from Harrison (1981) Patton Escarpment, North Pacific data is from Smith et. al. (1979).

Table 1 also shows the amount of organic carbon that was intercepted in sediment trap deployments as a function of distance from the outfall. While oxygen uptake (carbon utilization) increased by a factor of 13 between control and the 5 m outfall station, organic sedimentation increased by only a factor of 3. Organic content of bottom sediment remained relatively constant throughout the stations.

All fluxes of nitrogeneous dissolved substances, NH_4^+, NO_3^- plus NO_2^-, were positive, indicating release to the water column from the sediments. Mean NH_4^+ fluxes were highest near the outfall, and decreased with distance from the source of nutrient particulates. Ammonium flux at the station nearest the diffuser (2.2 mM $m^2 day^{-1}$) was very close to the ammonium flux measured in Kaneohe Bay (1.86 mM m^2 day^{-1}). Nitrate plus nitrite did not show the same distinct progressive decrease in magnitude with distance from the outfall.

Phosphate fluxes showed even higher variability since even the direction of flux changed from station to station. Such high variability appears to indicate that net phosphorous exchange is not significantly influenced by the effluent discharge.

Data from the City and County of Honolulu show that the ratio of particulate total N to P in the sewage effluent is about 5.5, while planktonic organic material has a N:P ratio of 16:1 (Ryther and Dunstan, 1971). The ratio of total N to P fluxed from the sediment at the Sand Island stations was 8.5. The low flux ratios of N:P may be due to metabolism of exogeneous sewage rather than natural sedimenting organics. However, Nixon (1981) also has measured N:P ratios of 7:1 in benthic fluxes in Naragansett Bay, Rhode Island. He theorizes that the low nitrogen fluxes are due to sequential nitrification of ammonium produced in aerobic metabolism, diffusion of nitrate and nitrite into the lower anaerobic sediment column, and subsequent denitrification to di-nitrogen. The end product is lost from the dissolved fixed nitrogen pool, and may be the cause for nitrogen limitation in some shallow marine systems.

Approximately 10^6 moles of particulate organic carbon are discharged each day from the outfall. Extrapolation of sediment trap fluxes to the total area of impact around the outfall structure indicate that only about 10^4 moles of this particulate carbon reaches the benthic surface. If these fluxes are of the correct order of magnitude, over 99.9% of the discharged material is dispersed in the water column under the normal regime of tide and current flow. While the proportions of material cycled within the benthic boundary layer are infinitesimally small compared with total effluent volume, it is significant that there is any increased signal at all indicating that benthic nutrient metabolic process are very sensitive to nutrient inputs.

DISCUSSION

Both community structure and community function analyses are useful approaches to determining ecosystem response to nutrient subsidy. Structural analysis of benthic macrofaunal community assemblages, including measures of species composition, abundance, diversity, trophic position and biomass, are aimed at determining the ultimate effect of a large scale nutrient subsidy on macrobiota. With this approach, however, there are no provisions to link structural characteristics of the community with changes in nutrient parameters via examination of metabolic pathways that are changed by the perturbation. Unless the trophic response of the macrofaunal community is extremely visible, as was the case at the shallow Sand Island outfall, there is little or no understanding of the causative relationships between biotic structure and the altered environment.

A community metabolism approach can, however, be used successfully to assess the effect of sewage stress or other nutrient subsidies on the marine ecosystem. Quantitative determination of rates of processes that cycle materials provide a means to estimate the fate and effect of organic material within the framework of the whole system. While this type of functional approach entails a higher level of technology, it may actually be easier and quicker than the purely structural approach, since the latter requires establishment of a statistically valid sampling procedure and tedious examination of large numbers of samples. Thus, assessing and quantifying cycling of natural materials by mass balances derived from the measure of nutrient fluxes may be used to identify material sources and sinks--important information for improving the potential to predict ecosystem response to other similar situations.

We have chosen to investigate the biogeochemical processes occurring within the benthic boundary layer because the sediments act as a storage reservoir of both particulate and dissolved nutrient material. Thus, it is at the sediment-water interface that one might expect to see the most subtle or the most intense alterations to ecosystem function. At this point in our research effort, we can already conclude that nutrient regeneration in the sediments and release to the overlying water has been responsive to nutrient loading from the Sand Island Outfall.

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METABOLISM OF INTERREEF SEDIMENT COMMUNITIES

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ABSTRACT

Metabolic and nutrient fluxes of lagoon sediment communities at Enewetak, Marshall Islands, were measured using hemispheric incubation chambers. Simultaneous determination of oxygen and carbon dioxide fluxes allowed empirical derivation of an RQ value of 1.5 and a PQ of 0.8. More carbon is respired by the sediment community than is produced, and both production and respiration are closely correllated with depth. Biotic and functional comparisons between Enewetak and Kaneohe Bay, Hawaii, suggest metabolic and structural similarities between these physiographically disparate coral reef systems.

INTRODUCTION

Ecosystem analysts increasingly are turning to coral reefs as foci for studies of community metabolism. However, most researchers have concentrated on the conspicuous and highly productive perimeters of reef systems; with a few exceptions (Sournia, 1976; Kinsey, 1979; Harrison, 1981), interreef areas have been largely ignored, despite the fact that these regions usually comprise the substantial areal majority of the coral reef ecosystem. Lagoon floor communities have long been regarded as sinks for the excess production of fringing reef crests. However, neither sediment community metabolic characteristics nor overall dimensions of the functional relationship between organic sources and sinks within reef systems have been adequately described.

Enewetak Atoll in the northern Marshall Islands has been the site of numerous pioneering investigations into coral ecosystem dynamic processes. Perhaps more than any other major system, Enewetak provides an opportunity to achieve an empirical synthesis of all the main components of coral reef ecosystems for an overall budgetary analysis of organic metabolism. There remain only two major system compartments needing detailed description: the lagoon water column, and the lagoon benthos. In this report, I intend to provide sufficient data to characterize the latter compartment, and I further hope to provide impetus to encourage pursuit of the final area of uncertainty, the lagoon planktonic community.

METHODS AND RESULTS

Clear acrylic hemispheres (domes) with a radius of 0.5 meters were used to isolate sample areas for metabolic and dissolved inorganic nutrient fluxes. Oxygen concentrations were measured polarographically; carbon dioxide fluxes were calculated from temperature, pH, and alkalinity measurements (Smith and Kinsey, 1978). Preliminary alkalinity determinations confirmed Smith and Harrison's (1977) suggestion that net $CaCO_3$ production of the sand-rubble component of the Enewetak marine environment is effectively zero. Thus, the majority of CO_2 calculations were based on temperature and pH measurements alone. Dissolved inorganic nutrient concentrations were determined using standard automated techniques.

Incubations at depths down to 35 meters were performed by use of SCUBA. At depths in excess of 35 m, the submersible, Makali'i was used to emplace and sample the domes. Oxygen data were normalized to a half-sine wave model of diurnal production and integrated to establish net production (Marsh and Smith, 1978). For lack of a more accurate estimate, nighttime respiration measurements were extrapolated throughout the day. A summary of the data is given in Tables 1 and 2. Due to equipment failures, reliable CO_2 data were obtained only for two of the six sampled depth intervals, yet the close correspondence between these figures suggests a uniformity of RQ and PQ values throughout the sampled depth range.

Table 1. Summary of Enewetak lagoon sediment metabolic data. Depth in meters; respiration and gross production means ± standard deviation. Units: mmoles O_2 m^{-2} day^{-1}.

DEPTH	n	RESPIRATION	PRODUCTION	RQ	NET PQ	TRUE PQ
4	10	60 ± 12.5	64 ± 16.7			
7	26	58 ± 34.9	64 ± 36	1.5 ± 0.6 (n = 21)	1.0 ± 0.7 (n = 22)	0.8
10	12	54 ± 8.6	50 ± 7.8			
16	32	36 ± 14.2	36 ± 13.2	1.5 ± 0.6 (n = 23)	1.0 ± 0.5 (n = 24)	0.8
27	9	30 ± 7.9	27 ± 9.8			
55	5	12 ± 19.8	13 ± 21.5			

Table 2. Enewetak lagoon sediment nutrient fluxes. Depth in meters; mean fluxes ± standard deviation. Sample size in parentheses. Negative sign denotes uptake by the sediments. Units: micromoles m^{-2} day^{-1}.

DEPTH	PO_4	$NO_2 + NO_3$	NH_4
4	-47 ± 62.3 (7)	-7 ± 24.5 (7)	131 ± 174.9 (6)
7	46 ± 352.7 (22)	38 ± 111.7 (23)	206 ± 523.2 (23)
10	7 ± 16.0 (7)	-10 ± 48.4 (7)	306 ± 563.8 (7)
16	-54 ± 190.8 (25)	-7 ± 94.2 (24)	132 ± 536.3 (25)
27	-2 ± 21.2 (5)	-11 ± 61.6 (5)	86 ± 1132.8 (5)
55	-18 ± 88.9 (9)	-40 ± 53.9 (9)	-45 ± 113.2 (9)

Oxygen data are depicted in the histogram (Figure 1) by depth. The evident depth trends of both respiration and gross production are not found in the sediment nutrient fluxes (Table 2). In general, nutrient fluxes, particularly phosphate and nitrite + nitrate, are barely above limits of detection. However, as noted in previously studied lagoon floors (Harrison, 1981), both oxygen and dissolved inorganic nutrient fluxes are highly variable.

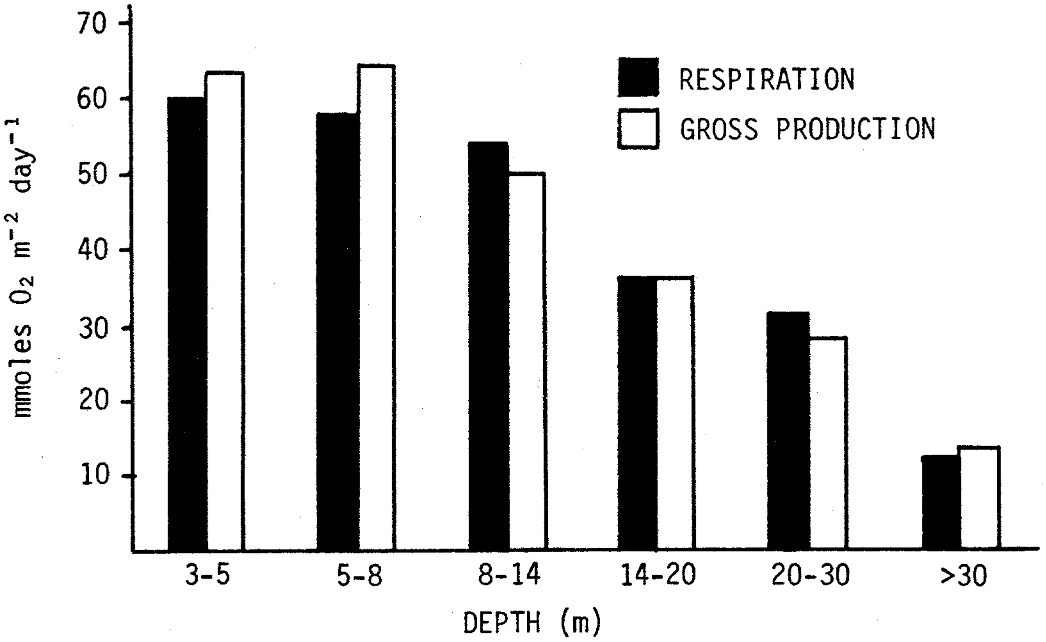

Figure 1. Histogram of pooled oxygen data: 24 hour respiration and gross production at increasing depths.

DISCUSSION

Depth dependence of community metabolism.

The evident balance between gross production and respiration throughout the depth range of Enewetak lagoon (Fig. 1) is misleading, as will be discussed subsequently. However, the figure clearly illustrates that both parameters are depth dependent. Based on the pooled data, gross production, regressed exponentially against depth, yields a decay coefficient of 0.031 m^{-1}, with a correlation coefficient (r^2) of 0.971. Similarly, the respiration decay coefficient is also 0.031 m^{-1}, with r^2 equal to 0.985. The close adherence to an exponential model establishes the correlation of sediment community metabolism with incident light. Unfortunately, the lagoon extinction coefficient has not been determined, but in the open ocean immediately east of Enewetak, the extinction coefficient is 0.045 m^{-1} (Colin, *et al.*, in prep.). Since the lagoon water column contains more particulate material than does the open ocean, the lagoon extinction coefficient cannot be lower than 0.045 m^{-1}. Thus, although production and respiration of lagoon floor communities are clearly light-driven, benthic community activity is increasingly efficient at greater depths.

Lagoon floor heterotrophy.

Assuming that the empirically determined values for RQ and PQ are uniform throughout the lagoon floor, production and respiration can be expressed as carbon equivalents. If measured oxygen fluxes are converted to carbon equivalents by use of RQ and PQ values, it turns out that more carbon is respired by the system than is produced, and the sediments are distinctly heterotrophic. Although no direct assays have been conducted, the RQ value of 1.5 indicates a substantial component of anaerobic metabolism in lagoon sediment communities. Kinsey (1979) likewise derived high RQ values for sand-rubble systems, also invoking anaerobic metabolism as an explanation. Net carbon deficits for each depth interval are presented (Table 3) along with depth distribution data from Emery, et al (1954) to derive a mean carbon requirement for Enewetak sediment communities of 41 mgC m^{-2} day^{-1}.

Table 3. Lagoon sediment community carbon deficits.

DEPTH (m)	AREA (km^2)	CARBON DEFICIT (mgC m^{-2} day^{-1})	AREAL DEFICIT (kg C)
3-5	22.8	121	2,759
5-8	22.8	74	1,687
8-14	25.4	216	5,486
14-20	50.8	110	5,588
20-30	40.6	138	5,603
>30	769.6	22	16,931
		Total lagoon deficit	38,054 kg C
		Total lagoon area	932 km^2
		Mean deficit	41 mgC m^{-2} day^{-1}

Preliminary calculations based on organic carbon production of windward reefs (Smith and Marsh, 1973) indicate that excess production of these reefs is probably more than sufficient to provide the carbon requirement of the sediment community. However, in the absence of detailed information on metabolism in the lagoon water column, mechanisms and precise characteristics of the trophic relationship between organic sources and sinks within Enewetak Atoll must remain speculative.

Macroinfaunal influences.

Inspection of the summarized results (Tables 1, 2) reveals substantial variability in both metabolic and dissolved nutrient flux data. Previous sediment metabolic surveys have related high levels of parameter variability to the presence of actively bioturbating infaunal communities in interreef lagoonal systems. In Kaneohe Bay, Hawaii, alpheid shrimps thoroughly mix the upper 30 cm of sediments, greatly enhancing rates of sediment community metabolism and nutrient cycling (Harrison, 1981). The lagoon floor at Enewetak contains an extensive population of callianassid shrimps actively turning over large volumes of sediment daily. Callianassid burrow systems penetrate in excess of 2 m below the sediment surface (Colin, et al., in prep.), providing direct routes for transport of organic detritus into the sediment column, and suggesting mechanisms for stimulation of the apparently high levels of anaerobic metabolism inherent in these communities. In this respect, and in others, there is a remarkable correspondence between both structural and functional characteristics of widely disparate reef ecosystems.

The substantial physiographic differences between a high island system such as Kaneohe Bay and an oceanic reef like Enewetak are reflected in the different levels of organic and inorganic supply to which their respective biota must adapt. High island reefs must withstand heavy nutrient and organic loading from terrigenous runoff; by contrast, external supply to atolls is minimal. Despite such opposition of material supply regimes, reef structure in the two environments is surprisingly similar. To be sure, systematic and morphological differences in coral reef communities are prevalent, but both oceanic margins are metabolically and structurally alike, as are the lagoon patch reefs. It would appear that the major metabolic differences between high island and oceanic reef systems are confined to interreef and possibly planktonic compartments. Reliable estimates of RQ and PQ values for Kaneohe Bay sediment communities are not available, so direct comparisons of Enewetak and Kaneohe Bay carbon metabolism cannot be made. However, the near-zero net balance of aerobic metabolism of Enewetak sediments (Fig. 1) contrasts with a daily oxygen deficit at the Kaneohe Bay floor of roughly 9 mmoles m^{-2}. The increased heterotrophy of the Kaneohe sediment community reflects the abundance of systemic material supply.

Despite metabolic and visual dissimilarities, the lagoon floors of Enewetak and Kaneohe Bay are functionally and biologically comparable. Such correspondence between major components of disparate reef systems supports the validity of general models of coral reef ecosystems.

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