CORAL REEF POPULATION BIOLOGY

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Edited by

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Dedicated to the memory of

EDWIN W. PAULEY

Results of the 1983 Summer Research Training Program
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EDWIN WENDELL PAULEY

JANUARY 7, 1903-JULY 28, 1983

DEDICATION

This volume is dedicated to the late Edwin W. Pauley, in recognition of the significant role that he played in the founding and development of the Hawaii Institute of Marine Biology on Coconut Island. In 1947, Mr. Pauley invited the University of Hawaii to establish a marine laboratory on Coconut Island (Moku o Loe) located in Kaneohe Bay, Oahu, Hawaii. This offer was accepted and Dr. Robert R. Hiatt was designated as the first Director of what was then known as the Hawaii Marine Laboratory. The original laboratory was housed in buildings donated by the Pauley family. Mr. and Mrs. Pauley took a very personal interest in the laboratory and they established close ties with the University community. This was especially apparent during the annual luncheon when they would invite the entire laboratory staff to their home on Coconut Island. Those who worked at the laboratory during this period have many fond memories of the Pauley's gracious hospitality at these gatherings. Mr. Pauley continued to be a good friend and provided considerable financial support to the laboratory over the years. He frequently visited the laboratory when he was in residence on Coconut Island in order to check on progress of various research projects and determine how he might help. When the original laboratory building was destroyed in a fire during 1959, he offered assistance and furnished funds to enable the University of Hawaii to begin construction of the present laboratory building which was completed in 1966. The laboratory continued to grow and prosper, until today it is one of the world's leading tropical marine research institutions.

At the marine laboratory we knew Mr. Pauley as a friend and as a person who had an abiding humanitarian interest in the advancement of science and in higher education. Mr. Pauley was, however, unique in many ways. He was a very successful businessman and recognized widely as an accomplished economist and diplomat. He had a distinguished career in government, education and private industry. He was a talented educator, a skilled educational administrator, an enlightened and judicious philanthropist and an enthusiastic promoter of arts and athletics.

Edwin Wendell Pauley was born in Indianapolis, Indiana, January 7, 1903, the son of the late Elbert L. and Ellen Van Patten Pauley. He graduated from Georgia Military Academy, College Park, Georgia, in 1918, enrolling the following year at Occidental College, Los Angeles, where he later served as a trustee.

After two years at Occidental, he transferred to the University of California at Berkley, receiving his Bachelor of Science degree from the College of Commerce and Business Administration in 1922.

His lifetime contributions in the field of education were enormous. Following graduation Mr. Pauley spent a year on the teaching staff at the University of California, Berkeley. His interest in education remained strong throughout his life, even though his primary occupation was in business and government service. He was appointed a Regent of the University of California in 1939. He was reappointed for a second sixteen-year term in 1954, and served as Chairman from 1956 to 1958 and from 1960 to 1962. He worked hard to shape the University of California into one of the world's greatest institutions of higher learning. In 1960-1961 Mr. Pauley played an active role in raising funds to establish KCET, Los Angeles' educational television station. He was awarded honorary degrees from the University of Santa Clara, and Pepperdine College, Los Angeles.

Mr. Pauley's principal business interest was the oil industry and in real estate development. After his teaching experience at the University of California, he became associated with his father in the Pauley Oil Company. In 1927, he organized the Petrol Corporation and operated it until 1948. He sold this company and subsequently engaged in the oil business under his own name. He did likewise in real estate and operated both businesses until the incorporation of the Pauley Petroleum Inc. in 1958. Mr. Pauley was involved in a variety of other business activities. He was a partner in the Los Angeles Rams Football Club, and a principal in the Riverside International Raceway and the Valley Music Theatre, Los Angeles. He was a director of the San Francisco - Oakland Television, Inc., which operated KTVU. In 1945, Mr Pauley purchased controlling interest in the Pacific Tire and Rubber Co. In 1951 he became interested in developing real estate in northern California and subsequently developed shopping centers and industrial parks in Southern California. The development of Hastings Ranch in Pasadena is an example. In addition, Mr. Pauley was a member of the Board of Directors of Western Airlines.

Mr. Pauley was an organizer and a leader in both business and government. In 1933, during the Great Depression, he represented the independent oil producers in the planning and coordinating committee under the National Recovery Act. From 1934 to 1938 he was president of the Independent Petroleum Association. He served as representative of the Governor of California at the Pan American High-

way Conference in 1939, and in the same year served as the Special Representative of the Governor of California on the National Resources Commission. With the approach of World War II, oil supply became vital to the defense of the United States. Mr. Pauley was appointed Special Representative of California on the Interstate Oil and Compact Commission in 1940 and was an organizer and member of the Defense Council of the State of California in 1941. In 1940 he was asked by President Franklin D. Roosevelt to serve as his Special Representative, acting as liaison between the United States and Great Britain. In 1941 he was also appointed by President Roosevelt to formulate plans for the Coordinator of Petroleum Industry, and later that year carried out missions in Europe as Special Representative of the Petroleum Coordinator for War. Mr. Pauley was economic advisor for the United States Government at the Potsdam Conference in 1945. From 1945 to 1946 he was the United States Representative on the Allied Commission on Repatriations, with the rank of Ambassador. From 1947 to 1948 he was Special Assistant to the Secretary of the Army.

In the Los Angeles community, Mr. Pauley's civic activities included the following: Director and Treasurer of the Hollywood Bowl Association, Member of the Board of Directors of the Los Angeles Chamber of Commerce, Member of the Board of Directors and President of the Los Angeles World Affairs Council, Member of the Southern California Committee for the Olympic Games, and Vice Chairman of the Board of Trustees of the California Museum Foundation. Mr. Pauley is one of the founders of the Los Angeles Music Center, which was established in 1964. He was an active supporter of the San Gabriel Valley Council of the Boy Scouts of America. He was a moving party and principal donor of land and new building which is the headquarters of the San Gabriel Valley Council. Mr. Pauley's other philanthropies included substantial contributions to the University of California.

Edwin Pauley died in July 1981 at the age of 78.

There is adequate evidence that Mr. Pauley was a man of great wisdom and vision who demonstrated a unique talent to identify areas of high potential success and to develop these areas. Perhaps it is not surprising that he recognized the importance of the marine sciences in the late 1940's some two decades before this area achieved national prominence. He had an abiding humanitarian concern for the potential role of marine science to address societal needs, particularly food production and resource management. Mr. Pauley correctly antici-

pated the important and unique role that the University of Hawaii was to play in the development of this area of research.

All of us at this laboratory recognize that Mr. Pauley gave up his privacy on Coconut Island when he invited the University to establish laboratories and share his beautiful estate. It is clear that he wanted this institution to grow and prosper. In this spirit, we have initiated a major summer research training program and have invited students and scientists from all over the world to participate.

The traditions started by Mr. Pauley have been perpetuated by his family and through the Edwin W. Pauley Foundation. Close ties have long existed between marine scientists from throughout the University of California system and HIMB due to joint programs initiated by Mr. Pauley. Mr. Pauley's wife, Barbara, takes an active, ongoing interest in the laboratory and has done much to promote marine science in Hawaii on her own initiative.

This volume represents only a tiny fraction of the research and training that has occurred at HIMB as a result of Edwin Pauley's foresight and generosity. The Hawaii Institute of Marine Biology is living evidence of Mr. Pauley's commitment to excellence in higher education and research in the marine environment. In a small way this dedication is a grateful recognition of our debt to this man.

Foreward

This volume is the result of research done by a group of highly motivated scientists and students who gathered at the Hawaii Institute of Marine Biology on Coconut Island in Hawaii during the summer of 1983 to participate in a program titled "Coral Reef Population Biology". This was officially labeled as a graduate course in zoology, but it was actually much more.

In an effort to extend the influence of the University of Hawaii as an institution striving for excellence, a number of the institute's staff who had participated in earlier, similar programs, conceived the idea for this one. They planned to make maximum use of the unique laboratory facilities and reef communities in the tropical environs of Hawaii, with the additional goal of making a substantial contribution to graduate education in marine biology.

The setting on Coconut Island contributed greatly to the success of this program. The island is in a protected bay with a variety of biotopes and is surrounded by a fringing coral reef that is protected as a marine sanctuary. This luxuriant reef is but a few feet from a well equipped laboratory, and only a few miles from a major university with even more sophisticated apparatus, research library, etc.

This program was all made possible through the vision and generosity of the Pauley Foundation, the University of Hawaii Foundation and the University of Hawaii Sea Grant Program. Not only was funding supplied, but also a great deal of personal interest and concern was shown by Mrs. Edwin Pauley and Mr. William Pagen of the Pauley Foundation, President Fujio Matsuda of the University of Hawaii (for the U.H. Foundation) and by Dr. Jack Davidson, Director of the Sea Grant Program at the University of Hawaii.

The format for this program consisted of a series of lectures presented by a group of outstanding scholars with a broad spectrum of approaches to the subject. Next followed intensive research through small group and individual projects. Because of the enthusiasm of the organizers for the high quality and intense interest of the applicants, the program surpassed the original expectation of participation by 12-15 students, and resulted in a final total of 29 students and 11 senior staff members. The atmosphere was scholarly, dynamic and

creative. The students had varied backgrounds - some having never observed the living corals or tropical environment. New techniques and approaches were introduced which allowed students to trace growth processes in order to elucidate reproductive regimes, as well as to explain ecological relationships in a variety of corals and organisms in the coral reef community. Seven of the students were already enrolled as graduate students at the University of Hawaii. Others came from six mainland states, Australia, the Philippines, Japan, Guam, Mexico and the United Kingdom. The students became a friendly, stimulated and strongly motivated group, and student-instructor relationships were highly conducive to the production of ideas that evolved into fruitful research. Each student arrived at the course with an approved research topic, having already communicated with one of the instructors.

Most of the research described in this volume was accomplished during the period extending from the first week in June until mid-August. Interests developed and nurtured during the summer persisted and several of the students stayed on to be part of the graduate program at the University of Hawaii in order to pursue the research that they had initiated in this course. Other students and instructors acquired interests and developed collaborative relationships with members of our staff. This endeavor was strongly influenced and given direction by the core staff consisting of Robert Kinzie, Paul Jokiel, Peter Glynn, George Losey, Robert Richmond, and David Krupp, as well as by some of the student participants in the course.

This volume stands as testimony that we can make substantial contributions to graduate education and advanced research training by exposing students to a rich tropical biota with a stimulating format of lectures, and at the same time advance our own knowledge of the particular discipline through research. It was my distinct privilege to have been associated with the outstanding group of scholars whose concerted efforts produced this work. We anticipate that this will be an annual program, and that it will continue to serve as an example of a unique and rewarding approach to graduate education.

Philip Helfrich

Coconut Island

6 June 1985

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We also wish to express appreciation to Bob Young, Frank Stanton and workers in the HIMB shop for many hours of uncomplaining assistance. They truly went beyond the required to help everyone have a profitable summer.

In addition to those participants on the regular staff, we also wish to acknowledge several others who volunteered their time to give special lectures and presentations for the program. These include Steve Smith, Satoru Taguchi, Ed Laws, and Kitty Ageqian, all of the Oceanography Department of the University of Hawaii, and Paul Ekern of Water Resource Research Center. We also wish to acknowledge all of the regular staff at The Hawaii Institute of Marine Biology who willingly gave advice and help upon request.

CORAL REEF
POPULATION BIOLOGY

Graduate Research and Training

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Hawaii Institute of Marine Biology

University of Hawaii

Structural Reefs of Kaneohe Bay, Hawaii: An Overview

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Abstract

The physiography and structural reefs of Kaneohe Bay, Hawaii are described in a synthesis of existing literature. The geologic background of the Kaneohe region is outlined and the watershed described in terms of its geography, climate and hydrology. Kaneohe Bay is divided into inshore, inner bay and outer bay zones for the discussion. The inshore zone consists of shoreline features, the fringing reef, and Mokolii Island. The inner bay includes the lagoon proper, with its array of patch reefs, and Moku o loe Island. Considerable variation occurs along the long axis of the inner bay necessitating its division into 3 sectors (Southeast, Central, Northwest) in the discussion. The outer bay is composed of the barrier reef complex, which is bisected by channels at either end. The barrier reef is described in terms of 5 physiographic zones based on geomorphology and substrate. The effects of human activities such as watershed modification, direct reef alteration, and sewage discharge on the reefs of Kaneohe Bay are also reviewed.

1. KANEOHE BAY REGION

1.1 Introduction

The Kaneohe region consists of a watershed and semi-enclosed embayment on the NE coast of Oahu, Hawaii (Fig. 1). The area is delineated on the landward side by the near vertical cliffs of the Koolau mountain range. The seaward limit of the region extends to the base of the steep reef slope of the barrier reef fronting Kaneohe Bay.

1.2 Geologic Background

The geology of the Kaneohe region was accurately described by Stearns and Vaksvik (1935). The once massive Koolau shield volcano is one of two Pliocene volcanoes forming the island of Oahu. Fluvial erosion, over the centuries, cutback the predominantly basaltic lava flows, leaving only three ridges extending across the present coastal lowlands. One of the ridges reappears as an island (Moku o loe or Coconut Island) in the bay, while a remnant basaltic sea stalk forms another island (Mokolii, or Chinaman's hat) at the northern end of the bay. Other ridges were worn away by the rains borne on the near constant trade winds and the valley heads coalesced to form an almost continuous cliff face (= pali of Hawaiian language) up to 800 m high.

Along the southern perimeter of the Kaneohe region, the drainage basin is defined by a breccia ridge which remains from the main volcanic vent. On Mokapu peninsula, which partially encloses the SE portion of the bay, the more recent Honolulu series of eruptions is represented by a volcanic cone about 225 m high. The coastal lowlands, which comprise over 60% of the terrestrial portion of the Kaneohe region, are made up of the deposited materials washed down the eroding valleys of the windward Koolau range. Of this alluvium deposition, 70% is older, more consolidated, and less permeable in nature, extending from an elevation of about 200 m down to marine sediments in the present day bay. From about 70 m above sea level and down to the bay, a layer of younger, reworked alluvium that is less consolidated and more permeable overlies the earlier deposits (Takasuki et al., 1969).

Sea level fluctuations due to periodic glaciation during Pleistocene and Holocene epochs subjected much of the Kaneohe region alternately to exposure and submergence, leaving a series of stream and wave cut terraces (Stearns, 1974). During lower stands of the sea, streams eroded winding paths through the alluvial plain. The current lagoon basin and the position of the two channels through the barrier reef are probably the result of stream valley cutting during periods of lowered sea level (Hollett, 1977). Fluvial erosion, in conjunction with subaerial erosion, led to the accumulation of sand in formation of beach ridges and dunes. Lithified dune material presently forms a portion of the barrier

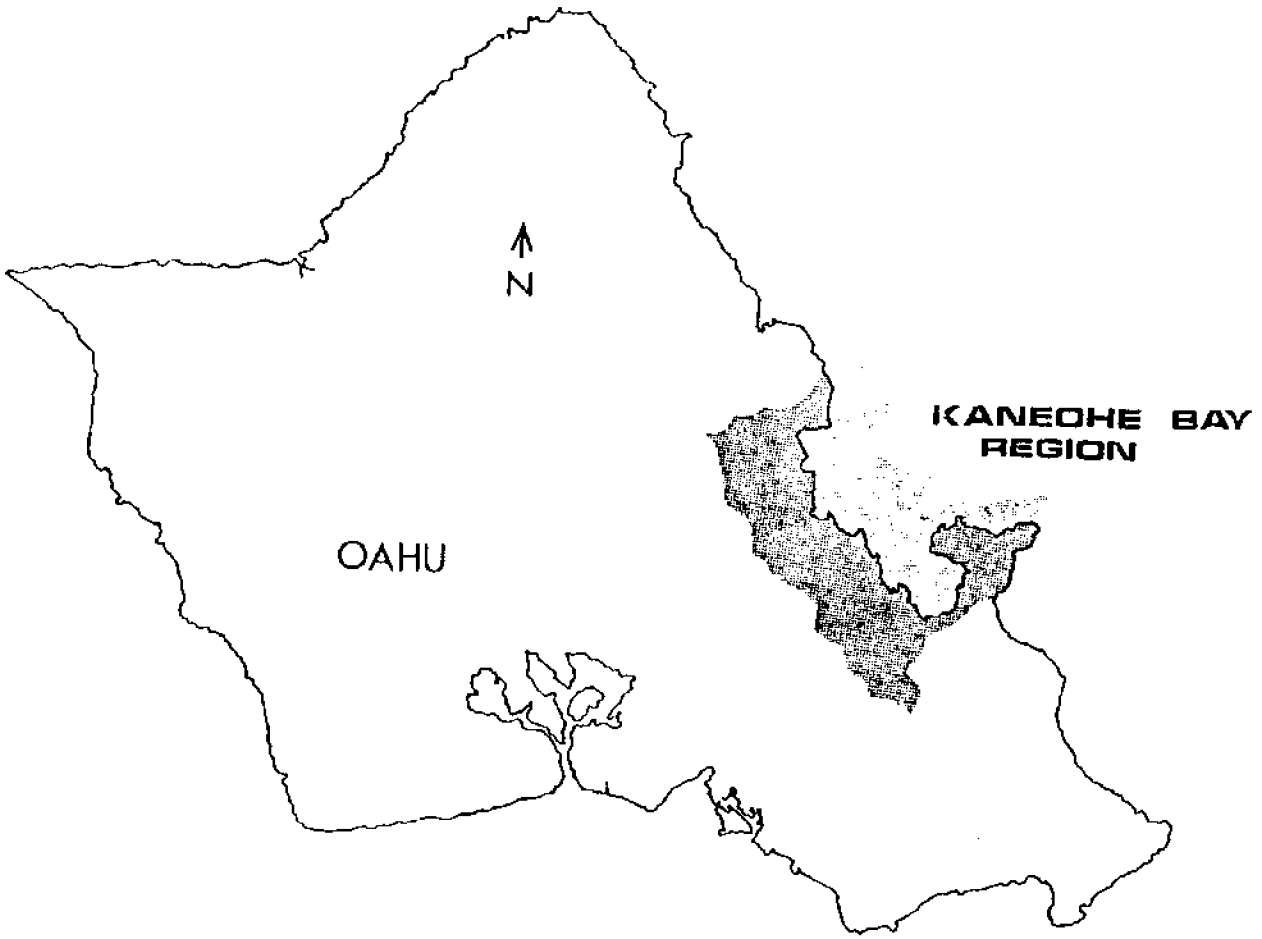

Fig. 1. Kaneohe Bay Region: showing watershed and bay.

reef ridge and its exposed island (Kapapa) and may underlie more extensive portions of the barrier reef ridge area (Roy, 1970).

During interglacial periods, reef growth kept pace with rising sea level, forming layers of reef and reef derived sediments 30 to 300 m thick which overlie the submerged alluvial formations (Stearns and Vaksvik, 1935). The present day reefs in Kaneohe Bay are represented by a fringing reef around the currently emerged shoreline, a barrier reef formed on an ancient ridge of deposited sediments and patch reefs of less certain origin and structure. The lagoon basin and barrier reef channels represent drowned stream valleys that are being progressively infilled by terrigenous sediments eroded from the surrounding watershed and reef sediments transported off the extensive barrier reef (Roy, 1970). More recent human disturbances of the Kaneohe region watershed and reefs have increased the rate at which the infilling of the bay is occurring (Roy, 1970; Hollett, 1977).

1.3 Watershed

1.31 Geography

The Kaneohe drainage area covers about 97 km^2 (Smith et al, 1981) although earlier studies calculated a figure of 46.6 km^2 (Chave, 1973). The Koolau ridgeline defines much of the watershed and reaches heights of up to 800 m. The coastal lowlands, which make up most of the watershed, are rolling hills 5 to 250 m in elevation, bissected by the three basaltic ridges crossing the plain. The soils of Kaneohe watershed have been classed into 9 types by Cline (1955) with lithosols and humiclatosols accounting for over 80% of the material. Erosion of these soils produces stream transported sediments of sand (10-45%), silt (25-55%), and clay (20-50%) sized particles (Fan, 1973).

1.32 Climate

Recent rainfall estimates for the area average about 2400 mm yr^{-1} for the watershed and 1400 mm yr^{-1} for the inner bay (Smith et al., 1981). The highest month's rainfall occurs in August, but maximum daily rainfall will usually take place in winter during storms which counteract the tradewind flow. Although yearly differences are large, a wet season from October to May is normally experienced. Evapotranspiration in the watershed averages about 1100 mm yr^{-1} and 1700 mm yr^{-1} in the inner bay (Takasaki et al., 1969). Combining these figures of rainfall and evapotranspiration gives an estimate of 117 x 10^6 m^3 yr^{-1} of average net fresh water input into the watershed and inner bay (Smith et al., 1981).

Air temperature ranges between 20 °C and 28 °C throughout the year. Winds blow out of the NE about 70% of the year, averaging about 10-11 knots and do not exhibit marked seasonality. These fairly constant trade winds force maritime air against and up the Koolaus creating an orographic uplift which results in large amounts of precipitation being released from the moist, rising air along a distinct gradient. The outer margins of the bay receive only 75-100 mm of rain each year while the ridge crest experiences a deluge of 380-500 mm average annual rainfall (Taliaferro, 1959). Occasional storms, not usually associated with tradewinds conditions, may cause locally violent, heavy rainfall.

1.33 Hydrology

The Kaneohe watershed is the source of fresh water flow, with accompanying dissolved and suspended materials, that enters Kaneohe Bay in the form of base stream flow, flood flow, and groundwater discharge. A review of the water quality and sediment situation for the streams and watersheds of Kaneohe Bay is provided in the Kaneohe Bay Water Resource Data Evaluation (Sunn, Low, Tom, and Horn, 1976). The dozen or so streams entering the bay presently produce a net runoff of 94 x 10^6 m^3 yr^{-1}, which excludes the 23 x 10^6 m^3 yr^{-1} of water which is diverted out of the watershed for domestic and agricultural use (Takasaki et al., 1969). Of the net runoff, over 50% enters the NW portion of the bay, while 25% is discharged into the SE basin (Bathen, 1968). Seven perennial streams provide most of the surface water discharge into the bay with an estimated long term average load of 200 tons per day of terrigenous sediments. The average annual sediment yield was estimated to be 37,000 tons (Jones et al., 1971). However, large volumes of runoff are a direct response of the short, steep stream channels to periods of intense rainfall. These sharp flood peaks result in huge amounts of sediment transport into the bay waters, with up to 8.9 X 10^6

kg per day estimated for one of the larger streams in flood (Fan, 1973). Detailed analysis of water quality, runoff, and sediment load for Kaneohe Bay were carried out for both dry season and wet season periods (Yonge et al., 1976; Law et al., 1976).

Agricultural and urban development which include natural vegetation removal, an increase of impervious surfaces and the channelization of stream courses has exacerabated the fresh water discharge and sediment load problem of Kaneohe Bay (Banner, 1974; Maragos and Chave, 1973). Coincident with increasing population growth and urbanization in the Kaneohe Bay watershed was the increasing amounts of sewage previously disposed of into the bay. Over 22,000 m^6 day^{-1} of sewage was estimated to have been entering Kaneohe Bay until 1978. At that time the effluent was diverted to an ocean outfall on the SE side of Mokapu penninsula. Smaller amounts of secondarily treated sewage continue to enter the north end of the bay (Smith et al., 1981).

Groundwater seepage into Kaneohe Bay is a function of the high permeability of the surface soils and rocks of the watershed along with the excess rainfall over evapotranspiration. The drainage area is considered to have four regions of somewhat different groundwater characteristics and a total discharge of about 22 x 10^6 m^3 d^{-1} of fresh water into the bay (Cox and Fan, 1973).

2. Physiography of Kaneohe Bay

2.1 Introduction

Kaneohe Bay, the largest sheltered body of water in Hawaii, forms a semi-enclosed embayment that contains components of both estuaries and coral reefs (Fig. 2). Along a northwest (NW) to southeast (SE) axis, the bay is approximately 12.8 km long and 4.3 km wide, enclosing a surface area of 60.56 x 10^6 m^2 at mean sea level (Bathen, 1968). About 2/3 of its length is open to the ocean, but protected by a barrier reef that is bisected by navigable channels at either end. Behind the barrier reef complex is a lagoon with scattered patch reefs. The SE portion of the lagoon is formed into a somewhat isolated basin by the Mokapu peninsula and Moku o loe (Coconut) Island. Along the bay's shoreline a near continuous fringing reef of variable extent borders the land.

The total volume of the bay waters out to the outer margin of the barrier reef was determined by Bathen (1968) to be 380.6 x 10^6 m^3. There is a net transport of ocean water over the barrier reef and into the bay, driven by wave action. Much of this input is deflected and flows out the adjacent channels. Current patterns are overall very consistent and are governed by tidal flow, winds, wave action and bathymetry (Bathen, 1968). The NW bay has fewer flow restrictions and experiences more active circulation then the rest of the bay, especially the restricted SE basin which has sluggish circulation and a slow rate of exchange (Bathen, 1968).

Average tidal variation for Kaneohe Bay is 0.68 m d^{-1} with a maximum range of 1.1 m, although wind direction and velocity will appreciably change the time and height of the tides. In his comprehensive study of the oceanography of Kaneohe Bay, Bathen (1968) determined that bay waters range in temperature from 20-27 °C around a mean of 25.1 °C. Salinity ranged between 33-35 parts per thousand, very near the oceanic average. More recent investigations (Smith et al., 1981) provide detailed information on lagoon water composition.

Kaneohe Bay has been dissected by most investigations into the area along both its long SE to NW axis and along a shorter profile from land to open ocean. In discussing the physiographic makeup of the bay, it is most illustrative to describe the bay in cross section across its narrow axis, moving from those areas most affected by terrestrial influences to those dominated by the oceanic environment. Superimposed upon this zonation there is a perpendicular gradient from SE to NW in the lagoon based upon circulation and ocean water exchange, wave activity, freshwater runoff and sedimentation.

Across the land to sea profile of Kaneohe Bay, three physiographic zones are distinguished: the inshore, inner bay, and outer bay zones. The inshore zone is composed of the marine/land interface at the shoreline, the fringing reef system and Mokolii Island. The inner bay zone consists of the lagoon proper, which is divided into SE, Central and NW sectors, the array of patch reefs, and Moku o loe Island. The outer bay is made up of the barrier reef complex, including

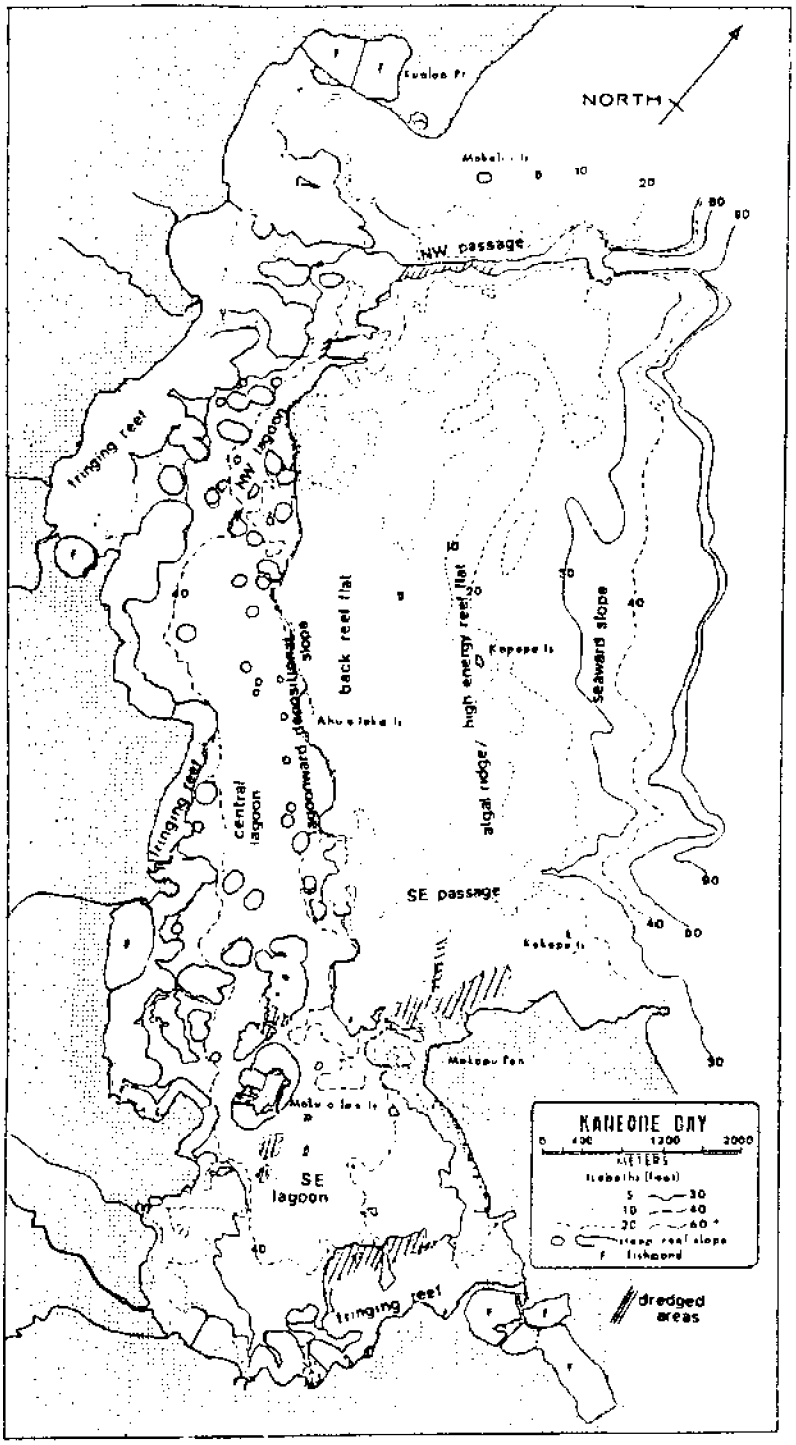

Fig. 2. Kaneohe Bay: Physiographic Zones and dredged areas.

Kapapa island, and the two channels bisecting the barrier reef. The components of each of these zones will be described in terms of their structure and substrate with relation to the degree of terrestrial and oceanic influences acting upon them (Fig. 3).

2.2 Inshore Zone

2.21 Introduction

The near shore margins of Kaneohe Bay consists of both natural and artificial shoreline including beaches and promontories, stream mouth deltas, mangrove swamps, fishponds, seawalls, and fill land. Extending various distances out from the shore is a near continuous border of fringing reef composed of an inshore flat, ridge crest and steep slope. At the NW end of the bay, Mokolii Island is situated on the wide fringing reef around Kualoa point and is therefore included in this discussion of the inshore zones.

The near shore areas of Kaneohe Bay are heavily influenced by the form and processes of adjacent terrestrial regions. Most important among these influences are the position and size of the streams emptying into the bay. The nature of the coastal geomorphology bordering the bay also affects the character of the nearby shore areas, as does proximity and extent of human alterations in coastal land use. Direct oceanic influences are very low in the inshore zone except in the more exposed NW section of the bay.

2.22 Shorelines

Of the approximately 28 km of shoreline along Kaneohe Bay, large portions are bounded by seawalls and landfill. This is especially true in the SE basin adjacent to the highly urbanized areas and the military facility at Mokapu penninsula. Prior to the creation of these recent artificial shore features, about 33 Hawaiian fishponds lined the bay, enclosing large portions of the reef flat and accounting for approximately 30% of the bay's shoreline (Aecos, 1981). Most of these ancient fishponds have fallen into disrepair or have been filled in to create additional bay front property, although 12 remain intact with 2 still actively used for aquaculture (Devaney et al., 1976).

Natural shorelines within the bay reflect the abundance of sediment loaded runoff and lack of wave activity. Where the deeply weathered basaltic ridges reach across the coastal lowlands to the bay, a 6 to 7 m high cliff or terrace drops steeply down to the inshore edge of the fringing reef. Against the base of these cliffs are accumulations of gravel talus along with fine terrigenous sands and mud. The low amount of wave action disturbing the bay coast allows for the buildup of small deltas at the mouth of the numerous small streams entering the bay. The deltas are composed of silt and sand sized particles eroded from the drainage basin and transported downstream, especially during periods of intense rainfall (Fan, 1973). The introduction and spread of mangroves in some of the stream openings have encouraged the deposition of sediments and the formation of swamps, altering the formerly estuarine conditions of these low lying areas (Walsh, 1967).

The remaining undisturbed shoreline along the inner edges of the reef flat consists of mixed deposits of terrigenous silt and fine to medium grained calcareous sand with some basaltic gravel (Fan, 1973). Extensive deposits of relatively clean calcareous beach sand are uncommon in Kaneohe Bay. Kualoa point at the extreme north end of the bay is a depositional plain and beach of calcareous sand accretion which forms a recurved spit to the south and west, nearly separating Moilii Fishpond from the bay (Aecos, 1981). Additional sand beaches formerly occupied much of the NW side of Mokapu Penninsula which has been extensively altered by dredging and filling (Devaney et al., 1976).

2.23 Fringing Reef

2.231 Fringing reef flat

A fringing reef flat averaging less than 1 m deep extends 300-800 m off most of the Kaneohe Bay shoreline (Aecos, 1981). Large portions of the reef flat, especially in the SE basin have been dredged to cut small boat channels, accomodate larger ships, and form a seaplane landing area. The nearly continuous band of reef is widest in the NW sector of the bay and also slightly deeper there. Interruptions in the reef flat occur where fresh water stream runoff and sediments have cut, or maintained open, shallow channels of silt and sand (Aecos, 1981).

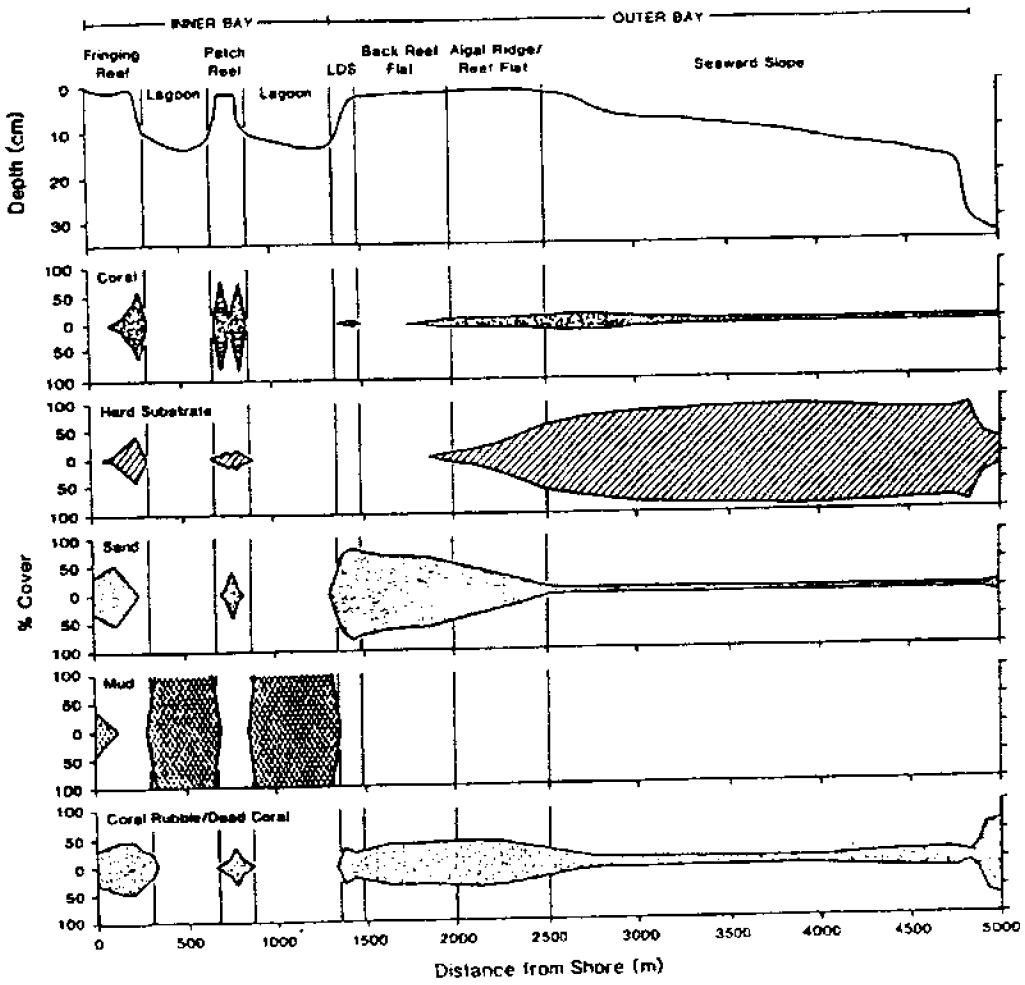

Fig. 3. Cross section of Kaneohe Bay: Physiographic zones and substrate composition. (Adapted from Smith and Kam, 1973).

Substrate on the stable environment of the fringing reef flat gradates from nearshore terrigenous sands and muds to poorly sorted coral rubble and boulders towards the reef margin, with a corresponding increase in the percentage of calcium carbonate in the sediments (Fig. 3; Smith and Kam, 1973). The inshore fine sediment deposits form a gradient from the SE basin, where they are mainly organic muds, to the NW coast, where inorganic sands predominate. Generally less than 5% of the bottom is live coral or hard substrate (Smith and Kam, 1973). At the reef flat edge, dead coral and rubble become consolidated to form a slight ridge or crest, except where disrupted by stream sediment channels (Roy, 1970).

The fringing reef flat receives little ocean wave energy, except those areas in line with the channels through the barrier reef, especially in the NW sector of the bay where the barrier reef is slightly deeper. The greatest fluctuations in temperature and salinity within the bay occur on the shallow fringing reef flats. In areas at stream mouths, water temperatures annually range from 19 to 28 °C and salinity from 31 to 35 parts per thousand. On wide reef flat expanses, low tide exposure combined with reduced circulation and high insolation may lead to extremes of 29 °C temperature and 36 parts per thousand salinity (Bathen, 1968).

2.232 Fringing reef slope

The outer fringing reef margin consists of a consolidated reef rubble crest and algal ridge at a depth close to MLLW, except in the NW bay where it is slightly deeper (Aecos, 1981). The ridge drops vertically down about 1 m to a narrow shelf and the main slope face then continues down at an angle of approximately 25° to depths of 9 to 12 m (Roy, 1970), although portions of the reef slope may be as steep as 45° (Maragos, 1972). Upper sections frequently have large blocks of reef rock which have slumped part way down the slope. Occasional reef blocks and coral rubble talus are mixed with increasing proportions of soft substrate further down slope. The fine sands and silt begin to predominate as slope angle decreases and then flattens out into the muds of the lagoon floor (Aecos, 1981).

Live coral cover on the fringing reef slope varies considerably within the bay. In the NW sector, where circulation and mixing are good, reef corals occur in greater abundance and to greater depths than on other fringing reef slopes (Maragos, 1972). Moving southward along the reef margin, live coral cover decreases and proportions of dead coral, coral rubble, and sediments correspondingly increase (Smith and Kam, 1973). The effects of episodic disturbances (Banner, 1968) as well as continued degradation of near shore reefs from pollution and sediment laden discharges (Banner and Bailey, 1970) are responsible for this trend. In the SE basin, reduced circulation and mixing coupled with silt and sewage pollution pressures have decimated what was once some of the finest coral gardens in Hawaii (Devaney, 1976; Banner, 1974). The fringing reef slopes have been reduced to a dead coral framework covered in a blanket of silt and bioeroded by filter feeding organisms (Maragos, 1972). Recent surveys indicate this situation may be reversing with the discontinuation of sewage disposal into Kaneohe Bay since 1978.

2.24 Mokolii Island

Although not usually associated with the inshore zone, Mokolii Island (Chinaman's Hat) is situated on the fringing reef flat around Kualoa point at the far NE end of Kaneohe Bay. This approximately .015 sq. km island is a 65 m high remnant seastack composed of bedded lavas from the Koolau volcano. The shallow reef flat around Mokolii consists of sand and rubble with occasional outcrops of reef rock and dead coral heads. In the lee of the island, a layer of sandy silt fans out across the reef flat (Aecos, 1981). The exposed windward side receives the impact of considerable amounts of wave energy which has led to the creation of small wave cut beaches and large basalt boulder talus. Seaward of the island, a mixed bottom of sand, coral rubble, and hard limestone outcrops with little live coral cover increases in relief towards the depths of the fringing reef slope and the NW (Mokolii) channel (Aecos, 1981).

2.3 Inner Bay Zone

2.31 Introduction

The inner bay zone of Kaneohe Bay can be considered to include everything seaward of the fringing reef slope up to the lagoon side of the barrier reef

complex, and the lagoon proper with its array of patch reefs as well as Moko o loe Island (Coconut Island).

The lagoon has been divided into three sectors based on the gradient reflecting differences in circulation and the relative degree of oceanic influence along the SE to NW axis (Bathen, 1968; Smith et al., 1981). The SE lagoon is a semi-enclosed basin of restricted circulation and exchange with the rest of the bay and ocean waters. Runoff from three major streams and, until recently, flow from two sewage outfalls discharge into this sector. The central lagoon is bounded to seaward by the barrier reef complex and receives a substantial influx of ocean water over the reef and through the passes, with an additional moderate input of stream water and sediments from the bordering terrestrial area. The NE lagoon is more nearly oceanic in its character with extensive mixture and exchange of ocean water, despite considerable fresh water inflow from a number of streams in adjacent areas of high rainfall.

Patch reefs in the inner bay reflect the conditions of the lagoon area in which they are situated. Substrate composition, especially living coral cover, is influenced by factors of circulation, sedimentation, and fresh water influx. Moku o loe Island (Coconut Island), situated between the SE and central sectors of the bay, contributes to the partial isolation of the SE basin. The island is home for the Hawaii Insitute of Marine Biology through which most of the research concerned with Kaneohe Bay has occurred.

2.32 Lagoon

The non-reef portions of Kaneohe's inner bay cover 180.37 x 10^6 m^2, over 70% of which is greater than 9 m deep (Roy, 1970). The depth frequency of the lagoon floor is bimodel, exhibiting 12.5-14.0 m depth mode for the flat lagoon bottom and 1.5-6.0 m depths for areas of stream delta deposition and dredging spoil disposal. In general, the lagoon floor is smooth and slopes gently downward from the base of the fringing reef toward the barrier reef.

Roy (1970) found that moats up to 1 m deep and over 30 m wide occur in the lagoon floor sediments around patch reefs. These moats may result from settlement of the reefs into the compressible bottom deposits, or from scouring by currents around the reef base, although lagoon currents are probably not strong enough to accomplish this. Some of the deepest parts of the lagoon are found where patch reefs are in close proximity to each other. This is thought to be due to increased erosion at the pass bottom (Roy, 1970).

Numerous studies have focused upon the sediments of Kaneohe Bay (Fan, 1973; Roy, 1970; Smith and Kam, 1973; Hollett, 1977). The viscous sandy mud of the lagoon bottom is described as a mixture of sand sized skeletal grains and indurated fecal pellets in addition to ubiquitous silt and clay sized calcium carbonate and terrigenous material. Sand material is slightly more predominant on the lagoon floor behind the back reef of the barrier system. Elsewhere muds are overwhelmingly dominant, exhibiting local irregularities due to burrowing organisms or the accumulation of organic debris. Roy (1970) estimates that 72% of Kaneohe Bay sediments are internally derived calcium carbonate materials but later studies reduce this figure to approximately 50% (Smith and Kam, 1973). The bulk of these deposits appear to be derived from the barrier reef and transplanted landward into the lagoon. The percentage of calcium carbonate in lagoon floor sediments thus decreases away from the barrier reef towards the shore, with a corresponding increases in terrigenous materials (Fig. 3; Smith and Kam, 1973). Natural depositional rates, along with sedimentation induced by human activities have led to an average shoaling of the lagoon floor by 1.7 m between 1927 and 1969 (Roy, 1970).

2.321 Southeast Sector of lagoon

The somewhat isolated SE basin has limited circulation and flushing, and receives about 25% of the Kaneohe watershed runoff. (Bathen, 1968). The proportion of terrigenous material deposited on the lagoon floor here is higher than in other sectors. Calcium carbonate sediments in the basin are mainly derived from degradation of the fringing reef and depositions associated with the extensive amounts of dredging that has occurred in this sector of the lagoon (Smith and Kam, 1973). Between 1927 and 1976, it is estimated that this portion of the lagoon floor shoaled an average of 1.6 m. Much of this was contributed by the stream borne sediment from the highly disturbed watershed surrounding the basin (Hollett, 1977).

2.322 Central Sector of lagoon

The Central sector of the lagoon is bounded by the barrier reef complex and receives abundant sediment input from the calcium carbonate materials biologically produced on the seaward reef slope and algal reef flat. These materials are eroded and transported across the barrier reef by wave action to the calm waters of the back reef and lagoon where they are deposited. Due to the small amount of stream flow entering this portion of the lagoon, all the floor here is composed of over 50% calcareous sediment (Smith and Kam, 1973). Low levels of wave energy inside the barrier reef and steady circulation of the lagoon water result in a very smooth lagoon floor that slopes gently toward the barrier reef base. The bottom in this sector has shoaled on average of 0.9-1.2 m in the 49 years to 1976 (Hollett, 1977).

2.323 Northwest Sector of the lagoon

The Northwest sector accounts for a relatively small portion of the lagoon floor, which becomes narrowed between the extremely wide fringing reef protrusions and the barrier reef. Circulation and flushing are much greater in the NW lagoon, resulting in water conditions close to oceanic (Bathen, 1968). Although about 50% of Kaneohe watershed stream runoff enters this sector, calcium carbonate sediment production on the wide fringing reef and adjacent barrier reef dominates the deposits. The current set in the NW lagoon funnels water and sediment out nearby Mokolii Channel. This flow, along with a lesser amount of reef and watershed surface disturbance, have resulted in an average shoaling of only 0.4 m between 1927 and 1976 (Hollett, 1977).

2.33 Patch Reefs

The 79 patch reefs in Kaneohe Bay approximate truncated circular cones rising from the lagoon floor in their appearance. Their surfaces range from 10-900 m in diameter. They have a collective area of 20.87 x 10^6 m^2 (Roy, 1970). Twenty five patch reefs have been partially or wholly dredged, most to a depth of 9 m, some to only 3 m. These reefs are not distributed randomly in the bay but rather are concentrated in the lagoon areas adjacent to the NW and SE passages through the barrier reef complex. Patch reef occurrence thus does not seem to be governed by basement configuration or substrate condition. Instead, factors associated with the influx of ocean waters and the strong currents and active circulation near the passes presumably are important in the origin and maintenance of these reef structures (Roy, 1970).

Two types of patch reefs are distinguished by Roy (1970): 1) simple reefs - with smooth, regular, circular to ovate outlines and 2) compound reefs - with multilobate outlines which appear to represent the coalescence of 2 or more simple reefs of independent origin. Simple reefs less than about 60 m in diameter are approximately circular while larger ones tend toward an ovate shape, elongated in a direction parallel to the NE tradewinds. Active growth appears to be stimulated on that part of the reef facing into the prevailing wind and currents. Large blocks of the reef structure may slump off from this growing margin providing suitable substrate for lateral expansion of reef building corals (Roy, 1970). Additional processes promoting elongation occur on the opposite side of patch reefs where reef sediment and rubble are transported across the reef and deposited down the leeward slope.

In patch reefs which are closely spaced, elongation is further induced by the formation of narrow channels in the sediment between their bases. In general, it is found that the further a patch reef is from another reef, the more circular it is. Extended, lobate portions of the fringing reef may also represent the assimilation of patch reefs into the larger reef structure. Thus, at some stage in the fluctuating sea level history of the bay, erosional processes followed by reef growth episodes enabled formerly independent reef units to merge into larger structures. Conversely, patch reefs in close proximity to the lagoonward edge of the barrier reef complex are being engulfed by the prograding depositional sand slope of that structure (Moberly and Campbell, 1969).

Hydrographic and oceanographic conditions on patch reefs are very much a function of reef position and location. Windward sides of the reef surface will experience the brunt of most wave energy. Circulation and exchange will thus be higher than the protected leeward side. Location in proximity to the barrier reef and, especially, nearness to the passes influences the amount of wave action and oceanic waters that will affect the patch reef surface and slopes.

Those situated closer to these areas will experience greater surge and circulation and reduce these effects upon patch reefs situated to landward.

2.331 Patch reef flats

Patch reef surfaces are generally flat and reach within 1 m of mean sea level, although a few patch reefs in the NW lagoon have tops 2-3 m deep. Dredged patch reef surfaces do show some recolonization and recovery of the coral communities (Maragos, 1972) but have not exhibited evidence of regrowth to the surface (Roy, 1970). Live coral cover drops off rapidly towards the inside of most patch reefs. Those larger than 30 m in diameter have centers composed of coarse, poorly sorted sand, gravel, dead coral, and coral blocks and rubble (Smith and Kam, 1973). A number of patch reef tops are anomalous in having nearly complete live coral cover and hard substrate. These include those patch reefs with deeper, submerged surfaces and a few other small reefs.

Consolidated limestone substrate and encrusting coralline algae form a ridge around the outer margin of patch reef tops. These are generally about 0.3 m shallower than the central portion of the patch reef flat and may be exposed at spring tides (Roy, 1970). This wave resistant reef crest is particularly well developed on the windward margin of patch reefs, especially on those patch reefs in the central lagoon (Smith et al., 1982). The ridge margin may be interrupted by breaks where reef flat sediments are transported over the leeward side of the reef.

2.332 Patch reef slopes

From about 1 m of water, the patch reef slope extends downward to the depth of 9-12 m, at an angle of about 26° (Roy, 1970). The foot of the slope would thus be about 18 m out from its upper edge. This relates closely to the minimum distance of about 30 m which Roy (1970) suggests separates adjacent, but independent, patch reefs. The upper portions of patch reef slopes often support the highest abundance of live coral cover found in Kaneohe Bay (Smith and Kam, 1973; Smith et al., 1981).

In this upper region of active coral growth, cracks often form in the reef edge and large blocks may slough off and slide down the slope face. These slump blocks and accompanying coral rubble are common in the mid levels of patch reef slopes, but are rarely found at the slope base (Roy, 1970). The extent of live coral cover varies from nearly 8 m deep in the well developed reef slope communities in the NW lagoon to almost nothing in the degraded SE basin reef slopes. Below the live coral and large slump blocks, patch reef slopes gradate from sandy mud with coral fragments to typical lagoon floor muds. Slope angle drops off rapidly in this lower portion and merges into the shallow depression ringing most patch reefs (Roy, 1970).

2.34 Moku o loe (Coconut) Island

Although not specifically a patch reef, the reef around Moku o loe (Coconut) Island displays many of the features common to patch reefs of the inner bay. Coconut Island, an extension of the ridge that forms Pohakea headland, is the only volcanic island in the inner bay. The original 20 m high basaltic hill and the surrounding fringing reef have been extensively altered. The dredging of harbors and ponds and expansion of the island with the fill material have created an area of 0.37 km². The island shores are all lined by seawalls and the dredged basins have muddy bottoms (Aecos, 1981).

The reef flat around Coconut Island is composed of coarse sand and coral rubble. Closer to the reef edge, live coral, reef boulders, and micro atolls are interspersed with sand and coral rubble. A well consolidated ridge crest margin bounds the reef flat, but is less well developed on the west and SW sides. The reef face consists of typical patch reef coral cover in the upper region, which diminishes quickly with depth. Large coral fragments and rubble grade into sandy mud downward along the steep reef face slope. At depths of 9-10 m, the slope rapidly levels out into the lagoon floor muds (Aecos, 1981).

2.4 Outer Bay Zone

2.41 Introduction

Kaneohe's outer bay zone consists of the barrier reef complex and the two channels which cut through it at either end. The barrier reef system is about 2

km wide and extends more than 5 km across Kaneohe Bay (Aecos, 1981). It consists of a series of physiographic zones that gradate from landward to seaward across the narrow axis of the reef, with considerable variation along the length of each zone. The reef passes bisect the barrier reef complex profile and provide access for oceanic water and wave energy into the inner bay. Originally shallower, the NW pass has been dredged to accomodate deep draft vessels, while the SE pass is relatively unaltered.

Wave energy is highest on the outer margin of the barrier reef where trade-wind and storm generated surf impinges unimpeded. The transport of water across the barrier reef and through the channels sets up the currents and circulation patterns that determine the character of the inner bay sectors. Oceanic influences are very high in the outer bay, diminishing across the width of the barrier reef, while terrestrial influences exert little or no impact upon the structures and processes of the outer bay.

2.42 Barrier Reef Complex

The reef system extending across the opening of Kaneohe Bay has been described in a number of studies, using different classification schemes (Roy, 1970; Smith and Kam, 1973; Aecos, 1981; Smith et al., 1981). In this synopsis the barrier reef is divided into 5 physiographic zones based on distinctive geomorphologic features and their substrate (Fig. 2). These zones lie parallel to the long axis of the reef and consist of: the lagoonward depositional slope, back reef flat, algal ridge/reef flat, Kapapa island ridge, and the seaward reef slope. The divisions between these zones are not always clear and their form and content exhibit variation along the length of each region as well.

2.421 Lagoonward depositional slope

The lagoon side margin of the barrier reef is composed of a sand and reef rubble depositional slope. Although some portions consists of consolidated limestone (Aecos, 1981), calcareous sands that are generated on and transported across the barrier reef represent the bulk of the material which has built a sand wedge up to 185 m thick (Smith and Kam, 1973; Moberly, 1969). These well sorted deposits spill down the lagoonward edge of the reef in a smooth, planar, prograding slope that appears to be engulfing nearby patch reefs (Roy, 1970). The steep slope rests at an angle of about 29° to depths of about 11 m, where it gradually merges into the flat lagoon floor muds at 14-15.5 m deep (Moberly, 1969; Roy, 1970).

2.422 Back reef flat

Sand produced by biological production and erosive wave action is transported from seaward portions of the barrier reef and deposited to form the wide back reef flat. Over 80% of oceanic water entering the bay flows across the barrier reef, providing the means to transport vast quantities of reef derived sediments to the lagoonward depositional flats and slope (Bathen, 1968). Much of the back reef flat forms an extensive shoaling body of calcareous sand that is less than 1-2 m deep. The sand body is up to 18.5 m thick containing at least 9.84 million m^3 of deposits that are marked by an exposed sand bar (Ahu o laka) (Moberly, 1969).

Although the central portion of the back reef flat is the focus of active sand deposition, the character of this zone changes along its length. Towards the NW end, the reef flat is still generally sand covered with some irregular microatoll formations. However, the reef is deeper there, reflecting the possibly older age of this part of the barrier reef. In the SE side of the back reef, the relief becomes more varied with many well developed microatolls. This live coral growth, interspersed among the sand and coral rubble just behind the algal ridge, may represent the younger stage of development of this end of the barrier reef complex (Roy, 1970).

2.423 Algal ridge/reef flat

This zone of the barrier reef forms a wide, 1-2 m deep, convex seaward arc that is referred to as both an algal ridge (Roy, 1970) and a high energy reef flat (Smith and Kam, 1973). The shallowest portion of this feature is a broadly defined algal ridge with an asymmetrical profile. On the lagoon side it rises quickly up from the back reef flat, with a near vertical slope of up to 1.5 m in sections of maximum relief. The ridge is about 0.3 m deep at its highest and

extends seaward at this depth for approximately 65 m after which it gradually slopes into the fore reef structure (Roy, 1970). The character of the algal ridge changes along the distance of its arc. At the NW end, it is reduced to a narrow zone of hard bottom composed of reef material consolidated by coralline algae and nearly covered by sand. In its central portion, lagoonward of Kapapa Island, the ridge exhibits greater relief and consists of encrusting coralline algae with some coral. Towards the SE, the live coral component increases and becomes predominant, especially on the lagoon side of the ridge (Aecos, 1981).

Landward of the steep lagoon side drop off, the algal ridge/reef flat region contains a series of short ridges. These are formed by the growth and coalescence of microatolls and coral heads which are partly covered with coralline algae (Roy, 1970). Microatolls consist of circular to ovate coral heads which have dead centers, but are actively expanding at their margins. In Kaneohe Bay, microatoll formations may grow to 6 m in diameter. As the algal ridge/reef flat merges into the sediment dominated back reef flat, the microatolls become less common. The seaward portion of the algal ridge/reef flat slopes gently oceanward from the almost flat, wide, shallow ridge. Sand bottomed gullies and coralline algae limestone ridges begin to form parallel to the direction of water movement across the reef. These gullies and ridges gradate into the spur and groove system of the seaward reef slope (Aecos, 1981).

The algal ridge/reef flat lies as much as 1 km inside the main line of breaking surf and receives gently rolling waves that are refracted in an arcate pattern along the fore reef. The calcareous sediments and organic material of the highly productive algal ridge/reef flat and upper seaward reef slope are then deposited as part of the extensive sediment body covering the back reef flat and building the lagoonward barrier reef slope.

The width of the barrier reef algal ridge in Kaneohe Bay, along with its gentle seaward slope and distance from the surf zone, distinguish it in form and process from typical algal ridges. It was suggested by Roy (1970) that the present algal ridge/reef flat structure may be a relict feature, such as a beach or dune ridge, that has been more recently covered by a veneer of coral and encrusting algae. The variations in the nature of the algal ridge/reef flat from an older, reduced feature at the NW to a younger, actively building structure in the SE thus possibly represent different steps in a developmental sequence for this zone (Aecos, 1982).

2.424 Kapapa island platform

Near the seaward margin of the barrier reef an area of elevated hard substrate is marked by Kapapa Island. Both the platform and island are constructed of lithified dune material which was subaerially deposited in the past when sea level was much lower (Roy, 1970). The island is now heavily eroded and has a 10 m wide bench on its windward side that is usually awash. Above this, a pitted and weathered second bench is exposed at 1-2 m above sea level and backed by a beach ridge of calcareous sand and coral rubble. On the leeward side a deep notch has been carved into the cemented dune sands by present sea level (Stearns, 1935). A broadly sloping platform spreads seaward from about 0.5 m depth adjacent to the island. This platform, of hard substrate similar to the lithified dune material of Kapapa, is heavily etched by boring sea urchins (Aecos, 1982).

Kekepa Island, although not on the barrier reef, is also a remnant island of the lithified sand dune sediments. It is located on the outer margin of the fringing reef at the NW edge of Mokapu Penninsula, just before the seaward reef slope. Kekepa Island has a prominent wave cut notch cut around its base (Stearns and Vaksvik, 1935). The proximity of both Kapapa and Kekepa islands to the seaward margin of Kaneohe Bay reef structures exposes them to considerable amounts of wave action. This accounts for the high degree of erosion experienced by the islands and results in a high level of oceanic water mixture and circulation around them.

2.425 Seaward reef slope

The small ridges and gullies of the algal ridge/reef flat exhibit higher relief as they slope seaward, until they become the well developed spurs and grooves of the upper seaward reef slope. This is a zone of breaking surf, which under normal conditions, is at about the 3 m isobath (Roy, 1970). The greatest amount of wave energy is produced by the nearly constant trade winds which occur

over a large portion of the year (Shimada, 1973). The formation of deep, narrow cracks in the limestone reef rock and lithified dune sediments is apparently contributed to by mechanical erosion resulting from the incessant wave action (Roy, 1970). The spur and groove systems reflect this high wave energy environment. The eroded sediments are chuted down the reef slope in the channels and the scoured, hard substrate of the spurs which are occupied only by wave resistent corals and encrusting algae (Smith and Kam, 1973).

The bathymetric configuration of the upper seaward reef slope appears to be a relict stream drainage pattern with more recent feature superimposed on it (Roy, 1970). The nature of the fore reef also changes along its length, especially NW of Kapapa where the reef front is less well defined. In this portion, a shoal has formed as a result of longshore drift and sediment transport from the heavier surf area around Kapapa Island to the SE. About 300 m seaward of the surf zone NW of Kapapa Island is a region of swell and swale topography. The mounds are 7-10 m wide, over 35 m long and rise up to 1 m above the depressions. These long, low ridges are covered with live coral and encrusting algae, while the low areas have sand and rubble deposits. Further towards the ocean, the mounds are narrower and show evidence of bioerosion by boring sea urchins (Roy, 1970).

In general, the seaward reef front slopes from the 3-4 m deep spur and groove features in the surf zone to a depth of 18 m over a distance of about 1 km (Aecos, 1981). The reef face is made up of consolidated reef limestone, coral rubble, and cemented dune sediments with small amounts of live coral cover. From 18 m, an eroded submarine cliff, with caves and overhangs, descends steeply to about 27 m (Roy, 1970). A notch cut into this cliff face at 24 m below present sea level is considered by Stearns (1974) to be evidence of a relatively long stand of the sea at that level. At the base of this cliff, sediments deposited down the front of the barrier reef and fanning out from the reef passage channels accumulates and spreads oceanward. This broad, gently sloping sand terrace gradually thins out over a distance of several kilometers. As the depth increases to about 100 m, this sand wedge diminishes almost entirely and the shelf upon which it rests continues to extend out to sea (Roy, 1970).

2.43 Barrier Reef Passes

At either end of the barrier reef complex, 2 relatively deep, sand filled channels about 5 km apart separate the barrier reef from the fringing reefs off Mokapu Penninsula and Kualoa Point. Seismic reflection data indicate the passes lie over deep infilled valleys. These channels may have been cut through the reef structure at lower stands of the sea or built up by reef growth at higher sea levels, or both. The deposition of transported sand has filled the valleys to their present depth and spills out onto the ocean terrace. These fan shaped wedges coalesce along the base of the barrier reef where they are almost 60 m thick, gradually thinning out to almost nothing about 1500 m further offshore (Roy, 1970). Although the passages allow water and sediment to be transported out of the bay, they also permit relatively unimpeded wave energy access to the inner bay, which influences circulation and mixing patterns (Bathen, 1968).

2.431 NW pass

At the NW end of Kaneohe Bay, Mokolii (Ship) Channel is a natural channel that was deepened by dredging in 1939. At the lagoon end of the passage there was a 6 m deep sill that was dredged to about 10-11 m. From the lagoon sill to the surf zone the channel is nearly horizontal and has shoaled about 1 m since 1949 (Hollett, 1977). From beneath the surf zone, the channel floor slopes very gradually down to about 20 m, and then continues even less steeply for another 800 m until it merges with the sand deposition fanning out from the submerged valley mouth. A majority of the inner bay's water flow and sediment transported are conveyed NW through the lagoon and then out through Mokolii Channel (Bathen, 1980).

2.432 SE pass

The SE end of the barrier reef is bounded by Kaneohe (Sampan) Channel which has not been dredged. Most of the bottom of this shallow passage is covered with calcareous, non-terrigenous sand with occasional elevated hard patches covered with encrusting coralline algae and some live coral (Roy, 1970). From the lagoon end sill, the channel slopes seaward very gradually for about 30 m at which point it intersects the cliff line of the seaward barrier reef slope (Roy,

1970). Some water and sediment transport out through the SW pass is noted, but not nearly to the extent as occurs at the NW pass (Bathen, 1968).

2.5 Physiographic Changes in Kaneohe Bay

2.51 Introduction

The history of the Kaneohe region is reflected in changes in the physical make up of the bay. The construction of walled fish ponds, which enclosed portions of the fringing reef flat, and the development of terraces and irrigation systems, which reduced runoff and sediment transport into the bay, were early modifications by ancient Hawaiians which did not greatly disrupt the marine environment of Kaneohe Bay (Devaney et al., 1976). With the advent of Western civilization and 20th Century technology, changes in the Kaneohe Bay region have become increasingly frequent and destructive. Disruption of the physiography of Kaneohe Bay has come about as a result of chronic, large scale alterations in the land use of the watershed punctuated by acute episodes of direct physical modification of structural features within the bay.

2.52 Runoff, Sedimentation, and Sewage

The changing patterns of land use in the Kaneohe drainage basin have resulted in rising rates of shoaling on the lagoon floor and degradation of living reefs through the effects of increased runoff of sediment laden freshwater. The removal of natural vegetation by cattle grazing and agriculture in the late 19th and early 20th centuries increased the amount of erosion and sediment discharge into the bay (Maragos and Chave, 1973). The effects of fresh water innundation and siltation on coral reefs in Kaneohe Bay have been documented for recent events (Banner, 1968) but can only be speculated on for earlier periods. However, the coral reefs in Kaneohe Bay were still considered some of the most luxurient in Hawaii even until the 1940's (Edmondson, 1946).

Since about 1940, land use changes in the Kaneohe watershed have taken the form of rapidly increasing urbanization, especially around the SE portion of the area. The numerous impacts of rising population on the Kaneohe Bay ecosystem have been dealt with in a number of studies (Banner and Bailey, 1970; Maragos, 1972; Banner, 1974; Maragos and Chave, 1973; Cox, et al., 1973; Smith, et al., 1981). Urbanization has led to further removal of vegetation and an increase in the proportion of impervious surfaces. These changes, along with the channelization of streams, allowed for increased runoff of sediment loaded, fresh water into the bay. As a result, the lagoon has shoaled about 1.6 m between 1927 and 1969, with approximately one half of the material from terrestrial sources (Roy, 1970).

The discharge of sewage from 2 treatment plants on the SE basin shores began in the 1950's and rose to about 20,000 $m^3 d^{-1}$ by 1978. The resulting degradation of the bay ecosystem has been mainly biological in nature, due to alterations of water quality and productivity in the water column (Smith et al., 1981). Live reef coral substrate was adversely affected by reduced light penetration in the turbid, nutrient rich water, and by the explosive growth of green bubble algae (*Dichtyosphaeria cavernosa*) which smothered living reef corals (Maragos, 1972; Banner, 1974). In the heavily impacted SE basin, the increasing abundance of filter feeding organisms boring into the reef framework may have led to the weakening or breakdown of reef structures. The diversion of sewage to outside the bay in 1978 appears to have slowed much of the degradation (Smith et al., 1981) and the recovery of coral reefs affected by sewage related stress seems to be taking place (Evans et al., this publication). Kaneohe Bay's water quality under existing conditions and alternative land use scenarios in the watershed were projected in a detailed computer modeling study by Dames and Moore (1977).

2.53 Dredging and Filling

Dredging accounts for the most extensive and permanent alteration of the physiography of Kaneohe Bay. Up until 1939, only minor dredging of fringing reefs took place in the development of shoreside boat basins and piers (Devaney et al., 1976). From 1939 through the World War II years, the construction of Kaneohe Marine Corps Air Station at Mokapu Penninsula involved the removal of 3.77×10^6 m^3 of reef material and landfilling of the shallow reefs at Mokapu. This occurred in the dredging of patch and fringing reefs to 3 m in the SE basin to create a seaplane runway, the deepening of the NW Pass to 10 m, the truncat-

ing of patch reefs to 10 m to clear a ship channel running the length of the bay, and the doubling of the land area at Mokapu Penninsula (Maragos, 1972; Devaney, 1976). Of the total dredge spoils, only 1.42×10^4 m^3 was permitted to be disposed of in the inner bay, the rest was used for landfill or disposed offshore (Banner, 1974). More recent investigations suggests that the volume of material dredged may have been much greater than this original estimate, contributing a significant amount of the calcareous sediments responsible for the lagoon floor shoaling (Roy, 1970; Devaney, 1976).

Dredging of channels across the reef flats by individuals has accounted for an additional 1.98×10^5 m^3 of reef removal. During the 1930's, Moku o Ioe Island reef was extensively dredged to create basins and channels and the spoils used for landfill to double the area of the island (Devaney, 1976). Between 1946 and 1948, nine fishponds of nearly 60 acres total area were filled, possibly with reef material dredged from adjacent reefs, to create additional bay front property mostly in the SE half of the bay. Since 1950, three more ponds have been filled but no other significant amount of dredging has occured in the bay (Devaney, 1976). Most of the fill areas along the shoreline are protected by sea walls or other artificial structures.

The effects of dredging upon coral reefs, beyond the physical destruction of the structure, include the creation of fine carbonate sediments which smother live coral and create an unsuitable substrate for coral planulae settlement. In Kaneohe Bay, these effects were exacerbated by the dispersal of dredge spoils in the inner bay where terrestrial sediment and pollution related disturbances already existed. Many of the dredged reef surfaces do exhibit evidence of the reestablishment and recovery of coral communities, but as yet do not show signs of significant vertical growth (Roy, 1970; Maragos, 1972).

Acknowledgements

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Coral Reef Communities of Kaneohe Bay, Hawaii: an Overview

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Abstract

Coral communities of the Kaneohe Bay region exhibit an overall abundance of coral. Within Kaneohe Bay there is considerable variation in coral distribution, abundance, and diversity. This variation is from shore to open ocean across both the inner and outer bay, along a gradient from the Southeast to Northwest sectors of the inner bay, and patchiness within localized portions of reef slope communities. Variations are attributed to abiotic factors at different levels of coral distribution for the fringing and patch reefs of the inner bay and the barrier reef complex of the outer bay. Coral communities of Kaneohe Bay have exhibited important temporal variation in distribution, abundance, and diversity as well as distinct spatial patterns.

Introduction

Kaneohe Bay, on the Northeast side of Oahu, includes the most extensive reef system in Hawaii. The area consists of a semi-enclosed inner bay with a near continuous fringing reef and numerous patch reefs. The outer bay is a wide barrier reef complex bisected at either end by two channels (Fig. 1). The physiography and structural reefs of Kaneohe Bay have been summarized (Holthus, this publication). An annotated bibliography of literature providing information of the corals and reefs of Kaneohe Bay up to 1975 is presented by Maragos (1975) along with a brief review of the status and importance of coral reef resources in the bay.

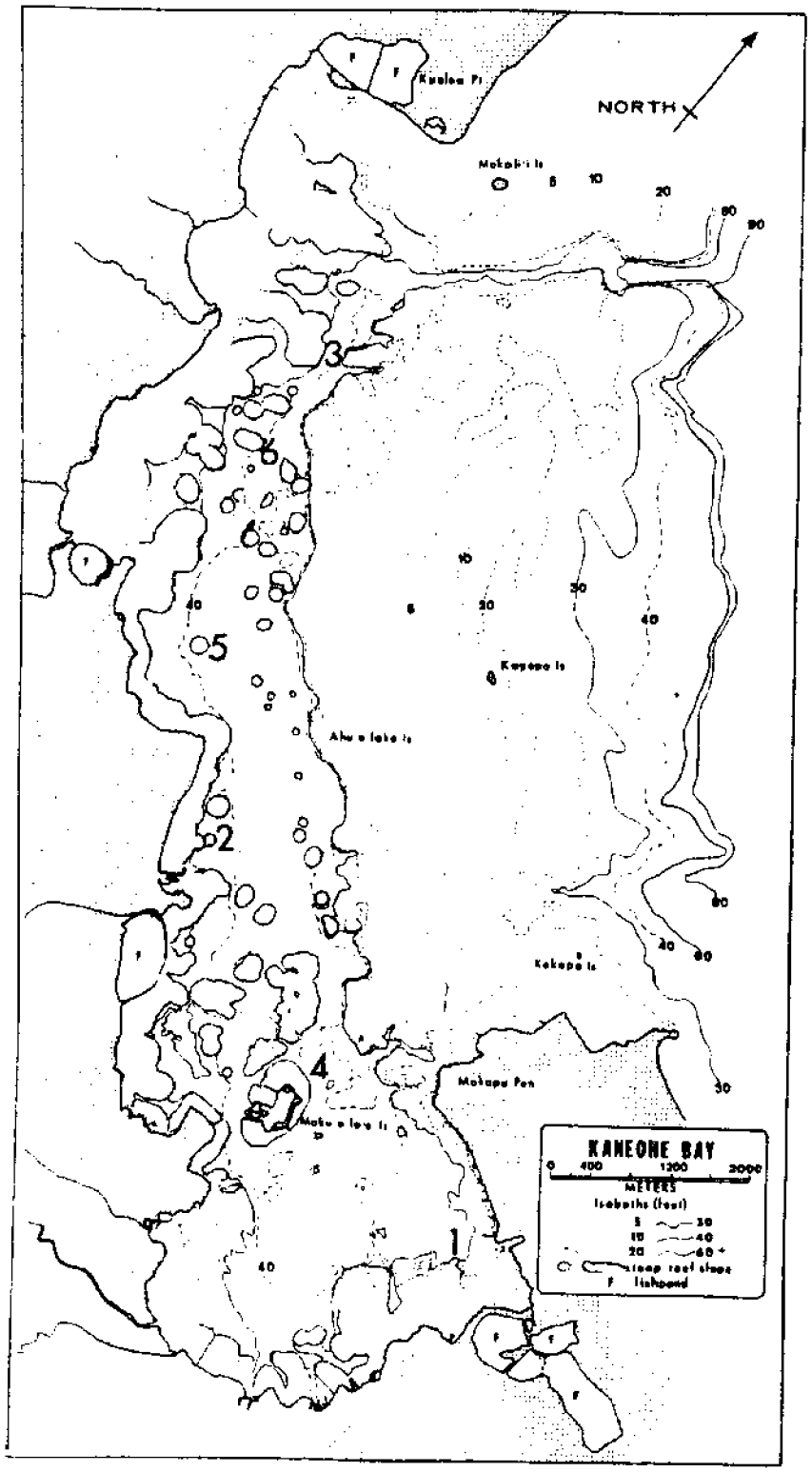
While the reefs of Kaneohe Bay in general display an abundance of hermatypic coral growth, the corals are restricted to certain habitats within the bay environs. Highest reef coral abundance occurs on the outer margins of the reef flats and upper portions of the lagoon reef slopes, with lesser amounts of corals found in the other zones of the bay (Maragos,1972). The patterns of coral abundance and distribution vary along a gradient from landward to seaward across both the inner and outer bay, along the southeast to northwest axis of the inner bay, and with localized patchiness in specific reef sections. The distribution and abundance of reef corals in the region are controlled by several factors, operating on different scales, which determine the location and composition of coral communities within Kaneohe Bay.

Coral Distribution

The distribution of reef forming coral species in Kaneohe Bay was determined by Maragos (1972) by extensive surveying of numerous sites throughout the bay. Coral occurrence, habitat, and relative abundance are summarized (Table 1). It is apparent that physical factors are important in the distribution of corals in Kaneohe Bay. However, the patterns of temperature, salinity, and nutrient concentration distribution for the bay waters investigated by Bathen (1968) do not exhibit variations similar to the local scale of observed variations in coral distribution. Factors considered by Maragos (1972) more likely to exert control over coral distribution and abundance include: hydrographic conditions, substrate composition, reef morphology, depth, sediment transport, and currents. These abiotic conditions may result in variations in coral growth rates, larval settlement behavior, competition for space among corals, and predation pressures in the coral communities.

Land to Ocean Coral Distribution

The broad patterns of coral abundance, diversity, and distribution from landward to seaward across a generalized cross section of Kaneohe Bay are adapted from Maragos (1973) (Fig. 2). The presence of reef corals is predominantly on the crest and slopes of reefs in the inner bay and on the algal ridge/reef flat and seaward slope of the barrier reef complex. Live coral cover is very low, or non-existent on the reef flats of the fringing and most patch reefs, and on the



ig. 1. Kaneohe Bay. Showing location of reef community profile sites (1-6).

Table 1. List of reef corals from Kaneohe Bay with indications on each species' most likely occurrence and relative abundance. (Adapted from Maragos, 1972).

	Abundant	Common	Scattered	Occasional	Rare
I. Shallow fauna:					
A. Species restricted or much more common in the lagoon					
Tubastraea aurea			*		
Porites compressa	*				
Fungia scutaria		*			
Montipora dilatata					*
Montipora verrilli			*		
Montipora verrucosa	*				
Montipora patula			*		
B. Transitions					
1) Species common both inside and outside of the Bay:					
Pavona varians		*			
Cyphastrea ocellina		*			
Leptastrea bottae		*			
Psammacora stellata				*	
Pocillopora damicornis	*				
2) Species most common on the barrier reef:					
Pocillopora ligulata				*	
Porites evermanni					*
Porites pukoensis					*
Psammocora (all species)				*	
C. Species most common outside the Bay in shallower water					
Pocillopora meandrina	*				
Porites lobata	*				
Pavona explanulata				*	
Montipora flabellata				*	
Pocillopora molokensis					*
Porites brighami					*
Leptastrea purpurea				*	
II. Deep fauna:					
A. Species most common outside the Bay in deeper water					
Pocillopora modumanensis					*
Cycloseris vaughani			*		
Leptoseris incrustans					*
Leptoseris digitata					*
Coscinaraea ostreaeformis					*

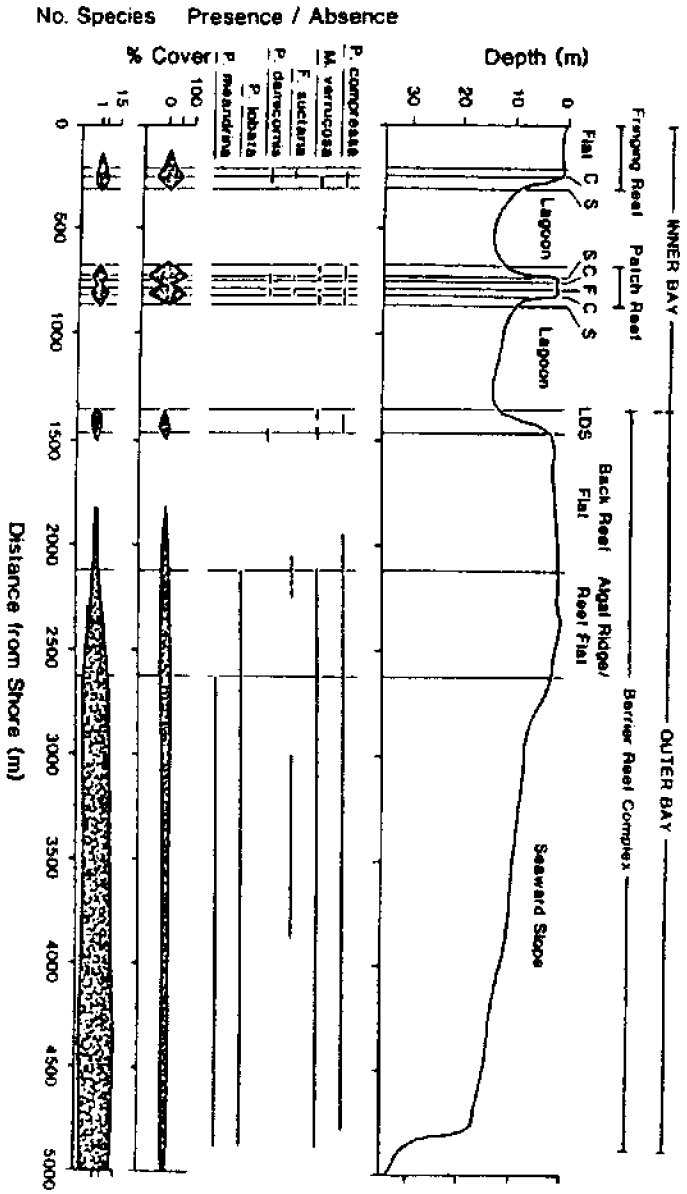


Fig. 7. Cross section of Kaneohe Bay: Physiographic zones and coral distribution, abundance and diversity (adapted from Maragos, 1973).

lagoon-ward depositional slope and back reef flat of the barrier reef due to the sand and rubble dominated substrate. The lagoon floor of the inner bay is similarly devoid of coral as a consequence of its viscous mud composition which is unsuitable for coral establishment.

Where corals do occur in Kaneohe Bay, the high abundance and low diversity of reef slopes in the inner bay contrasts with the low abundance and relatively high diversity of the oceanward zones of the outer bay. Mechanical erosion and scour from suspended particles caused by wave activity is thought to inhibit coral development on the exposed barrier reef slopes (Maragos, 1972). Reef slopes of the sheltered inner bay do not experience these physical disruptions and coral growth proceeds relatively undisturbed. This distributional pattern supports the proposed coral reef community successional pattern developed by Grigg and Maragos (1974) on the island of Hawaii. They conclude that in exposed situations, succession is constantly interrupted by physical processes of swell and surge activity, maintaining the coral assemblage at a pre-climax stage of low abundance and high diversity. Conversely, on reefs sheltered from wave disturbance, succession is able to proceed to a stage of high coral cover which often results in interspecific coral interactions, dominance by a single species, and low diversity (Grigg, 1983). This pattern is not only represented in coral community differences from inner bay to outer bay in Kaneohe, but also in a dichotomy between the coral assemblages on the windward and leeward patch reef slopes.

Southeast to Northwest Lagoon Coral Distribution

Within the inner bay region of Kaneohe Bay, coral communities vary considerably from the semi-isolated southeast (SE) basin to the ocean influenced northwest (NW) sector. The condition of reef communities reflects a gradient from the SE basin where sewage was discharged until 1978 and high rates of freshwater runoff and sedimentation occur, to the NW portion of the lagoon where mixing and circulation of ocean water is good (Banner, 1974). In the SE basin the coral reefs were severely degraded by dredging, high levels of sewage related nutrients, and sediment discharge resulting from disturbance of the surrounding watershed (Banner and Bailey, 1970). Recent surveys show settlement and growth of reef corals on the denuded reef framework, possibly as a result of the cessation of sewage input and a decline in sediment-laden runoff (Aliño, this publication). In the central lagoon area of Kaneohe Bay, much of the reef slope coral coverage has been smothered by mat-forming growth of the green bubble algae, Dictyosphaeria cavernosa. The explosive growth of this algae seems to be a response to sewage related nutrients in the water. The algae is able to out compete corals for space at mid-depth along the reef slopes (Maragos, 1972). Since the stoppage of major sewage inputs, a decrease in the amount of algae and a corresponding increase in coral cover and growth have been documented for the central lagoon (Evans et al., this publication). In the NW sector of the inner bay, coral growth is vigorous and continues to cover greater area, to greater depth, than elsewhere in Kaneohe Bay (Maragos, 1972; Evans et al., this publication).

Vertical Coral Distribution

A vertical pattern of coral zonation is either very simple or not distinct in the reef slope coral communities of the inner bay. In general, several species of corals are common in the upper 1 to 10 m of the steep reef slope, their extent depending on the conditions of that particular location in the bay (Table 2). Where Dictyosphaeria cavernosa is common, it will dominate the lower portions of this band of coral distribution, apparently taking advantage of depth where circulation and light are sub-optimal for coral growth (Maragos, 1972). The lower limits of coral presence are determined by the decrease in available hard substrate and increasing dominance of sediments at the bottom of reef slopes in the inner bay. Maragos (1972) pointed out the mutual exclusiveness of high coral cover and high sediment cover, but did note that there is a threshold of sediment accumulation up to which corals would survive.

In the variable depth zone of highest coral abundance, coverage may reach 80 to 100% of the substrate, but without a distinct zonation pattern down the face of the reef slope. Two factors are probably responsible for this. First, none of the common coral species appears to have a distinct depth range within the relatively shallow extent of reef slopes within the inner bay (generally less than 15 m). Secondly, in this protected environment where succession may pro-

ceed relatively uninterrupted, the competitively superior Porites compressa which accounts for 85% of coral cover in the bay, overwhelmingly dominates the community and overshadows any zonal trend (Maragos, 1972; Grigg, 1983). Even so, a generally observable pattern of coral distribution does seem to occur. On reef flats near the slope edge and upper slope, Pocillopora damicornis and Fungia scutaria are most commonly found. Towards the bottom of the area of greatest live coral coverage, Montipora verrucosa becomes more prevalent. In between, the dominance of Porites compressa may be nearly complete, although other corals may be found in very small amounts (Maragos, 1972).

Table 2. Vertical zonation of corals in Kaneohe Bay (Helfrich, 1973).

Depth (feet)	Number of Species
0-10	21
11-20	13
21-30	13
31-40	7
41-50	6
51-60	4
61-70	8[1]

[1]four of these species are restricted to the escarpment between 65 ft and 70 ft.

Coral Communities

The coral communities of Kaneohe Bay may be best analyzed in relation to the structural reefs of the region which have been summarized earlier (Holthus, this publication). Coral assemblages will thus be outlined for the fringing and patch reefs of the inner bay and the various portions of the outer bay's barrier reef complex. Variations in coral communities along the SE to NW axis of the inner and outer bays can be substantial and must also be considered in the description. Actual reef slope profiles and the extent of coral coverage are presented to exemplify the coral reef communities in each portion of the bay. The data from which these profiles and bottom coverage diagrams were constructed were collected in recent surveys of reef slope coral communities in Kaneohe Bay (Evans et al., this publication).

Inner Bay

Fringing reefs

Along the nearly continuous fringing reef of variable width which lines the shores of Kaneohe Bay, corals are generally restricted to the outer margins of the reef flats and upper portions of the reef slopes (Maragos, 1972). The amount of coral coverage and the depth to which it extends varies considerably along the length of the bay. The effects of terrestrial influences, especially those generated by human activity are important in determining the condition of coral communities on the fringing reef.

In the SE basin, coral cover is generally very low, only 1 to 10% in most areas. The degraded status of coral reefs in this region are evidenced by the high degree of sediment and hard substrate on the reef slope (Figure 3a). The shallow, sediment dominated base of the reef face reflects the large amount of silt accumulation which had occurred in the SE basin as a result of extensive dredging and watershed disturbance. The coral coverage which does occur is limited to colonies at mid-depths which have avoided direct effects from dredging at the upper slope, and sediment burial at the lower slope. Recent surveys show recruitment and growth of new coral colonies to be occurring. On the reef flats, Montipora verrucosa and Pocillopora damicornis appear to be forming colonies from planula settlement (Allen, this publication). Along the slope, Montipora verrucosa is the dominant coral at most depths, which reflects its ability to better withstand the disturbed conditions of the SE basin (Maragos, 1974).

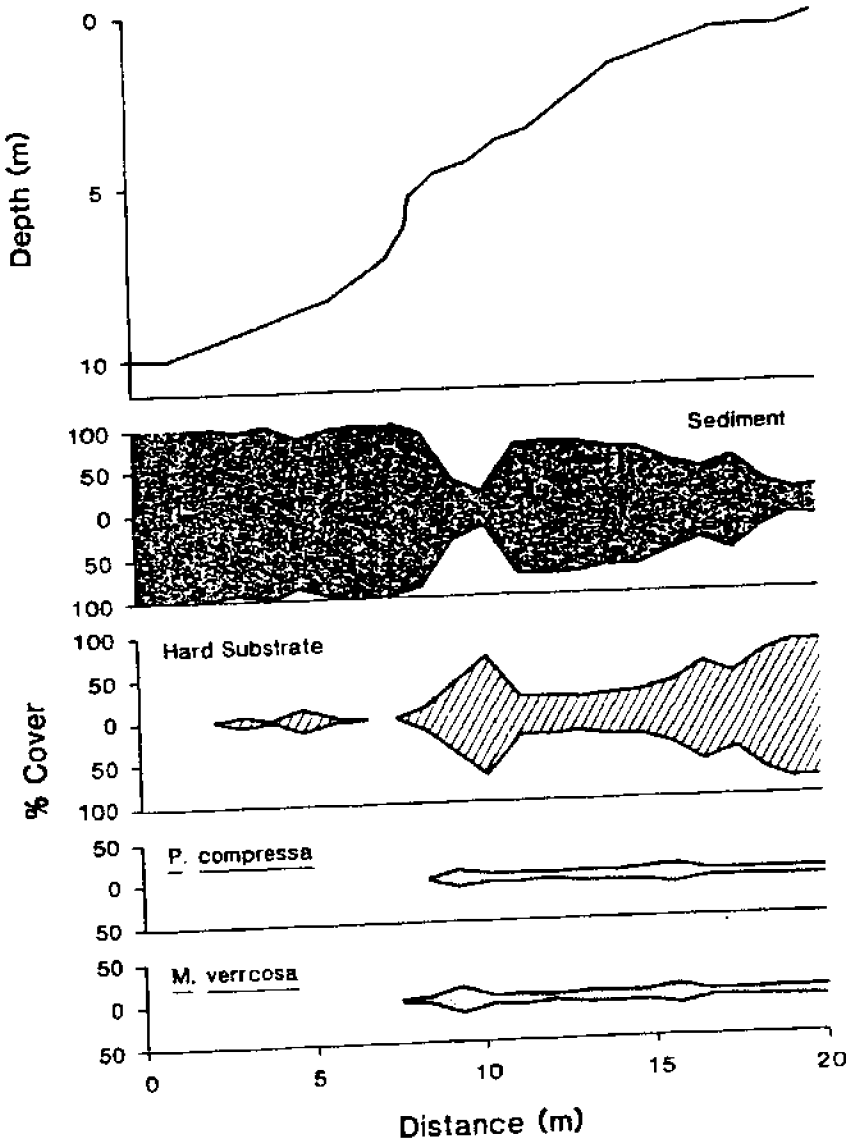


Fig. 3a. Fringing reef slope, Southeast lagoon (Fig. 1, site 1).

The fringing reefs facing the central inner bay support a substantial cover of live coral along slope depths of 1 to 8 meters, while the reef flat remains relatively barren (Aecos, 1981). The high degree of available hard substrate on the reef flat may be a result of periodic low tide exposure or fresh water runoff. Below the 1 meter depth, coverage by Porites compressa may reach 60 to 70% (Figure 3b). Montipora verrucosa and other corals (Pocillopora damicornis, Fungia scutaria, and Cyphastrea ocellina) intermittantly account for up to 5% of the cover. Dictyosphaeria cavernosa abundance is an important component at mid to lower depths. Below about 8 meters deep the algae and coral cover both drop rapidly off. Coral cover in this central inner bay area generally increases towards the NW, although proximity to stream mouths create silty sections where abundant coral cover is suppressed. The depths to which corals can be found also generally increase towards the NW, with the lowest portions of the reef slope still dominated by sediments or sediment coated reef rubble.

The fringing reef coral communities of the NW sector exhibit a moderate degree of variability due to the convoluted outline of the reefs. Where the reef is narrow, there is usually a large amount of silt and sand sediments which preclude much coral development. At the extended lobes of the fringing reef, coral cover may be higher than any where else in Kaneohe Bay (Aecos, 1981). On the outer reef flat margins, Porites compressa is dominant, but Fungia scutaria and Cyphastrea ocellina are also common. Total live coral coverage is still less than 10 to 20% in portions of the reef flat, with much hard substrate available (Figure 3c). On the reef slopes, Porites compressa is overwhelmingly dominant, with the other corals often occurring as less than 1% of the cover, if at all. In general, live coral cover may approach 60% at the crest of extended reef fingers and reach 100% at depths of 3 to 4 m (Aecos, 1981). Dictyosphaeria cavernosa occupies considerable segments of the reef slope in parts of the NW sector and may be increasing due to growing human disturbance and sewage discharge in this portion of the Kaneohe Bay watershed. Overall greater coral coverage occurs to greater depths along fringing reef slopes in this area.

Patch reefs

The patch reefs and reefs around Moku o loe Island of the inner bay exhibit trends similar to those on nearby fringing reefs. However, these reef surfaces are less disrupted by terrestrially derived impacts, although a number of patch reefs and reefs around Coconut Island have been dredged. The majority of patch reefs are located in the lagoon where the two passages cut through the barrier reef. They are thus subject to considerably more oceanic influence than the fringing reefs.

In the SE basin, a number of patch reefs were dredged to depths of 3-9 m. These have some remnant coral coverage on their lower slopes and have recently begun to develop extensive live coral cover on the upper dredged surfaces (mainly Montipora verrucosa). Reefs around the island of Moku o loe have about 5 to 10 % coral cover on the reef flats, which increases towards the reef crest. Pocillopora damicornis is the most common on the flats, with Porites compressa, Montipora verrucosa, and Fungia scutaria also found at the reef crest. On the slopes, Porites compressa is dominant, with some Dictyosphaeria cavernosa also occurring (Figure 4a). At the lower extent of coral coverage, Montipoa verrucosa becomes dominant with a mixture of other corals (Pocillopora damicornis, Cyphastrea ocellina) interspersed throughout the slope. The large amount of hard substrate on the reef slope may represent areas formerly occupied by the green bubble algae, which is now rapidly declining in abundance in this sector of the bay (Evans et al, this publication). The large patch reef just north of Moku o loe Island is one of the few areas where Montipora dilatata has been recorded in Hawaii and formerly contained patches of abundant Tubastraea coccinea (Maragos, 1972).

In the Central sector of the inner bay, the windward sides of patch reefs often have coral communities of somewhat higher diversity than the leeward facing side. Porites compressa, though, continues to be dominant, with up to 70 to 80% coverage in the upper slope (Figure 4b). Montipora verrucosa is a small component of the community, but is more prevalent on the lower portion of the slope. Pocillopora damicornis, Cyphastrea ocellina, Pavona varians, and Montipora verilli are all found intermittantly in patch reef slope coral assemblages in this area. Patch reef flats may have up to 20 to 25% coral cover near the crest margins, consisting mostly of Pocillopora damicornis, Montipora verrucosa, and Fungia scutaria (Aecos, 1981). Towards the NW end of this sector, coral communities begin to extend down the patch reef slopes to depths of 10 m.

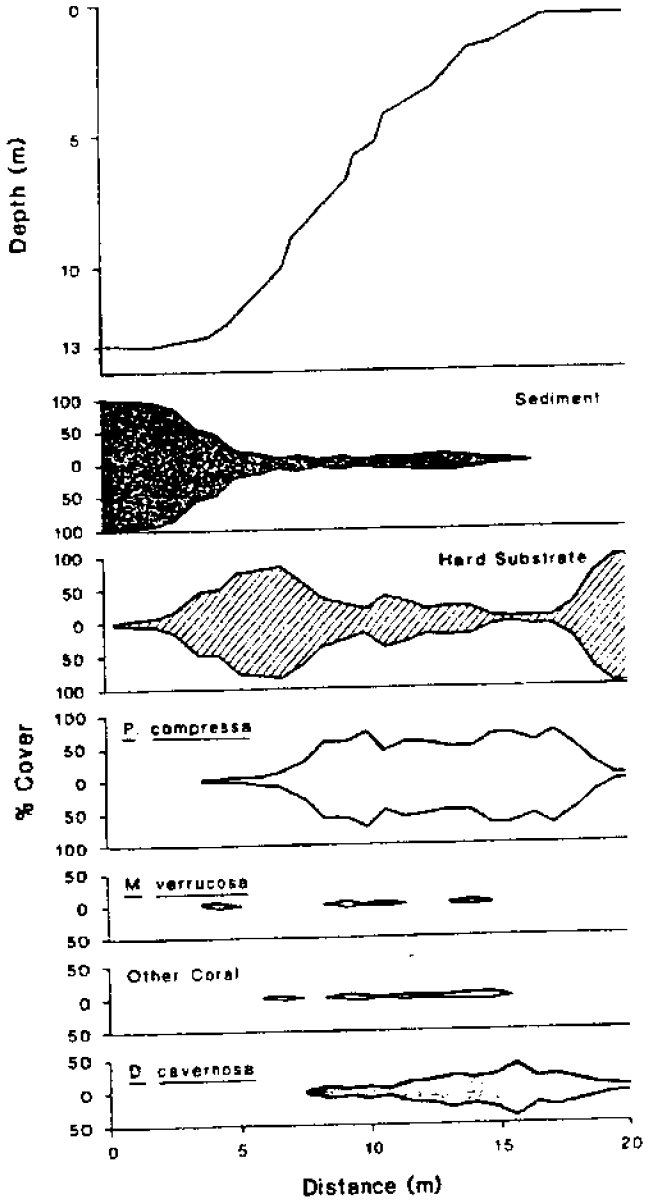


Fig. 3b. Fringing reef slope, Central lagoon (Fig. 1, site 2).

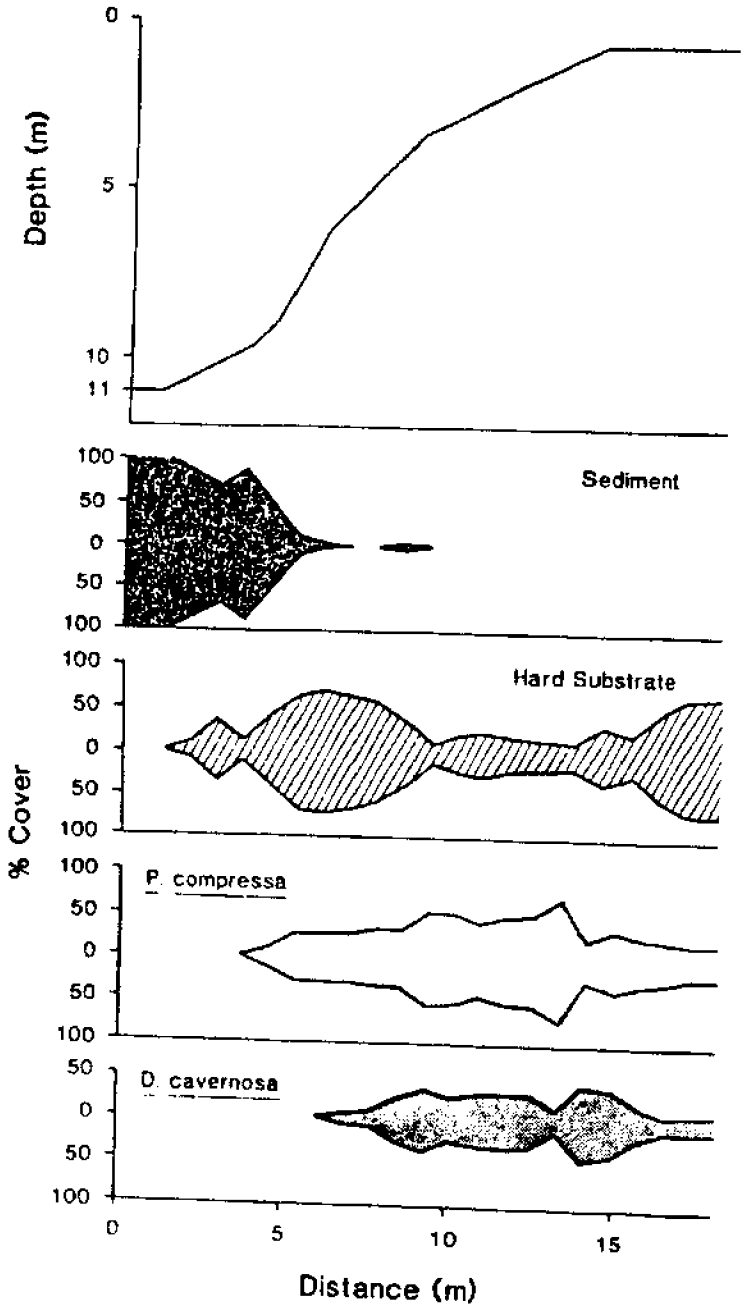


Fig. 3c. Fringing reef slope, Northwest lagoon (Fig. 1, site 3).

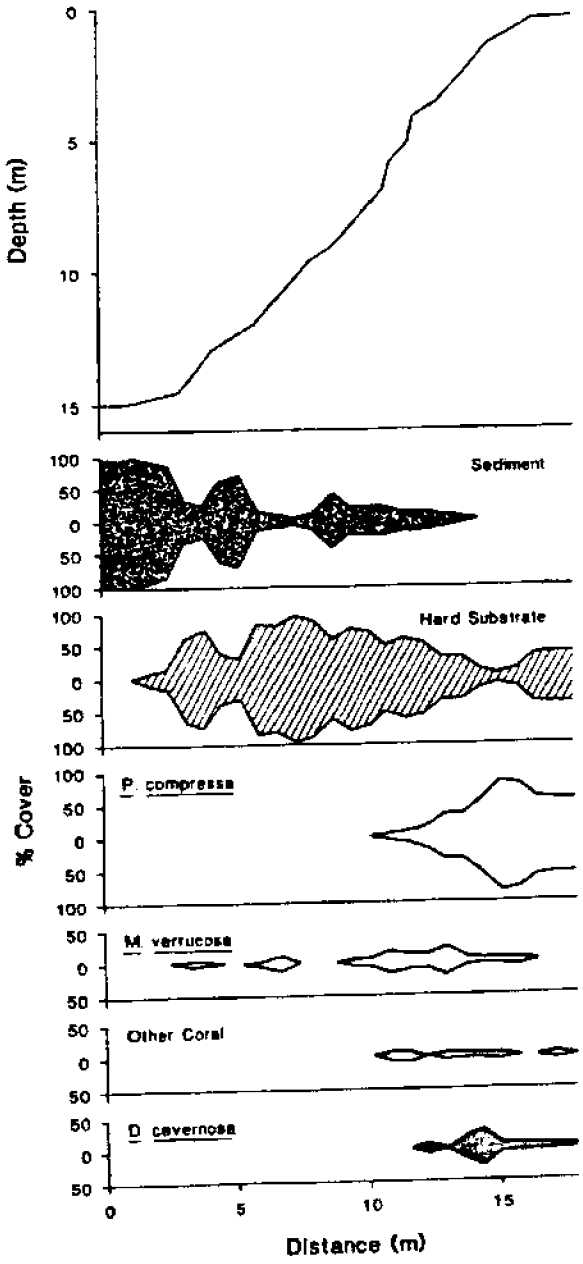


Fig. 4a. Reef slope - Southeast lagoon. Windward Mokuoloe Island (Fig. 1, site 4).

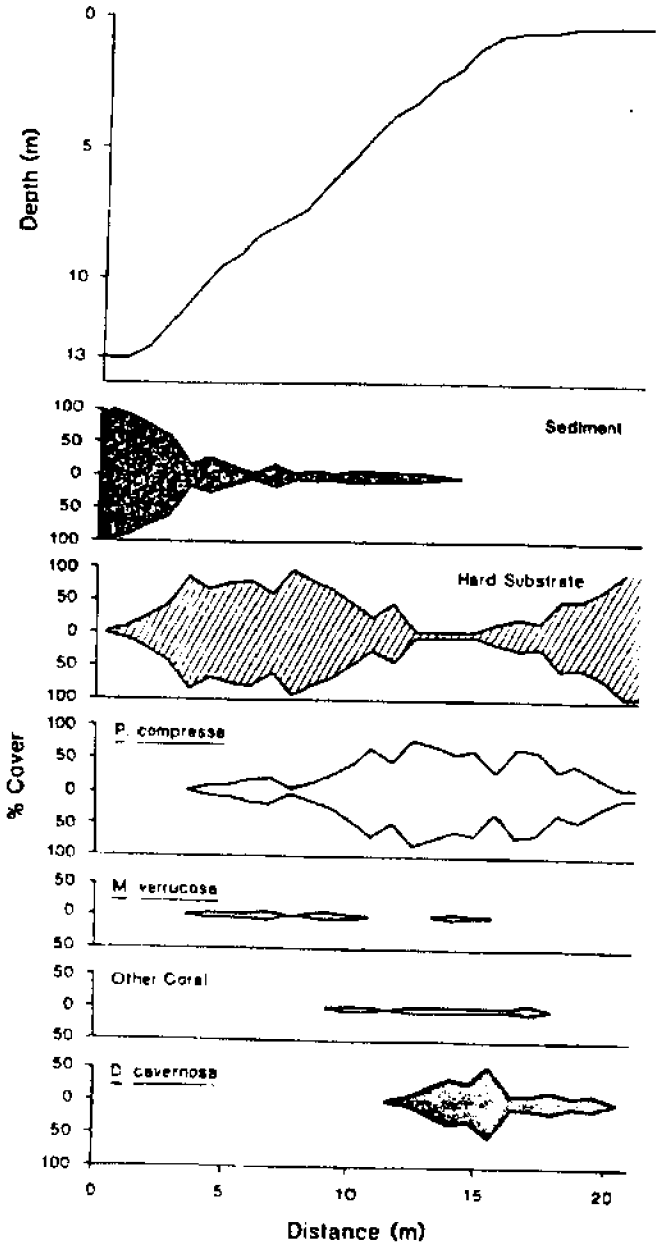


Fig. 4b. Windward patch reef slope, Central lagoon (Fig. 1, site 5).

Patch reefs in the NW sector are very similar to those in the central inner bay. Reef flats commonly have widely scattered heads of Pocillopora damicornis. A few patch reefs have submerged surfaces 1 to 2 m below sea level with almost complete coverage of Porites compressa and Montipora verrucosa. Along the reef face, Porites compressa is dominant, often achieving over 80% cover (Figure 4C). Montipora verrucosa, Pocillopora damicornis, Cyphastrea ocellina, and Fungia scutaria add little coverage to the slope community, but may be more common on the reef crest or reef flat margin. Towards areas of more oceanic influence and wave activity, Porites lobata and Pocillopora meandrina may also be found (Aecos, 1981).

Outer Bay

The barrier reef complex of the outer bay, although much greater in extent, contains a relatively small proportion of the coral coverage found in Kaneohe Bay as a whole. Most of this coral development occurs in the oceanward zones of the barrier reef slope.

Lagoonward depositional slope

Overall coral cover is very low on this sand and coral rubble slope which extends from lagoon bottom depths of about 15 m up to the 1-3 m edge of the back reef flat. In a few locations, patch reefs are being engulfed by the prograding depositions (Roy, 1970). In these situations, the reef slope community is much the same as patch reefs from the central inner bay. Coral coverage is moderate, 30 to 40% at most, and consists mainly of Porites compressa with some Montipora verrucosa in the lower areas. At the NW end of the barrier reef lagoon-ward slope, sections of hard substrate are covered with well developed Porites compressa thickets, extending down to 10 m depths (Maragos, 1974). A similar, smaller thicket occurs near the SE end of the barrier reef opposite the SE channel.

Back reef flat

Little or no coral development occurs on this extensive reef flat of 1-3 m depths of calcareous sediments, until near the algal ridge/reef flat where micro atolls of Porites compressa are found (Roy, 1970). These may be single ovate colonies, or a number of coalescing colony heads, ranging up to 1 m tall and 4 to 5 m across. Further seaward, large massive heads of the coral Porites evermanni are widely space over the generally barren bottom achieving diameters of 1-3 m.

Algal ridge/reef flat

This structure consists of a broad ridge and high energy reef flat. There is a 1 m drop to the back reef flat along portions of its lagoon side, while a gradual slope extends seaward extent of this region. In the SE section of this feature, lagoonward of the wide algal ridge, micro atolls and thickets of Porites compressa become fairly common. These begin to grow together and form ridges or rudimentary reef front spurs perpendicular to the angle of wave incidence (Roy, 1970). NW of Kapapa Island along the algal ridge/reef flat, scattered colonies of Porites lobata, Pocillopora meandrina and some Pocillopora damicornis are encountered (Aecos, 1981).

Kapapa Island platform

The elevated hard substrate of lithified dune material and the calcareous material covering much of this feature from depths of 0.5-2 m generally exhibit less than 5% live coral coverage. On the high wave energy, scoured hard substrate of the windward side of the island, widely scattered heads of Pocillopora meandrina and small encrusting colonies of Porites lobata are the most common species.

Seaward barrier reef

Coral cover on the ocean reef face, which slopes from 3-6 m down to about 27 m, does not exceed 10%. Porites lobata is the most abundant species, with Pocillopora meandrina also common. Both corals occur in greater numbers on the slope areas NW of Kapapa Island (Maragos, 1973). Small colonies of Montipora verrucosa, Porites compressa, Pocillopora damicornis, and lesser amounts of other more rare corals may be found in this area of largely bare substrate.

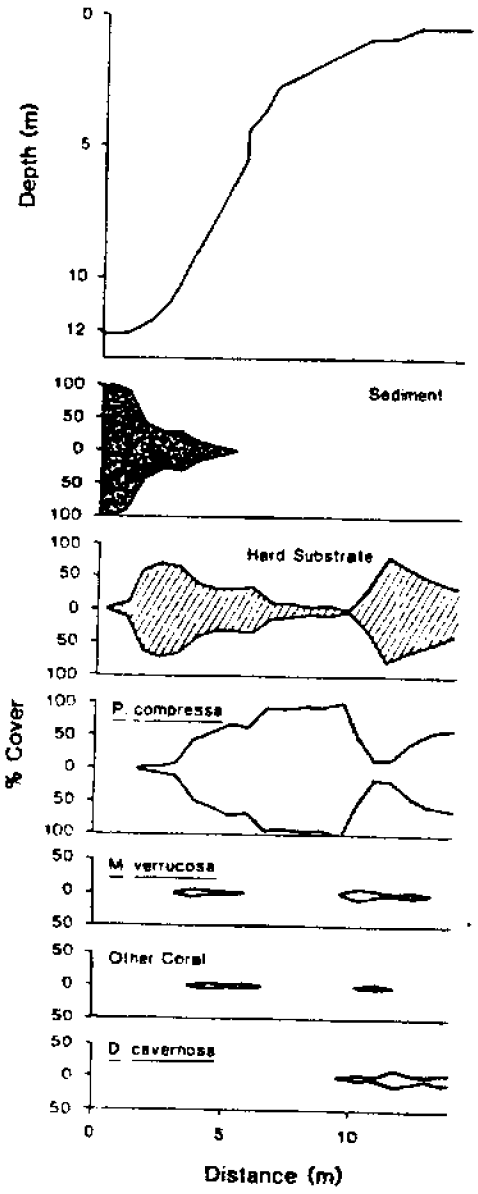


Fig. 4c. Windward patch reef slope, Northwest lagoon (Fig. 1, site 6).

Conclusion

The variation in coral reef communities in Kaneohe Bay not only displays a spatial pattern at all levels, but also has changed considerably over time. The physical factors, and to a lesser extent, biological factors are responsible for controlling coral distribution, abundance, and diversity. However, the impacts of human activities are the most influential in the present temporal, and some of the spatial, patterns to which the coral communities of Kaneohe Bay are still responding and changing.

Acknowledgements

I would like to thank Mr. Paul Jokiel, Dr. Jim Maragos and Dr. Bob Richmond for their review and comments of this paper.

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Bryozoan assemblages in modern coral reefs of Kaneohe Bay, Oahu

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Abstract

Modern coral reefs of Kaneohe Bay, Oahu, host abundant bryozoans. Most prominant are encrusting cheilostomes, but tuft-like and reteporid cheilostomes as well as lichenoporid and tubuliporid cyclostomes are common. Other cheilostomes and cyclostome groups are present in limited numbers.

Bryozoans occur as small (1-10 cm) hidden encrusting colonies on the undersides of coral heads and within cavities in the reef framework. Suitable substrate is of primary importance to bryozoan occurrence. Centers of abundance and diversity are thus limited to coral- and bedrock-dominated habitats of reef environments; bryozoans are virtually absent in sediment-dominated habitats of coastal, reef flat, and lagoon floor environments.

Environmental preferences of the 57 bryozoan species collected indicate three distinct assemblages. Observed species distributions reflect not only availability of substrate but changes in environmental factors (general environmental stability, terrigenous influence, ambient light) with depth and distance from shore. Fringing and patch reef crests and slopes yield predominantly Celleporaria, Cleidochasma, Fenestrulina, Holoporella, Lichenopora, Pollaplocecium, Rhynchozoon, and Tubulipora. Of interest also are large (20-30 cm) erect branching colonies of Schizoporella on artificial substrates in quiet waters. A wave-swept barrier coralgal flat is characterized by limited numbers of Rhynchozoon and Thallamoporella. Stenohaline, deeper ocean slope-bench localities yield abundant Parasmittina, Reteporellina, Schizoporella, and Steginoporella, with moderate numbers of Celleporaria, Holoporella, Lichenopora, Petraliella, Pollaplocecium, and Tubulipora.

Introduction

Many studies offer understanding of modern bryozoan occurrence in estuarine, deltaic, continental shelf, and reef environments (see Dade, 1983 for a list and brief discussion). Of those studies investigating bryozoan faunas of modern or ancient reefs, emphasis has been placed on delineating structural roles and environmental zonation (Cuffey, 1971a, 1971b, 1972a, 1972b, 1973, 1974; Cuffey and Kissling, 1973; Cuffey and Gebelein, 1975; Fonda, 1976a, 1976b; Cuffey and Fonda, 1977; Cuffey, et. al., 1977; Vasseur, 1977; Jackson and Winston, 1982; Cox, 1983).

In general, reef bryozoans are an abundant and diverse group showing well-defined environmental preferences. They are involved in complex competitive relationships due to space limitations. Bryozoans function in reefs as hidden encrusters and, very rarely, as frame builders or cavity infillers. Bryozoans do not contribute significant amounts of material to reef sediments, although skeletal fragments have been observed in sand-sized fractions.

The purpose of this study is to document the tentative identities, relative abundances, and time-averaged distributions of commonly found bryozoans in the shallow waters (less than 20 m depth) of Kaneohe Bay, Oahu. Although taxonomic understanding of the Hawaiian bryozoan fauna has been developing for many years, no discussion of bryozoan distribution has been offered. The information available for Hawaiian bryozoans is in the form of taxonomic descriptions and keys (Bush, 1884; Canu and Bassler, 1927; Soule and Soule, 1968, 1970, 1973) and a discussion concerning faunal affinities (Soule and Soule, 1967). At this time, no attempt was made to reconcile taxonomic problems. An illustrated catalog (Dade and Honkalehto, this volume) enabling at least partial identification of common bryozoans of Kaneohe Bay was completed. Although subject to future revisions, this will facilitate study of this interesting group.

Information on the relative abundances and distributions of the Kaneohe Bay bryozoans would be invaluable to future workers. It would enable comparison of bryozoan assemblages along environmental gradients within Kaneohe Bay and between different geographic localities. Furthermore, a study of this type would provide a basis for future paleoecological interpretation of fossil reefs found in Hawaii and elsewhere.

The Study Area

Kaneohe Bay is a semi-restricted embayment on the northeast windward coast of Oahu. The bay hosts a complex of barrier, patch, and fringing reefs. General environmental descriptions are available in Smith, et al., (1981) and Holthus (this volume).

Methods and Materials

During the months of June and July 1983, 29 sites across the Kaneohe Bay reef complex were visited (Fig. 1). Localities were chosen to cover environments recognized by the authors listed above. Collections of substrate material were made by snorkeling and use of SCUBA with approximately equal effort invested at each site by the same person (B. Dade). Emphasis was placed on collection of live specimens although dead material was taken as it reflects time-averaged distributions.

Material were returned to the Hawaii Institute of Marine Biology and examined for bryozoans. Intact, isolated colonies were air dried or preserved in isopropyl alcohol (70%). Approximately 1100 specimens were identified to the taxonomic level possible given available time and resources. Detailed systematic treatment is now underway.

Simple calculations used in this study (relative frequency abundance, Shannon-Weiner diversity index) are discussed in Brower and Zar (1977). Following the arguments of DeLaubenfels (1954), Coffey (1973), Done (1977), and Kinzie (1978), such easily applied measures are preferable when seeking broad classifications of site groups. It must be emphasized that relative frequency used herein as a measure of abundance does not <u>directly</u> reflect differences in species density or colony size among sites, but rather expresses probability of encounter in a given environment as a function of absolute abundance.

The Bryozoan Fauna

A total of 57 species of ectoproct bryozoans were collected during the summer of 1983, in and around Kaneohe Bay. Included in the collection were 45 cheilostome, 11 cyclostome, and 1 ctenostome species. Of these, 39 species have been identified with confidence and assigned specific titles. More complete taxonomic treatment is forthcoming. No revision of published nomenclature was made. Moreover, this list is not a complete list of bryozoan species previously reported in Hawaiian waters. Bryozoans that have been described from Circum-Pacific as well as subtropical and tropical waters world-wide (Harmer, 1915, 1926, 1934, 1957; Canu and Bassler, 1927, 1928, 1929; Hastings, 1930; Osburn, 1914, 1940, 1950, 1952, 1953; Soule 1961; Lagaaij, 1963; Cook, 1968; Fonda, 1976a; Winston, 1982; Cox, 1983) are also potential members of the Hawaiian fauna not collected during the course of this study.

Commonly found bryozoans of Kaneohe Bay may be placed in easily recognized colony form groups (Table 1). Descriptions of groups and member species may be found in an additional paper by Dade and Honkalehto, this volume.

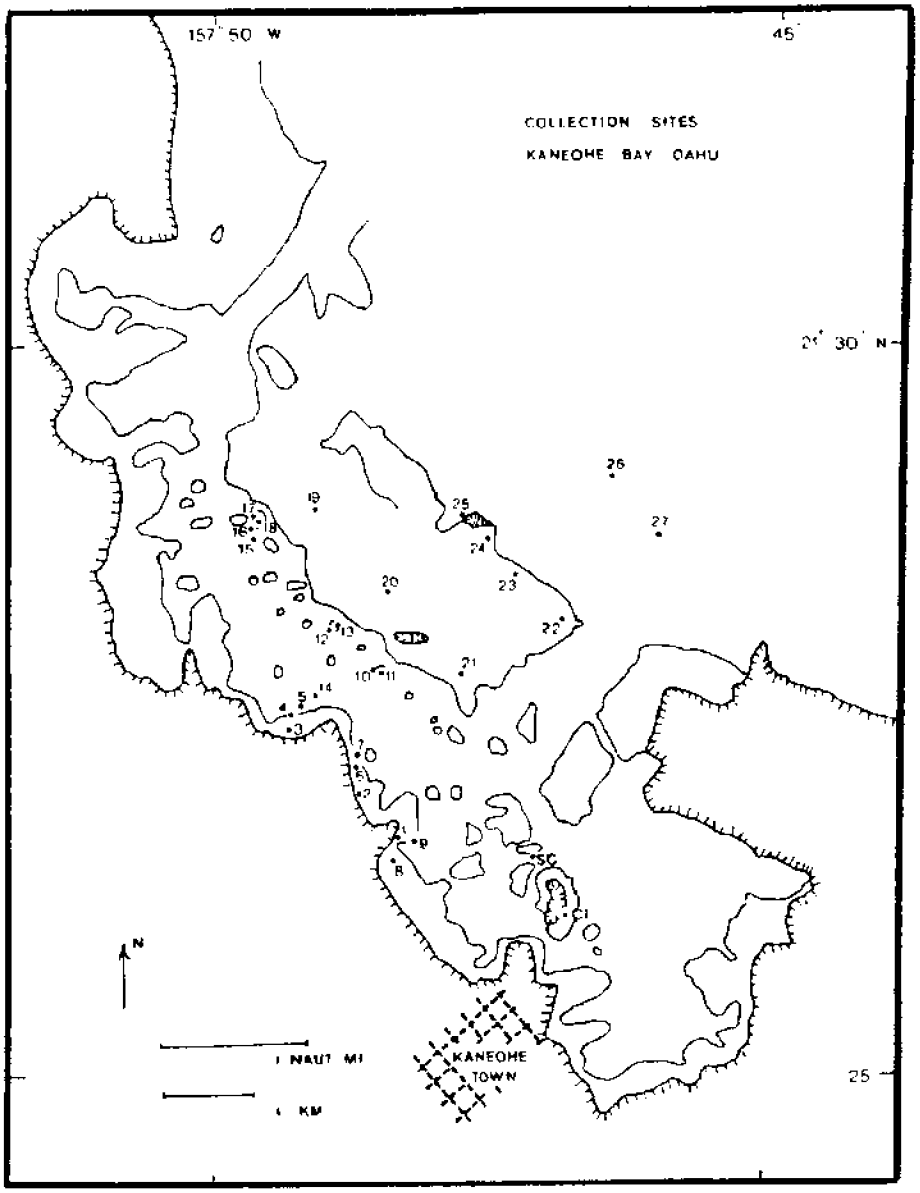


Fig. 1. Collection sites in Kaneohe Bay, Oahu. Solid line represents reefs at or near water surface.

Table 1. Bryozoans of Kaneohe Bay, Oahu, Hawaii.
(**) = abundant (greater than 5% of total fauna)
(*) = common (1% to 5% of total fauna)

Encrusting cheilostomes
Antropora sp.
Arthropoma cincinata (MacGillivray, 1868)
Celleporaria vagens (Busk, 1881)**
Cleidochasma sp.*
Coscinopsis fusca (Busk, 1884)*
Crepidicantha poissonii (Audouin, 1826)
Cribilaria radiata (Moll, 1803)*
Fenestrulina malusii (Audouin, 1826)*
Hemismittoidea corallinea Soule and Soule, 1973
Hippopodina feegensis (Busk, 1884)
Holoporella albirostris (Smitt, 1873)*
Holoporella pilaefera Canu and Bassler, 1929
Bastigaphora penanseris (Smitt, 1873)
Membranipora sp.
Microporella ciliata (Pallas, 1873)*
Parasmittina crosslandii (Hastings, 1930)*
Parasmittina parsevaliformis Soule and Soule, 1973*
Parasmittina serrula Soule and Soule, 1973
Parasmittina uncinata Soule and Soule, 1973*
Parellisina curvirostris (Hincks, 1862)
Petraliella albirostris Canu and Bassler, 1927*
Rhamphostomella sp.*
Rhynchozoon sp. b**
Encrusting cheilostomes
Rhynchozoon sp. c
Rhynchozoon sp. t
Schizoravella sp.
Schizoporella decorata Canu and Bassler, 1927*
Schizoporella unicornis Waters
Steginoporella lateralis MacGillivray, 1895
Steginoporella magnilabris (Busk, 1852)**
Thallamoporella stapifera (Levinsen, 1909)*
Thornelya sp.
Watersipora edmondsonii Soule and Soule, 1968*
Disk-like holoporellid cheilostomes
Holoporella sp.*
Aeteid cheilostomes
Aetea truncata *
Beaniid mats
Beania dircodermiae (Ortmann, 1889)
Beania hirtissima (Heller, 1867)

Table 1 (continued).

Tuft-like cheilostomes
Bugula californica Robertson, 1905
Bugula neritina (Linneaus, 1758)
Pollaploecium brevis Canu and Bassler, 1927**
Scrupocellaria sinuosa Canu and Bassler, 1927*
Tubocellaria sp.
Reteporid cheilostomes
Reteporellina denticulata Busk, 1884**
Lichenoporid cyclostomes
Lichenopora boski Harmer, 1915**
Lichenopora sp. a
Lichenopora sp. b*
Tubuliporid cyclostomes
Oncousoecia sp.
Proboscina major Johnston, 1847
Proboscina sp. a
Stomatopora sp.
Tubulipora pulchra MacGillivray, 1885**
Tubulipora sp. a*
Tubulipora sp. b*
Filifascigerid cyclostomes
Filifascigera robusta Canu and Bassler, 1927*
Crisiniid cyclostomes
Crisina radians Lamarck, 1758
Diaporecia californica (d'Orbigny, 1852)
Ctenostome tufts
Aspathia distans Busk, 1886

Biogeography

Of the 39 identified species, a summary of published distributions appears in Table 2. Zoogeographic affinities of Hawaiian ectoprocts may be most simply interpreted as follows: bryozoans typically have short-lived pelagic larval stages (some membraniporids are exceptions) (Ryland, 1970). Long distance dispersal very likely depends on raftings of adult colonies on logs, alga, and artificial substrates. A large component (46%) of the Hawaiian fauna is therefore cosmopolitan and potentially capable of dispersal throughout circumtropical waters. There is an association with the Indo-West Pacific fauna (21%) and some commonality with the East Pacific species (10%). Of all species reaching the Hawaiian islands, some have undergone speciation. The resulting endemism (23%) is comparable with other marine invertebrate groups (Kay, 1979), and probably reflects inherent genetic variability of certain species coupled with both regional isolation and/or patchy, heterogeous environments typical of a mid-oceanic archipelago. Thus the affinities of the bryozoan fauna so far described from Kaneohe Bay reflect:

1. the relative isolation and environmental heterogeity of the Hawaiian islands; and

2. intermittant exchange width primarily western but also eastern Pacific fauna.

Table 2. Summary of biogeographic affinities of some bryozoans found in Kaneohe Bay, Oahu

	Per cent of identified fauna (N=39)	Number of species
Cosmopolitan-Circumtropical (Atlantic-Pacific-Indian Oceans)	41%	16
Circum-Pacific only	5	2
Indo-west Pacific only	21	8
East Pacific only	5	2
East Pacific-Atlantic only	5	2
Endemic	23	9
	100 %	39

Environmental Distribution of Bryozoans

Substrates

Bryozoans are found on a variety of substrates, but predominatly on the undersides of live and dead branching plate-like corals (Porites, Pocillopora, Montipora), dead solitary corals (Fungia), coralgal rubble, and within reef-rock cavities. Membranipora sp. occurs on glass floats found occasionally in the Bay. Crusts of Watersipora edmondsonii were collected from mangrove roots in Coconut Island lagoon (CI in Figure 1), although none were observed in natural habitats along the coast. "Weedy" species (those that colonize primarily artificial substrates: Amathia distans, Bugula spp., Schizoporella unicornis) were collected from a submerged steel platform (SC in Fig. 1), submerged pilings, and the undersides of docks in Coconut Island lagoon.

Habitats

Habitats are intermediate scale settings that include substrate and surrounding area to 10 m². As such they reflect primarily bottom composition. In Kaneohe Bay there are sediment-dominated habitats of the mangrove coast (sites 1, 2 in Fig. 1), fringing reef flats (sites 3,6,8) leeward barrier reef flat (sites 19-21) and lagoon floor (sites 14,15) environments. These habitats, and subsequently, the corresponding host environment, yield no-to-very restricted bryozoan populations. Coral-dominated habitats are found in fringing and patch reef flats, crests, and slopes (sites 4,5,7,9,10-13,16-18 in Fig. 1), and less importantly in barrier coralgal flat (sites 22-25) and ocean slope-bench (sites 26,27) environments. Bed rock-dominated habitats are characterized by coralgal reef rock and rubble and are most prominant in barrier coralgal flat and ocean slope-bench localities (sites numbered above), but are also found occasionally on fringing and patch reef crests and flats (sites numbered as above). Bryozoan abundance and diversity are centered about coral- and bed rock-dominated habitats.

Environmental Zones and Bryozoan Assemblages

Environmental zones are topographically defined areas (100 m²) of characteristic physical and biological aspect. Recognition of biotic assemblages requires an understanding of the distributions of diversity, abundance, important growth forms, and where possible, dominant species. Diversity is presented here as number of colony forms (Sc), number of species (Ss), and Shannon-Weiner index (H') across the environmental zones developed in Kaneohe Bay (Figure 2). That last measure (H') is less sensitive to differences in collection effort or incomplete observations for rarer species; moreover, the Shannon-Weiner index provides a partial measure of evenness that simple species richness (Ss) does not (Brower and Zar, 1977). Abundance of bryozoans overall and major colony forms are expressed as relative frequency (ni/N, where ni = number of form i in a particular environment and N = total number of all forms in all environments). Examination of Figs. 2 and 3 indicates that centers of overall bryozoan abundance and diversity occur in coral-dominated settings of the lagoon (FC,FS,PS,PC,FF) and ocean slope-bench (OS) environments. Faunas are greatly restricted in the sediment-dominated habitats of coast, reef flat, and lagoon floor environments (MC,FF,LF,BF) and somewhat so in the high energy breaker zone of the barrier reef coralgal flat (BZ).

Major features of the bryozoan fauna are as follows: encrusting cheilostomes are the most frequently encountered forms in all environments. They compose from 70% to 100% of the colonies found on coral reef flats, and about 50% of the colonies taken from lagoon reef crest, slope, and ocean slope-bench settings.

Cheilostome tufts make up approximately 10% of the total Kaneohe Bay collection. They are found in all environments providing adequate substrate. Although tuft-like cheilostomes are prominant members of shallow lagoon reef crests (relative to other forms), their overall abundance appears to increase with depth.

Beaniid mats are not numerous, but are conspicuous on the shallow lagoon reef crests and flats to which they are restricted.

Disk-like holoporellid cheilostomes possess a well-developed center of abundance on lagoon reef slopes.

Peteporid cheilostomes are found in moderate numbers only in deeper, ocean slope-bench environments.

Both lichenoporid and tubuliporid (=idmoneid of Cuffey, 1973, in part) cyclostomes are prominent and widespread members of the overall collection. Their centers of abundance appear on lagoon reef slopes.

Columnar filifascigerid cyclostomes and delicate crisiniid cyclostomes are found rarely in lagoon reef localities and deeper, ocean slope-bench sites, respectively.

Vine-like aeteid cheilostomes occur very sparingly on available substrates throughout the reef complex.

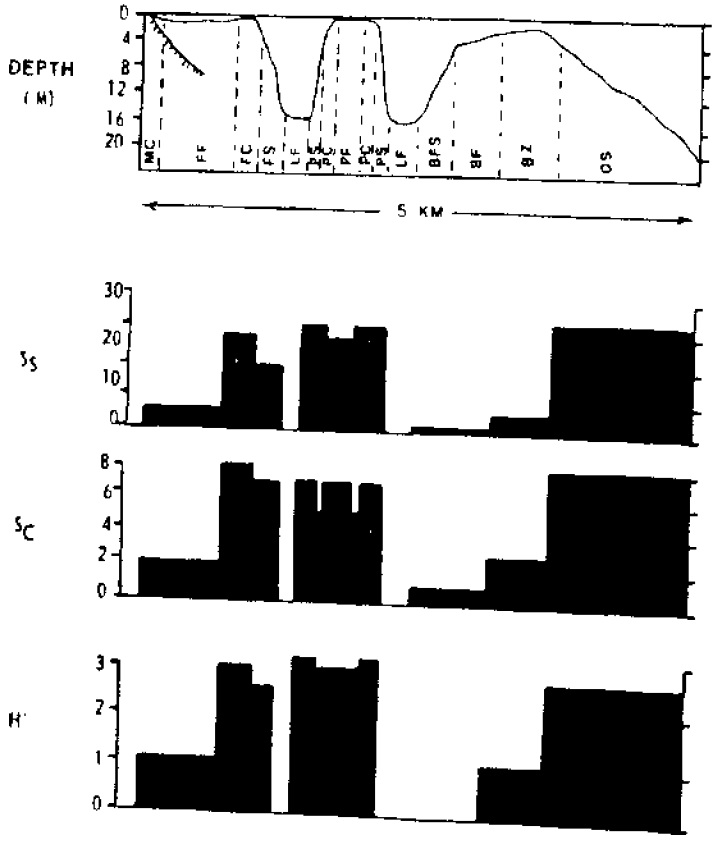


Fig. 7. Diversity of bryozoans in Kaneohe Bay, Oahu. Ss = number of species; Sc = number of colonies; H' = Shannon-Weiner Diversity Index; MC = mangrove coast; FF = fringing reef flat; FC = fringing reef crest; FS = fringing reef slope; LF = lagoon floor; PS = patch reef slope; PC = patch reef crest; PF = patch reef flat; BFS = barrier reef flat-slope; BF = barrier reef flat; BZ = breaker zone of barrier reef algal flat; OS = ocean slope-bench. (Profile from Smith et al., 1981).

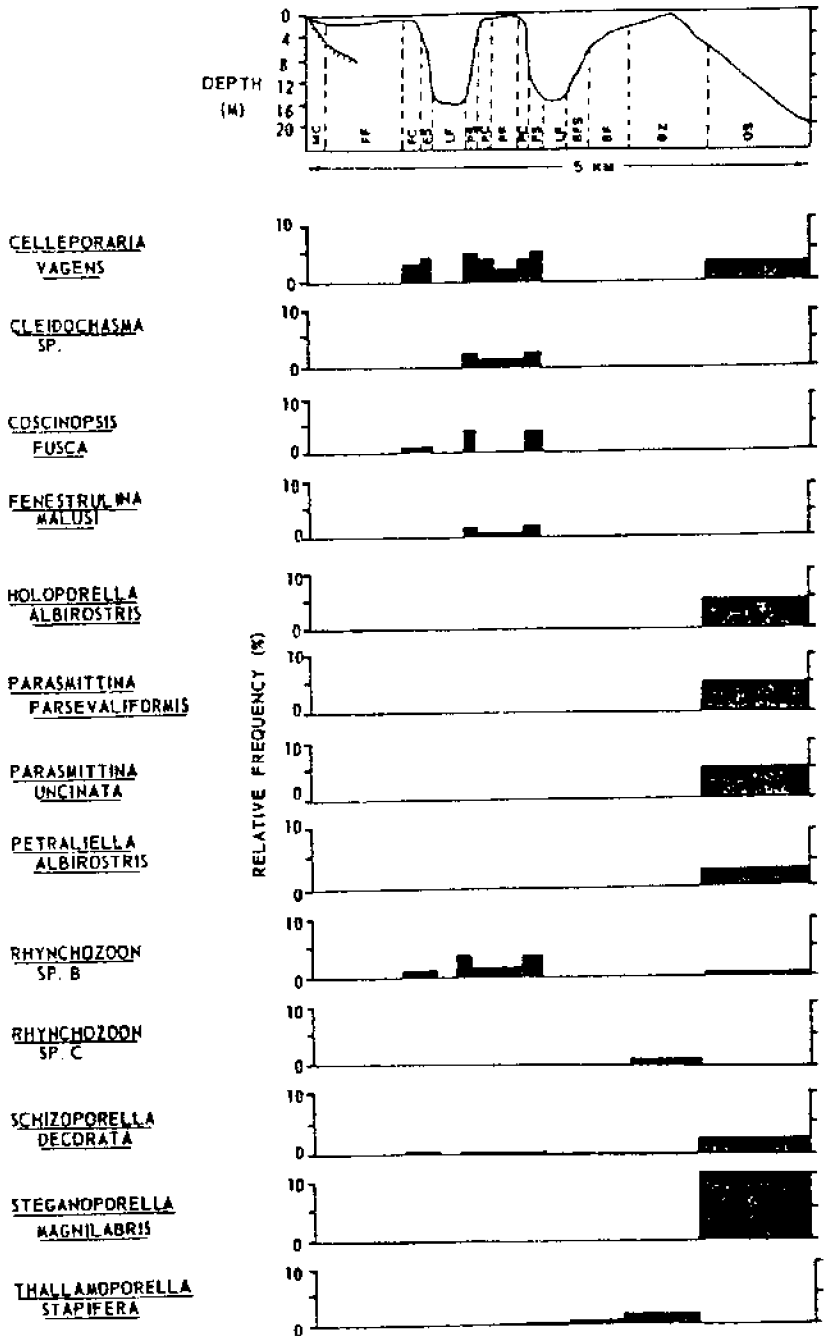


Fig. 3. Abundance of bryozoans in Kaneohe Bay, Oahu. Abbreviations same as Fig. 2.

Most colony forms include one or a few dominant species (Table 1) and for these discussions will be limited to form groups. Encrusting cheilostomes, however, are an abundant and diverse group. Several species are found in such sufficient numbers that environmental preferences may be recognized with confidence (Figure 4). Species shown here make up 1% or more of the total fauna and exhibit distinct zonation (greater than 50% of individual species occurrences in same environment).

Celleporaria vagens, although ubiquitous, is abundant and the dominant encrusting species in lagoon reef environments. Cleidochasma sp., Coscinopsis fusca, Fenestrulina malusii, and Rhynchozoon sp. b have centers of abundance on lagoon reef slopes. Rhynchozoon sp. c and Thallasoporella stapifera occur in limited numbers in barrier reef environments. Parasmittina parsevaliformis, Parasmittina uncinata, and Steginoporella magnilabris are dominant members of and restricted to deeper ocean slope bench localities. Schizoporella decorata, although occurring in a range of environments, is most abundant in offshore localities. Holoporella albirostris and Petraliella albirostris are limited in abundance and restricted to ocean slope-bench waters.

Environmental Factors Affecting Bryozoan Distribution

Generally, distibutions of bryozoan species and morphological groups reflect variability and time-averaged values of significant abiotic and biotic factors (temperature, light, salinity, availability of substrate and nutrients, turbidity, rates of sedimentation, water motion, competitive relationships, and predation) as they change with depth and/or distance from shore (Schopf, 1969; Cuffey, 1970; Jackson, 1979).

Distributions of bryozoans observed in Kaneohe Bay exhibit such limitations. As a whole, bryozoan occurrence is primarily determined by availability of substrate offering refuge from both biotic and abiotic stress. Jackson (1979) suggested that encrusting and erect forms so prevalent throughout Kaneohe Bay (as elsewhere) are well suited for maintaining colonial integrity in competition for substrate. In the same discussion, Jackson also concluded that closely adherent crusts are relatively better suited (than other forms) for environments characterized by high disturbance, water motion, or predation, and predicted relative success for more complexly structured forms in low disturbance, food-limited environments. Compare these predictions with the observed dominance of encrusting cheilostomes in the wave-swept barrier reef coralgal flat (BZ, Figure 3) and restriction of erect, reticulate-to fenestrate reteporids to deeper, stable marine localities (OS).

Among environments with adequate substrate in coral- and bedrock-dominated habitats, average, maximum, and total abundance of bryozoans increases with depth (Figure 5a). These trends most probably reflect a combination of environmental stability (with respect to the factors listed above), availability of substrate (as competition with coral and encrusting alga decreases), and decrease in ambient light levels with depth and distance from shore.

However, diversity is both restricted and variable in waters shallower than 1.0 m in depth (Sc=1-2; Ss=1-4; H'=0.0-1.39), but much higher and fairly constant for depths of 1.0 to 20.0 m (Sc=8; Ss=29-33; H'=2.86-3.04) (Figure 5b). Some species do show environmental preferences (as discussed above). Assemblage transition occurs, then, by member replacement in consistently structured associations in depths greater than 1.0 m. Maintenance of diverse and evenly structured associations may reflect the nature of competitive relationships among coexisting species despite varying levels of environmental stability (see Honkalehto and Dade, this volume, for discussion).

Constructional Roles and Potential for Preservation:
Paleoecological Application

Bryozoans of Kaneohe Bay, as in other reefs (Cuffey, 1974), typically occur as small bidden, calcareous encrusters. They are not framework organisms or major contributers to reef sediments. However, one species, Celleporaria vagens, sometimes forms multilamilar encrustations. Large branching colonies of Schizoporella, similar to those of Kaneohe Bay in form and occurence, have been described as potentially significant contributers to reef sediments in Western Atlantic waters (Cuffey and Ponda, 1976).

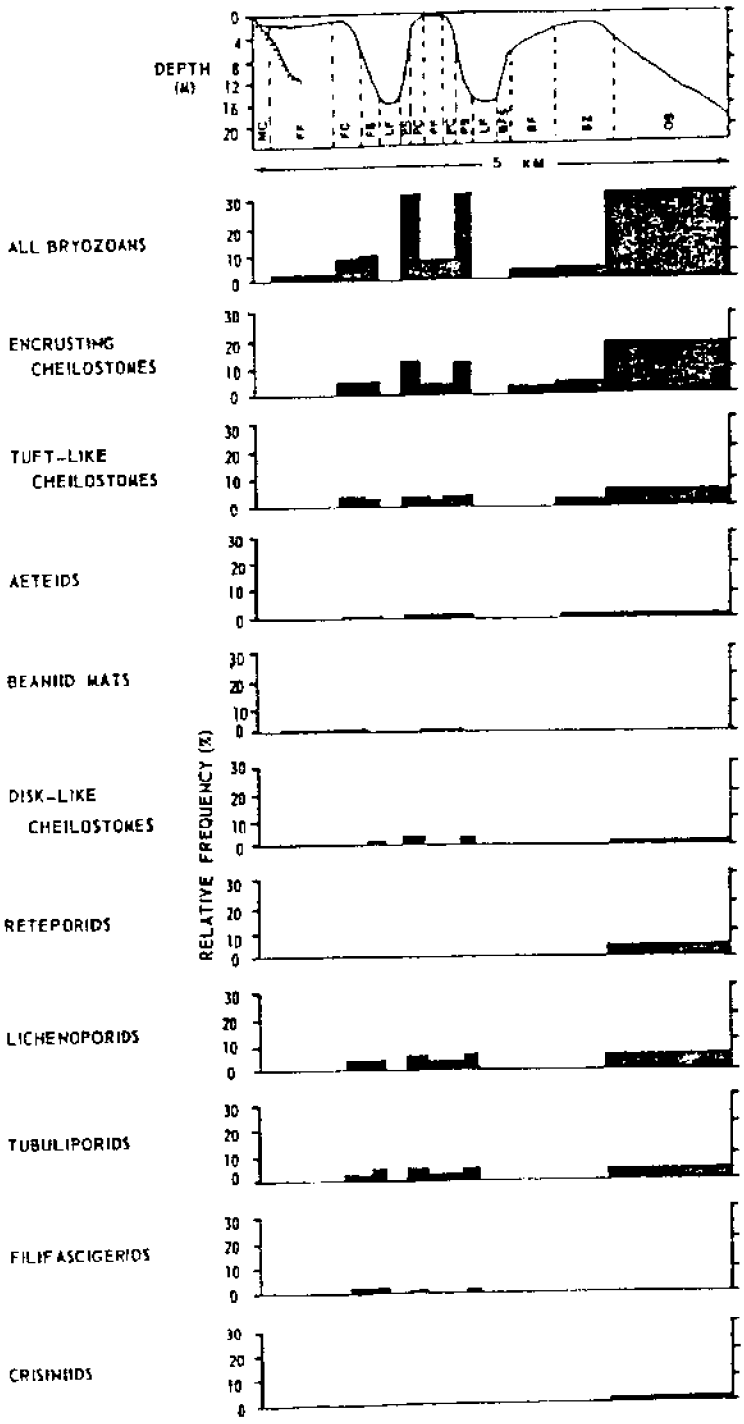
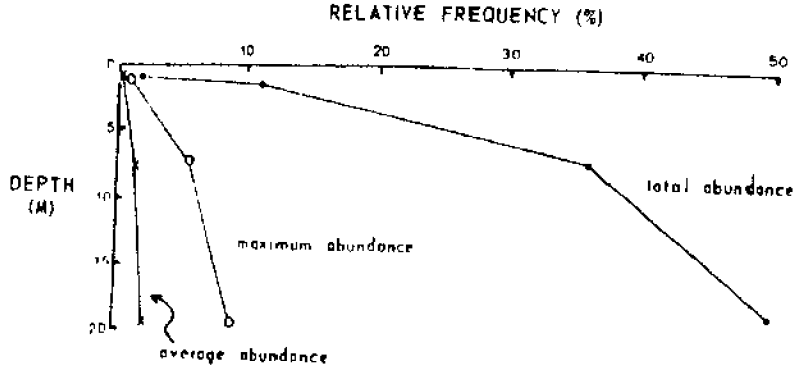


Fig. 4. Environmental zonation of dominant encrusting cheilostomes in Kaneohe Bay, Oahu. Abbreviations same as Fig. 2.

A ABUNDANCE



B DIVERSITY

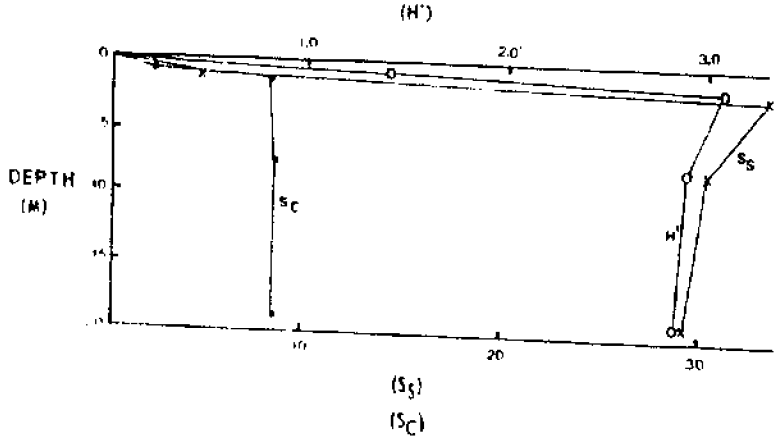


Fig. 5. Bryozoan abundance and diversity with depth in Kaneohe Bay, Oahu. (a) Abundance, (b) Diversity. SS = number of species; Sc = number of colonies; H' = Shannon-Weiner Diversity Index. Data pooled from localities dominated by coral and bedrock habitats.

Bryozoan occurrence as cavity dwellers with calcitic exoskeletons in viable, actively growing reefs (subject to as much as 3.2 cm/yr growth rates; Kinsey, 1978) suggests a likelihood of *in situ* preservation of dominant calcareous forms. The assemblages described herein thus hold potential as valuable tools in paleoecological analysis of fossil reefs.

Summary and Conclusions

Bryozoans are an abundant and diverse group in the reefs of Kaneohe Bay. This study identifies 39 of 57 species (43 cheilostome, 13 cyclostome, 1 ctenostome) collected during June and July 1983.

Common form groups include (in order of importance, with dominant species members): encrusting cheilostomes *Celleporaria vagens*, *Rhynchozoon* spp., *Steginoporella magnilabris*, *Parasmittina* spp., *Coscinopsis fusca*, *Schizoporella decorata*) lichoporid cyclostomes (*Lichenopora buski*) tuft-like cheilostomes (*Scrupocellaria sinuosa*, *Pollaplocium brevis*, *Bugula* spp.); Tubuliporid cyclostomes (*Tuliporа pulchra*) reteporid cheilostomes (*Reteporellina denticulata*) disk-like cheilostomes (*Holoporella* sp.); columnar filifascigerid cyclostomes (*Filifascigerid robusta*) aeteid cheilostomes (*Aetea truncata*) beaniid mats (*Beania* sp.); and crisiniid cyclostomes (*Crisina radians*). In addition, artificial substrates yield specimens of erect, branching colonies of the cheilostome *Schizoporella unicornis* and the cyclostome *Diaporecia californica*. The tuft-like ctenostome *Amathia distans* is found in profusion on the undersides of docks.

Biogeographic affinities of the Kaneohe Bay fauna reflect the geographic isolation of and the importance of chance dispersal to the mid-oceanic Hawaiian archipelago.

Bryozoans occur as hidden encrusters on the undersides of coral colonies, coralgal rubble, and reef-rock cavities. They are not major contributers of framework or sediment material.

Bryozoans are found in greatest abundance and diversity in coral- and bedrock-dominated habitats greater than 1.0 m depth, thus reflecting the importance of suitable substrate. Given substrate, overall abundance increases with depth. Species and colony form distributions are the result of environmental gradients with depth and/or distance from shore.

Resulting bryozoan assemblages are recognized for the following topographically defined environments:

1. *Lagoon reefs* (fringing and patch reefs; 1.0-8.0 m depth) characterized by a diverse and abundant association of encrusting cheilostomes (most prominantly *Celleporaria vagens*, *Rhynchozoon* spp. b, *Coscinopsis fusca*, and *Cleidochasma* sp.) as well as beaniid mats, tuft-like and disk-like cheilostomes, lichenoporid and tubuliporid cyclostomes.

2. *Barrier reef coralgal flat breaker zone* (1.0-2.5 m depth) characterized by a restricted fauna dominated by encrusting cheilostomes (*Thallamoporella stapifera*, *Rhynchozoon* sp. c).

3. *Ocean slope-beach* (15.0-20.0 m depth) characterized by a diverse and abundant association of encrusting cheilostomes (most prominantly *Steginoporella magnilabris*, *Parasmittina parsevaliformis*, and *Schizoporella decorata*), reteporid cheilostomes, tuft-like cheilostomes, and both lichenoporid and tubuliporid cyclostomes.

Bryozoan occurrence as hidden encrusters in centers of calcification and reef accretion will result in their *in situ* preservation. Knowledge of bryozoan distribution in the modern day reefs of Kaneohe Bay can contribute significantly to paleoecological understanding of fossil reefs.

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Common ectoproct bryozoans of Kaneohe Bay, Oahu

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The following is a catalog of short descriptions and illustrations of bryozoans collected during the summer of 1983 in Kaneohe Bay, Oahu. Collection sites and the nature of bryozoan form group and species occurrences are discussed elsewhere (Dade and Honkalehto, this volume). Terminology used in the descriptions of bryozoan skeletal features are defined in The Treatise on Invertebrate Paleontology, Volume G. Simplified representations of generalized features of encrusting bryozoans are shown in Fig. 1. To facilitate identification, classification here is based on colony form, degree of calcification, and shape of zooecial aperature. Proper taxonomic placement may also be found in the Treatise.

I. Encrusting cheilostomes: calcareous, rigid, closely adherant linear or fan-shaped colonies of box-like zooecia;

A. Anascans: frontal wall membranous or very thinly calcified, giving a lacy appearance

1. frontal wall completely membranous, with vestigial frontal calcification in form of embedded, marginal shelf (cryptocyst).

Antropora sp. -- well-developed cryptocyst; small, rounded avicularia paired at proximal corners of zooecia.

Membranipora sp. -- occurring as lacy, unilaminate sheets on floats.

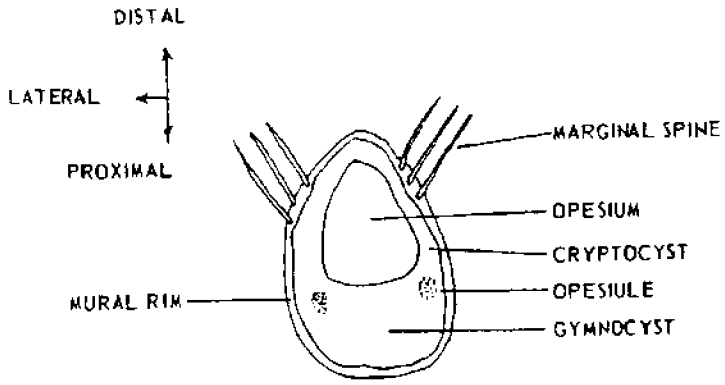
Parellisina curvirostris -- zooecia separated by distinct grooves; cryptocyst narrow and beaded, mural rims poorly developed; avicularia interzooecial, large, curved; ovicell hyperstomial, small, globose, finely granulated. (Fig. 2)

2. frontal wall membranous with well-developed thinly-calcified shelf (cryptocyst) extending across opesium to aperture.

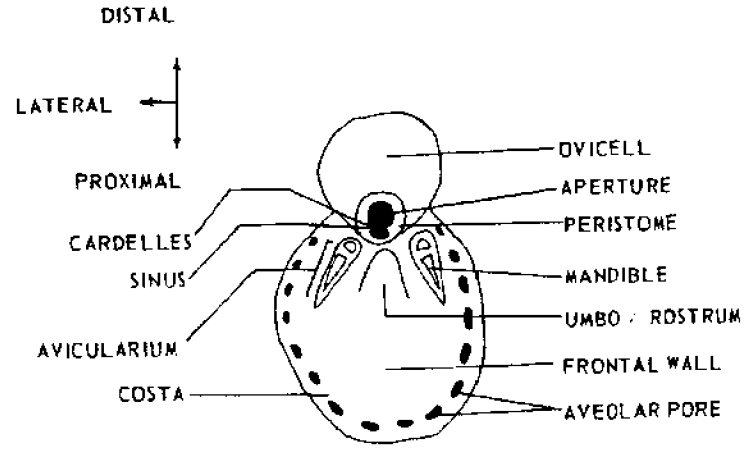
Steginoporella lateralis -- brown crusts; 2 kinds zooecia; all zooecia elongate with well-developed ria, especially at rounded distal end; cryptocyst extending over proximal half of frontal opening; border of apertural covering possesses a distinct, dark brown "-shaped thickening (sclerite). (Fig. 3)

Steginoporella magnilabris -- as above, but crusts are bright red-to-brown and sclerite is a distinct ~ -shape. (Fig. 4).

Thallamoporella stapifera -- aperture large and broadly curved; cryptocyst beaded and extending over entire frontal opening, bearing 2 asymmetrical holes (opesiules). (Fig. 5).



A. MORPHOLOGICAL FEATURES OF ANASCANS



B MORPHOLOGICAL FEATURES OF ASCOPHORANS

Fig. 1. Morphological features of encrusting bryozoans. (a) Anascans; (b) Ascophorans. Adapted from Fonda, 1976b.

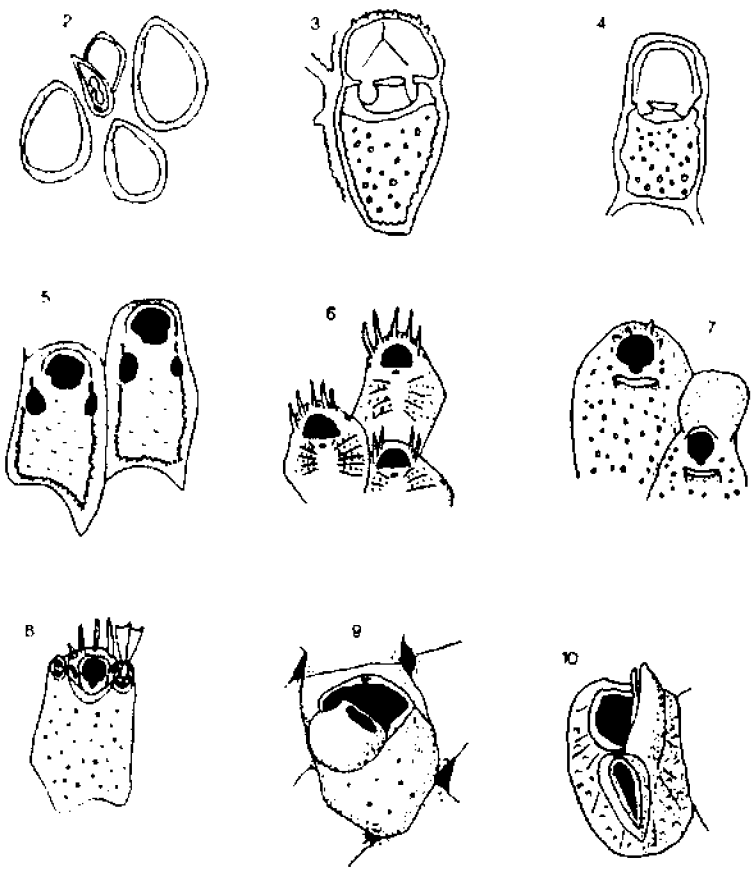


Fig. 2 - Patellicina curvirostris: zooexia; from Osburn, 1950.

Fig. 3 - Steganoporella lateralis: zooecium; after Harmer, 1926.

Fig. 4 - Steganoporella magnilabris: zooecium; after Harmer, 1926.

Fig. 5 - Thallasoporella stapifera: zooecia; from Harmer, 1926.

Fig. 6 - Cribilaria radiata: zooecia; from Osburn, 1950.

Fig. 7 - Arthropoma circinata: zooecia with ovicell; after Osburn, 1953.

Fig. 8 - Mastigophora pesanseris: zooecium; after Osburn, 1953.

Fig. 9 - Rhamphostomella sp.: zooecium.

Fig. 10 - Rhynchozoon sp.: zooecium.

3) frontal surface characterized by transverse ribs:

Cribilaria radiata -- small white crusts; zooecia separated by distinct groove; frontal opening covered by fused, radiating ribs (costae); aperture small, semicircular, with or without spines; large, elongate interzooecial avicularia sometimes present. (Fig. 6).

Ascophorans: frontal wall completely calcified:

1. aperture bearing a sinus or notch on proximal border:

Arthropoma circinatum -- sinus a narrow deep slit; peristome low, bearing 6 spines; proximal to aperture is a small arcuate process; frontal smooth, perforate; ovicell hyperstomial, smooth, imperforate, not closed by operculum; no avicularia. (Fig. 7).

Mastigaphora pesanseris -- small semicircular aperture with deep, narrow notch; raised peristome bearing several distal spines; avicularia paired lateral-oral, with distinctive "bat's wing" appearance. (Fig. 8).

Rhamphostomella sp. -- sinus asymmetrical; aperture surrounded by low peristome; avicularia forming raised mound along peristome, directed laterally or distally; juncture of 5-6 zooecia characterized by large pore. (Fig. 9).

Rhynchozoon spp. -- marginal and older zooecia very dissimilar in appearance; apertures possess beaded arch within:

sp. b -- sinus broadly arcuate; marginal zooecia smooth and possessing 2 spines (sometimes wanting); proximo-oral rostrum long, at placed recurved, and possessing basal or ascending avicularium; frontal knobby or irregularly ribbed, bearing a raised avicularium directed proximally (sometimes wanting); ovicell small, semicircular, flat, smooth, imperforate, and descending into aperture. (Fig. 10).

sp. c -- young zooecia possessing peristome with lateral avicularium; older zooecia with cuspate peristomes; peristomal avicularium raised and oblique or immersed in aperture, ovicells small, flat, descending into aperture.

sp. t -- similar to sp. b but rostra possessing irregular processes (appears 'spiked') and circular, basal avicularia; frontal avicularia long, acute, directed proximally, not raised.

Schizomavella sp. -- sinus shallow, small, arcuate; frontal perforate with distinct marginal groove; small, circular, median suboral avicularium on umbo; ovicell perforate, hyperstomial, flat, and closed by operculum. (Fig. 11).

Schizoporella decorata -- pale pink-to-white in color; rounded sinus; perforate frontal wall; small, rounded avicularia occurring singly or on both sides of aperture, or rarely, on frontal surface; ovicell imbedded and perforate. (Fig. 12).

Schizoporella unicornis -- orange-to-brick red in color; rounded sinus; perforate frontal wall (many small pores); paired or singular acute lateral-oral avicularia; ovicell hyperstomial and perforate; often a small umbo median-proximal to aperture is present.

Watersipora edmondsonii -- darkly pigmented reddish-brown; sinuate aperture with small processes (cardelles) and dark, heavily chitinized operculum; frontal wall perforate; no avicularia, no spines, no ovicells. (Fig. 13).

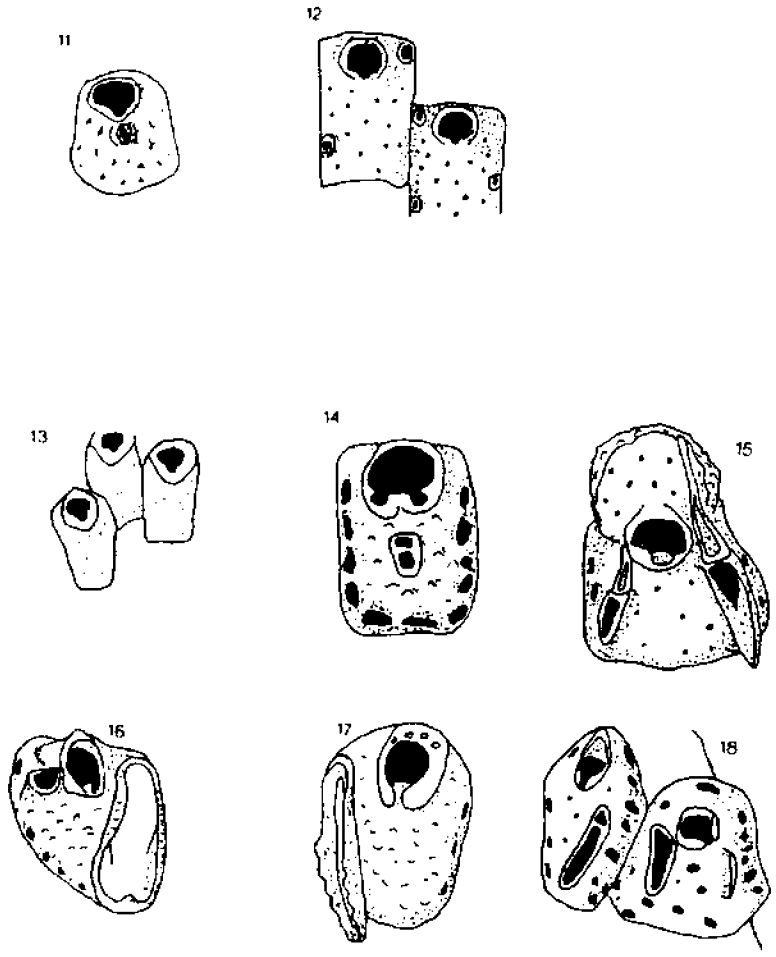


Fig. 11 - Schizosavella sp.: zooecium.

Fig. 12 - Schizoporella decorata: zooecia; after Canu and Bassler, 1927.

Fig. 13 - Watersipora edmonsonii: zooecia; after Soule and Soule, 1968.

Fig. 14 - Hemismittoidea corallinea: zooecium; after Soule and Soule, 1968.

Fig. 15 - Parasmittina crosslandii: zooecium with ovicell; after Soule and Soule, 1973.

Fig. 16 - Parasmittina parsevaliformis: zooecium with giant avicularium; after Soule and Soule, 1973.

Fig. 17 - Parasmittina serrula zooecium; after Soule and Soule, 1973.

Fig. 18 - Parasmittina uncinata: zooecia; after Soule and Soule, 1973.

2. aperture subcircular (not sinuate), bearing a distinct collar (peristome) that is sometimes discontinous or appearing notched; frontal wall bearing pores (areolae) along margin:

   Hemismittoidea corallinea -- white crusts; zooecia elongate, rounded distally; aperture with low, sinuate peristome, sometimes bearing 6 spines and wide denticles; single, small, median avicularium. (Fig. 14).

   Parasmittina crosslandii -- white-to-tan crusts; denticle narrow, slanting downward; aperture sometimes bearing 2-5 spines; avicularia variable, usually paired about aperture: 1 small ovate, and 1 proximally directed, elongate, with acute smooth or finely serrated tips; frontal wall beaded with small areolae; ovicells perforate and brimmed by distal segment of peristome. (Fig. 15).

   Parasmittina parsevaliformis -- yellow crusts, sometimes foliaceous; peristome high, particularly on sides of aperture; denticle not wide; lateral-oral avicularium large, rounded-to-triangular and pointed to aperture; giant frontal avicularium tongue-shaped with bilobate tip; frontal wall glassy possessing small areolae; ovicells bearing a few pores and occasional bulbous avicularium. (Fig. 16).

   Parasmittina serrula -- similar to P. crosslandii, but avicularia occasionally long, recurved, oriented proximally and bearing strongly serrated sides; ovicells possessing many large, irregular pores. (Fig. 17).

   Parasmittina uncinata -- orange-to-yellow foliose crusts; zooecia large and irregularly heaped; peristome high, with proximal narrow slight-like notch and occasional distal protuberance; frontal wall glassy with large areolae; avicularia variable, usually elongate, rounded at ends, and oriented proximally. (Fig. 18).

3. aperture circular or semicircular; no notch or sinus along proximal border:

   Celleporaria vagens -- zooecia brown pigmented with large white-tipped rostra, giving a "hob-nailed" appearance to colony; aperture subcircular with 3-4 denticles along proximal margin; peristome tubular and irregular; median suboral rostra bearing basal avicularium and notch; frontal wall imperforate, granular, and bearing small marginal pores; occasional interzooecial avicularia variably oriented with distinct tri-lobed mandibles; ovicells shallow, open sometimes bearing a process on top margin. (Fig. 19).

   Coscinopsis fusca -- aperture elongate, rounded with cardelles ("hoof-shaped"), collared by a peristome laterally and distally; single or paired lateral-oral acute avicularia oriented distally and inwards; frontal wall beaded and brown pigmented; ovicells large, hyperstomial, closed by operculum, and resembling frontal wall in texture. (Fig. 20).

   Crepidicantha poissonii -- aperture rounded distally with a wide shallow poster proximal to well developed cardelles, overall outline resembling an English derby; frontal wall smooth, inflated, with distinct marginal grooves; whip-like avicularia paired and placed symmetrically and proximally to aperture; numerous spines around zooecial margin. (Fig. 21).

   Fenestrulina malusii -- glistening white crusts of irregularly hexagonal zooecia; frontal wall smooth, inflated, bearing numerous conspicuous stellate pores, a small lunate ascopore, and a distinct marginal groove; aperture semicircular with low peristome, spines may be present; ovicell prominent, perforate, and possessing areolar pores around the base; no avicularia. (Fig. 22).

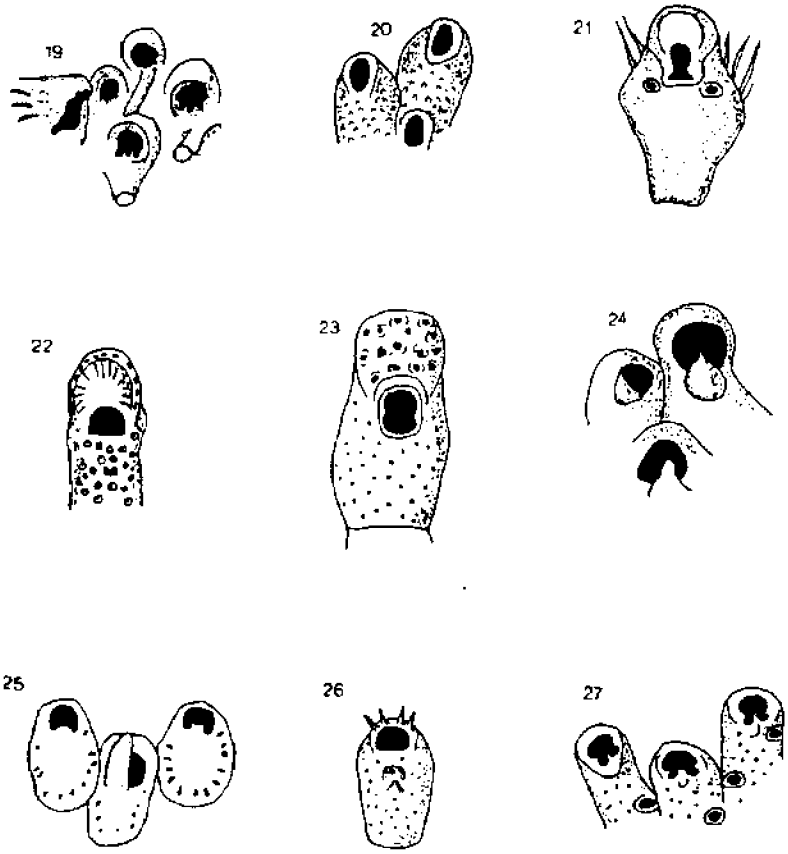


Fig. 19 - Celleporaria vagens: zooecia and avicularium; after Harmer, 1956.

Fig. 20 - Coscinopsis fusca: zooecia; after Canu and Bassler, 1927.

Fig. 21 - Crepidicantha poissonii: zooecium; after Osburn, 1953.

Fig. 22 - Fenestrulina malusii: zooecium with ovicell; after Harmer, 1956.

Fig. 23 - Hippopodina feegensis: zooecium with ovicell; after Osburn, 1953.

Fig. 24 - Holoporella albirostris: zooecia with ovicell; after Osburn, 1953.

Fig. 25 - Holoporella pilaefera: zooecia; after Harmer, 1956.

Fig. 26 - Microporella ciliata: zooecium; after Osburn, 1953.

Fig. 27 - Petraliella albirostris: zooecia; after Canu and Bassler, 1927.

Hippopodina feegensis -- zooecia large; aperture elongate, round ("hoof-shaped"), peristome low; frontal lightly calcified, slightly inflated, and bearing numerous very small pores; single elongate oral avicularium variably oriented; ovicell deeply imbedded in distally adjacent zooecium, perforate, and separated from aperture by distal wall of zooecium. (Fig. 23).

Holoporella albirostris -- very similar to Celleporaria vagens, but frontal smooth and aperture margin lacking denticles; occasional large interzooecial avicularia spatulate but not tri-lobed as in C. vagens. (Fig. 24).

Holoporella pilaefera -- aperture semicircular, no denticles on proximal margin; median suboral process variable in size, bearing a basal avicularium but no notch; frontal wall smooth with distinct marginal pores and commonly with large, projecting spatulate avicularium. (Fig. 25.)

Microporella ciliata -- glistening white crust; aperture semi-circular with low perisome and 5-7 oral spines; frontal wall perforate with small median lunate ascopore; single setose avicularium located proximo-laterally to ascopore, and oriented disto-laterally; ovicell prominent and globose, varying in surface texture. (Fig. 26.)

Petraliella albirostris -- dark brown crusts; aperture large, subcircular, and bearing large lyrule and denticles along proximal border, 3-4 short spines along distal border; operculum darker brown than thickly calcified perforate fronter wall; numerous small circular avicularia placed around aperture and margins of zooecia. (Fig. 27).

Thornelya sp. -- aperture elongate, round ("hoof-shaped"), possessing cardelles; poster broadly arcuate; peristome complete, wide collar bearing 3-7 long oral spines; 1, 2, or rarely up to 4 ascending avicularia located about the aperture; frontal wall with many tubercles and numerous small pores; ovicells hyperstomial, globose, closed by operculum, and bearing a process on top; operculum with distinct, marginal thickening (sclerite). (Fig. 28).

4. aperture key-hole shaped:

Cleidochasma sp. -- colony pink-orange when alive, drying white; aperture with deep, arcuate poster and well developed cardelles curving proximally, giving characteristic shape; frontal wall smooth or finely granular, bearing small marginal pores; 1 or 2 triangular avicularia located on sides of aperture and oriented disto-laterally; occasionally a small suboral median process is present; no ovicells observed. (Fig. 29).

II. Disk-like holoporellid cheilostomes: small (2-4 mm) calcareous, encrusting discoidal colonies of short box-like zooecia with terminal, round apertures:

Holoporella sp. -- small pink colony consisting of a cup- or saucer-shaped plate perched on a short stem; upper surface concave and bearing round terminal apertures of zooecia; aperture surrounded by a wide ridge and 4-8 oral spines; small, ovate interzooecial avicularia. (Fig. 30).

III. Aeteid cheilostomes: thinly calcified, vine-like colonies; post-like zooecia arising from stolen "runner":

Aetea truncata -- colony consists of white creeping stolon with erect tubular zooecia; these tubules smooth, finely perforate textured, with distal end truncated. (Fig. 31).

IV. Beaniid mats: chitinous, light brown, delicate, flexible, loosely adherent colonies attached by rootlets projecting from lower (dorsal) surface; box-like zooecia lacking a frontal wall, interconnected by tubules giving a reticulate appearance:

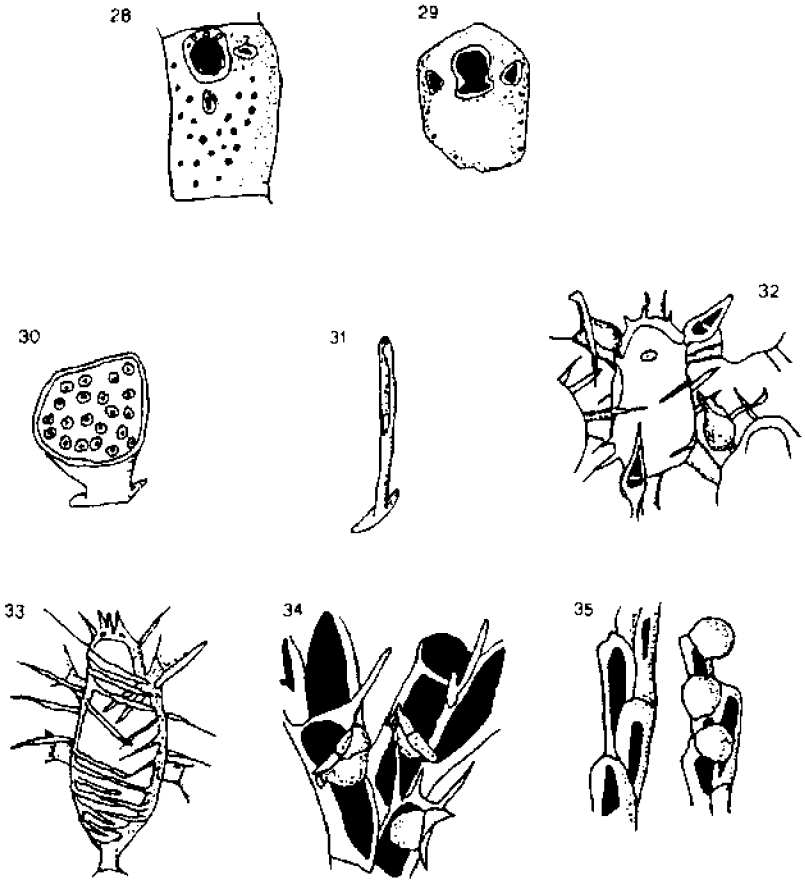


Fig. 28 - Thornelva sp: zooecium; after Harmer, 1956.

Fig. 29 - Cleidochasma sp.: zooecium.

Fig. 30 - Eoloporella sp.: colony.

Fig. 31 - Aetea truncata: zooecium; from Osburn, 1950.

Fig. 32 - Beania discodermiae: zooecium and avicularia; from Harmer, 1926.

Fig. 33 - Beania hirtissima: spined zooecium; from Osburn, 1950.

Fig. 34 - Bugula californica: zooecia and stalked avicularia; after Osburn, 1950.

Fig. 35 - Bugula neritina: zooecia and ovicells; from Soule and Soule, 1968.

Beania discodermiae -- as above; 6 connecting tubules; fenestrae symmetrical, ovate, smaller than zooecia; 10-12 frontal spines; avicularia unilateral or paired, located and oriented distally; avicularium shape globose proximally, elongate distally. (Fig. 32).

Beania hirtissima -- as above, but avicularia wanting and spines very long and numerous, including 5-6 dorsal spines. (Fig. 33).

V. Tuft-like cheilostomes: erect, flexible colonies of box-like zooecia:

A. Anascans: colonies chitinous or very thinly calcified:

Bugula californica -- large white colonies of spirally whorled branches; side walls of zooecia bearing large and small stalked avicularia, distal wall bearing 3 spines and centered, globose ovicell. (Fig. 34).

Bugula neritina -- large, bushy, reddish-brown to purple colonies; no spines or avicularia, ovicells large, rounded, placed on distal axial corner of zooecium; distal outer corner pointed. (Fig. 35).

Scrupocellaria sinuosa -- colony white, usually small and delicate; branches usually consist of seven zooecia, separated by semi-transparent joints; alternating zooecia possess a long bristle (vibraculum) on side wall, and an irregularly shaped shield (scute) over the frontal opening; dorsal sides of branches marked by a distinct sinuous line. (Fig. 36, 37).

B. Ascophorans: colonies calcareous with chitinous, flexible joints:

Pollaplocecium brevis -- colony small, white, attached by chitinous rootlets, and dichotomously branched; branch segments consist of 3-5 zooecia; aperture small, wider than long, and bearing a sinus on proximal border; frontal wall inflated and finely perforate. Ovicell large, and imbedded in zooecium. (Fig. 38).

Tubucellaria sp. -- colony white, attached by dark chitinous rootlets; articulated branches separated by dark chitinous joints; branch segments variable in length and number of zooecia; zooecia imbedded in round stem, with tubular peristome projecting at an angle.

VI. Reteporid cheilostomes: erect, rigid, fenestrate or irregularly reticulate foliaceous colonies; lacy appearance:

Reteporellina denticulata -- colony brown-to-yellow in color; tubular peristome well developed, bearing several cusp-like processes; frontal avicularia large, arched, and bifurcate at tips; ovicells small, smooth, and possessing a median longitudinal slit. (Fig. 39).

VII. Lichenoporid cyclostomes: calcareous, encrusting disk-like or hemispherical colonies of tubular zooecia:

Lichenopora buski -- zooecia radiating uniserially near colony center and arranged in staggered fashion near colony margins; zooecia not attached (connate); peristomes elevated on central side, spined or pointed, and sloping marginally; spines occasionally located over cancelli; central area variable. (Fig. 40).

Lichenopora sp. a -- zooecia attached (connate), radiating unicerially or quincuncially; peristomes appearing square and bearing posts or tubercles at corners; apertures and cancelli equal in size; zooecial radii seperated by 1-2 rows of cancelli; central area flat and low; colony often complex, with many small "subcolonies" of radiating zooecia; purple in color.

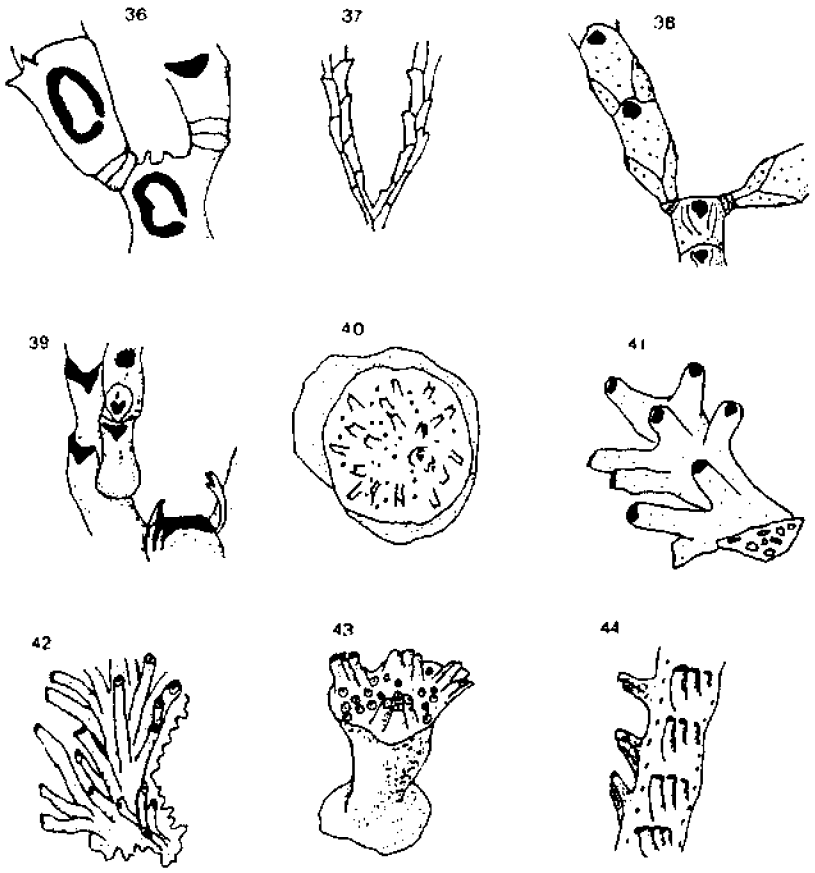


Fig. 36 - Scrupocellaria sinuosa: zooecia; after Canu and Bassler, 1927.

Fig. 37 - Scrupocellaria sinuosa: dorsal surface of colony: after Canu and Bassler, 1927.

Fig. 38 - Pollaploecium brevis: segments of branching colony: after Canu and Bassler, 1927.

Fig. 39 - Reteporellina denticulata zooecia, ovicell, and avicularium; after Harmer, 1956.

Fig. 40 - Lichenopora buski: colony; after Harmer, 1915.

Fig. 41 - Proboscina major colony: after Osburn, 1953.

Fig. 42 - Tubulipora pulchra: colony: after Osburn, 1953.

Fig. 43 - Filifascigera robusta: colony; after Canu and Bassler, 1927.

Fig. 44 - Crisina radians: segment of colony; after Harmer, 1915.

Lichenopora sp. b -- zooecia attached (connate), radiating uniserially in long primary rows and shorter more marginal secondary rows; central area flat or slightly depressed; apertures and cancelli equal in size; pin-sized spicules abundant in cancelli.

VIII. Tubuliporid cyclostomes: calcareous, encrusting, linear or fan-shaped colonies of tubular zooecia:

A. colony rounded, fan-shaped:

Oncousoecia sp. -- zooecial tubules long, projecting from surface, not seriated or bundled.

B. colony linear or strap-like:

Proboscina major -- colony cream colored; zooecial apertures round and little elevated from colony surface; apertures occurring randomly or in transverse rows of 2-4; surface of colony minutely porous. (Fig. 41).

Proboscina sp. a -- as above, but zooecial tubules arranged uniserially or biserially; surface minutely wrinkled.

Stomatopora sp. -- zooecial tubules long, projecting from surface: tubules arranged uniserially.

Tubulipora pulchra -- colony small, white; zooecia singular; lower (dorsal) surface of colony with small attachment processes giving colony edge a serrated appearance. (Fig. 42).

Tubulipora sp. a -- very similar to T. pulchra, but zooecia attached (connate).

Tubilipora sp. b -- cream-colored branching encrustrations; zooecia arranged singly or in transverse rows of 2-3, long salient; apertures round, surface minutely porous and wrinkled; similar to Proboscina spp., but peristomes well developed in Tubulipora.

IX. Filifascigerid cyclostomes: colonies erect, calcareous, rigid, stout columns of tubular zooecia:

Filifascigera robusta -- colonies are erect bundles or fascicles of 17-25 tubules arising as columns from an encrusting base; cream-to-tan in color; terminal apertures subcircular to polygonal in outline. (Fig. 43).

X. Crisiniid cyclostomes: calcareous, erect, rigid, branching colonies of tubular zooecia:

Crisina radians -- small, delicate, bluish-white colonies of bifurcating branches attached by a short stem; tubular zooecia arranged in transverse rows of 2-3, separated by a median longitudinal groove on the frontal surface; cancelli well developed; dorsal side of branches bearing distinct longitudinal ridges and rows of pores; ovicells perforate, place between tubule bases. (Fig. 44, 45).

Diaporecia californica -- similar to Crisina radians, but colonies larger and more robust; zooecial tubules long, recurved, arranged in bundles of 4-5 irregularly placed over frontal surface; tubules at branch bases sometimes fuse giving a reticulate appearance; ovicells large swollen areas spread amongst tube-like zooecia at bases of branches; dorsal side also striated, as in Crisina radians. (Fig. 46).

XI. Ctenostome tufts: erect or semi-erect chitinous, flexible, bushy colonies of small post-like zooecia arising from stem-like stolon:

Amathia distans -- light brown, straggly tufts; branching regularly dichotomous; zooecia short, attached (connate), arranged spirally in biserial pairs about stolon segments. (Fig. 47).

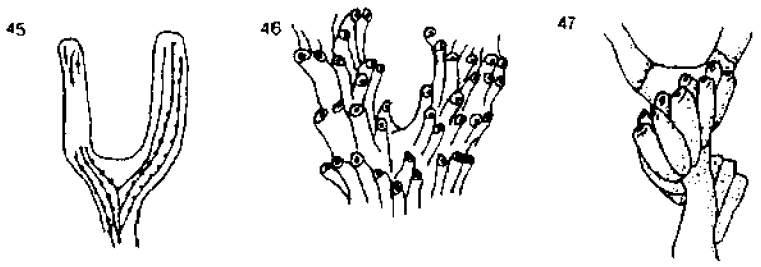


Fig. 45 - Crisina radians: dorsal surface of colony: after Harmer, 1915.

Fig. 46 - Diaporecia californica: colony branching; from Osburn, 1953.

Fig. 47 - Anathia distans: colony segment; after Osburn, 1953.

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Coral reef recovery subsequent to the fresh water kill of 1965.

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Abstract

The recovery of the coral reef community on a patch reef near Kahaluu in Kaneohe Bay was studied. This reef was denuded of live coral by a "fresh water kill" in 1965. The present study (1983) is a resurvey using methods of an earlier (1973) study. The species, abundance, and distribution of corals on the patch reef in 1983 were measured and recorded along a series of transects. Results show large increases in the size and numbers of colonies and coral area coverage. Analysis of distribution reveals an extension of coral coverage further down the reef slope, but with highest abundance in the upper 5 m. Community diversity decreased slightly as the fast growing Porites compressa became more dominant. The pattern of succession at this sheltered site appears to be consistent with results from other investigations in the Hawaiian Archipelago. Recovery appears to be rapid in protected, low wave energy, infrequently disturbed environments of Kaneohe Bay. Almost 20 years after a major reef kill, the Kahaluu patch reef slope coral community appears to be approaching its pre-disturbance condition.

Introduction

Because of the complexity and longevity of coral reef systems, few long term studies have been made of coral community dynamics, especially in the quantitative assessment of coral reef recovery from natural or man-made disturbances. In 1965, Kaneohe Bay, Hawaii experienced heavy rains in conjunction with low tides. This killed many nearshore coral communities (Banner, 1968). In the Central Sector of the bay, a patch reef slope facing the entrance to Kahaluu Stream was completely denuded of live corals. The initial recovery of this coral reef was monitored from 1968 to 1973 (Maragos, 1974). The present study is a resurvey of the Kahaluu patch reef slope coral community to determine the extent of its recovery 18 years after the original disturbance.

Coral reef communities are subject to a variety of destructive events (Stoddart, 1969; Johannes, 1975). Relatively few instances of coral reef recovery have been documented (Endean, 1976). Pearson (1981) defined reef recovery as the restoration of a coral assemblage to a degree comparable to its original state and suggested that this may require several decades following major natural disturbances. The reestablishment of coral reef communities was studied on dated lava flows, and long term succession of coral assemblages was documented (Grigg and Maragos, 1974). The patterns of coral colonization and succession in a newly created habitat were followed in detail over an 11 year period at Honolulu, Hawaii (Maragos, 1983).

The coral reef slope communities throughout Kaneohe Bay were resurveyed in 1983 to document their recovery five to six years after sewage input was diverted to outside the bay (Evans et al., this publication). In other areas, the recovery of reef assemblages disrupted by natural disturbances are considered to be mainly a function of time (Loya, 1976). The response of coral reefs to both man-made and natural perturbations in a variety of locations is reviewed and discussed by Pearson (1981).

In the present study, a series of transects are used to replicate earlier investigations and provide comparative information on the size, abundance, and distribution of corals along the Kahaluu patch reef slope.

Materials and Methods

In July, 1981, a resurvey of the coral community on Kahaluu patch reef, Kaneohe Bay, was carried out. Ten survey stations were evenly spaced along the southern and western (stream facing) slopes of the patch reef, very closely approximating the sites surveyed in earlier studies (Fig. 1). At each station, coral colony size, species composition, and number of species was obtained using the exact methods of Maragos (1974). A 1 m^2 frame was positioned on the reef flat at the slope edge. The maximum diameter and species of each coral colony lying at least 50% within the quadrat were recorded. The frame was then moved down the slope in a series of consecutive 1 m^2 units. Information was gathered in each successive quadrat until no corals were encountered. Thus, a transect 1 m wide beginning at the patch reef crest and extending 6 to 10 m down the reef slope was surveyed at each station.

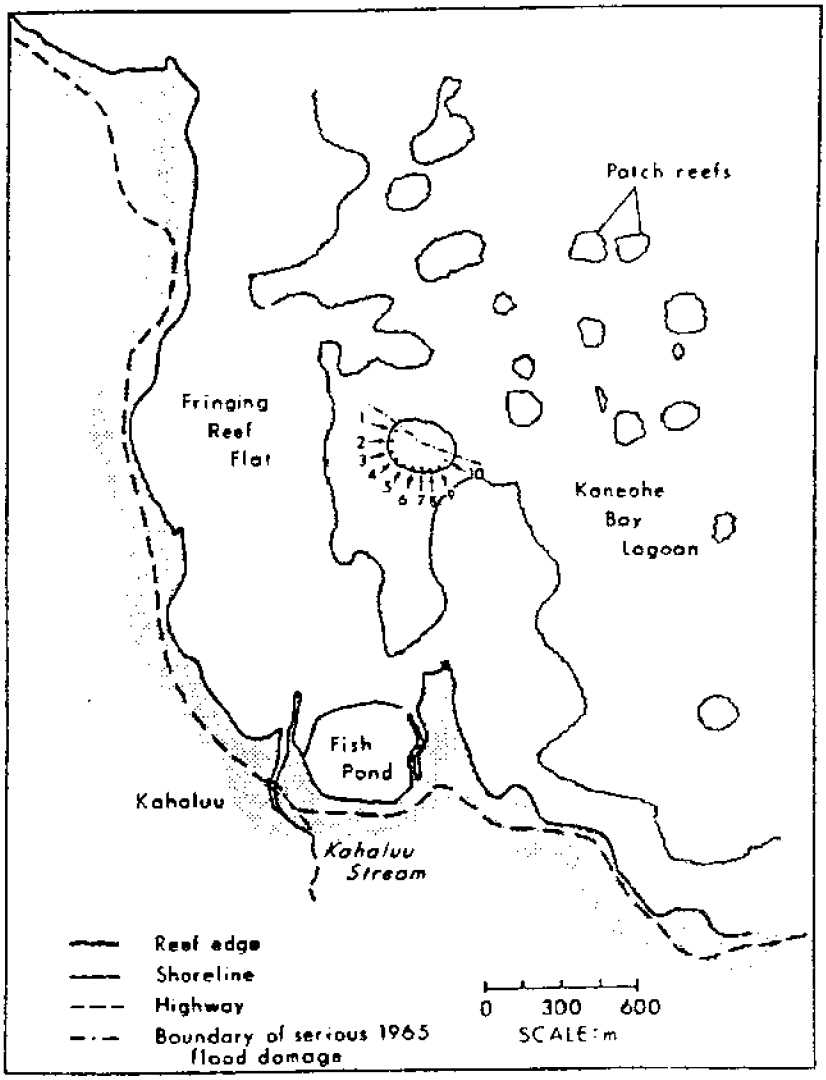

Fig. 1. Location of the patch reef near the Kahaluu Stream where a series of 10 surveys were conducted along a reef face denuded of corals during the 1965 freshwater kill (from Maragos, 1974).

The reef flat edge at this site is a feature of fairly uniform depth composition and relief in relation to patch reef slopes in Kaneohe Bay (Roy, 1970). The reef crest thus served as a reasonable reference point in relocating the start of each slope transect. In quadrats of high per cent coral cover, colonies may abutt and grow together, forming aggregate heads of more than one colony. In this situation, discernable color and morphological differences enabled individual colonies to be counted separately. A few larger colonies had dead central and upper portions. These were measured as whole live colonies unless highly fragmented, in which case the distinct live portions were measured. In addition to specific data, photos were taken and general observations regarding water quality, substrate composition, and other organisms present were noted.

Field data were compiled and compared to data from the earlier survey of Maragos (1974). This allowed us to determine the extent of recovery. Species composition was examined in terms of total numbers of colonies and total area cover. To calculate area coverage, colony diameters were converted using the formula Area=3.14 r^2 where r= 1/2 the diameter. This conversion formula may be biased in favor of flat, encrusting corals over multi-dimensional branching colonies. Also, per cent coverage per quadrat m^2 may be distorted. For this reason absolute amounts of coral cover are used in making comparisons and not per cent cover per quadrat.

Coral distribution was analyzed both vertically and horizontally along the patch reef slope. Horizontal zonation was examined by plotting coral abundance, as expressed in numbers of colonies and total coral area coverage for each transect station. Vertical zonation was displayed by plotting both the number of colonies and total coral area coverage per quadrat meter measured down the reef slope. The maximum growth rate for each species was calculated by averaging the diameters of the largest five colonies for each species, in both 1973 and 1983. Coral community diversity was measured and compared by applying the Shannon-Wiener Index to the information collected.

Results

On Kahaluu patch reef in Kaneohe Bay, between 1973 and 1983, coral abundance increased in colony numbers and and area coverage (Table 1). Coral coverage increased by over 660% while the total numbers of colonies rose about 150%. The same four coral species (Porites compressa, Montipora verrucosa, Pocillopora damicornis, and Cyphastrea ocellina) constitute nearly all of the coverage and colonies encountered. Size frequency distribution reveals the shift towards greater numbers of larger colonies for Porites compressa, Montipora verrucosa, and Pocillopora damicornis (Table 2). In 1973, no colonies greater than 30 cm were found. By 1983, over 25% of the colonies measured were larger than that size. In contrast, Cyphastrea ocellina displayed a marked increase in the number of smaller colonies in 1983, which may be as a result of its response to decreased sewage in Kaneohe Bay (Evans et al., this publication).

The changing distribution of coral abundance was examined horizontally along the reef face and vertically along the patch reef slope. No distinct patterns related to distance from the surviving reef slope community were obvious in the measurement of total coral coverage or number of colonies (Table 3, Table 4). Vertically down the reef slope, in 1973 a zone of high coral coverage and colony numbers occurs in the upper five quadrat meters. By 1983, the coral coverage in this zone has expanded greatly while the total numbers of colonies has not increased much (Table 5, Table 6). Although the extent downslope at which corals are encountered had nearly doubled by 1983, the main zone of high coral abundance extends only slightly further downslope.

Growth information for each species revealed Porites compressa and Montipora verrucosa to be growing rapidly. Pocillopora damicornis showed a gradual increase, while Cyphastrea ocellina growth leveled off after 1973 (Table 7). The shift in coral community composition is apparent in the increasing dominance of Porites compressa (Table 1). As the reef slope coral assemblage returns to its former condition, the number of colonies per m^2 decreases gradually as coverage per m^2 increases, especially in the case of Porites compressa (Table 8). This change is reflected in a slight decline in community diversity, from 0.50 to 0.45, as measured by the Shannon-Wiener Index of community diversity.

Discussion

The study of coral reef recolonization and recovery in the Hawaiian Islands is facilitated by the relatively small number of coral genera present and the

Table 1. Summary of transect data for the two surveys.

Species	1973 SURVEY Area (cm^2)	1973 SURVEY Area % of Total	1973 SURVEY Number of Colonies No.	1973 SURVEY Number of Colonies % of Total	1983 SURVEY Area (cm^2)	1983 SURVEY Area % of Total	1983 SURVEY Number of Colonies No.	1983 SURVEY Number of Colonies % of Total
Porites compressa	52,882	86.3	346	73.1	358,066	97.8	530	74.9
Montipora verrucosa	6,259	10.2	54	11.4	39,196	9.6	61	8.6
Pocillopora damicornis	1,963	3.2	67	14.2	4,433	1.1	72	10.2
Cyphastrea ocellina	152	0.3	6	1.3	393	0.1	41	5.8
Montipora patula	0	0	0	0	5,792	1.4	3	0.4
Porites lichen	0	0	0	0	3	<0.1	1	0.1
Totals	61,256	100%	473	100%	407,883	100%	708	100%

Table 2. Size frequency distribution for combined transect data. Table values are number of coral colonies for each size class.

	Colony size class (diameter in cm) 0-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100
Porites compressa										
1983	114	112	117	90	62	29	4	1	0	1
1973	166	128	52	0	0	0	0	0	0	0
change	-52	-14	+65	+90	+62	+29	+4	+1	0	+1
Montipora verrucosa										
1983	23	19	4	5	3	3	3	1	0	0
1973	33	19	2	0	0	0	0	0	0	0
change	-10	0	+2	+5	+3	+3	+3	+1	0	0
Pocillopora damicornis										
1983	62	7	3	0	0	0	0	0	0	0
1973	62	5	0	0	0	0	0	0	0	0
change	0	+2	+3	0	0	0	0	0	0	0
Cyphastrea ocellina										
1983	41	0	0	0	0	0	0	0	0	0
1973	6	0	0	0	0	0	0	0	0	0
change	+35	0	0	0	0	0	0	0	0	0
Other (Montipora patula, Porites lichen										
1983	2	0	0	0	0	1	1	0	0	0
1973	0	0	0	0	0	0	0	0	0	0
change	+2	0	0	0	0	+1	+1	0	0	0
TOTAL										
1983	242	138	124	95	65	33	8	2	0	1
1973	267	152	54	0	0	0	0	0	0	0
change	-25	-14	+80	+95	+65	+32	+7	+2	0	+1

Table 7. Horizontal zonation: Area coverage (cm^2) of coral in all quadrats at each station.

	Station									
	1	2	3	4	5	6	7	8	9	10
Porites compressa										
1983	53754	31353	34040	41688	49250	50727	34098	42536	42884	27051
1973	5881	4129	5552	6281	5785	3169	4574	4921	7915	4674
change	+47207	+24886	+26753	+28916	+24541	+40238	+29217	+36549	+29417	+17462
Montipora verrucosa										
1983	361	1980	1682	5635	17455	7260	291	986	3304	243
1973	699	292	1484	1270	694	1095	521	0	126	79
change	-338	+1688	+198	+4365	+16761	+6165	-230	+986	+3178	+164
Pocillopora damicornis										
1983	242	358	41	742	1450	52	16	20	180	832
1973	80	523	13	98	314	570	57	184	30	93
Change	+162	-165	+28	+644	+1136	-518	-41	-164	+150	+739
Cyphastrea ocellina										
1983	64	3	13	110	20	8	0	60	13	103
1973	0	3	0	0	20	122	0	0	7	0
change	+64	0	+13	+110	0	-114	0	+60	+6	+103
Others (*Montipora patula*, *Porites lichen*)										
1983	0	0	0	3	0	0	0	0	2054	3737
1973	0	0	0	0	0	0	0	0	0	0
change	0	0	0	+3	0	0	0	0	+2054	+3737
TOTAL										
1983	53754	31353	34040	41688	49250	50727	34098	42536	42884	27051
1973	6661	4948	7049	7649	6813	4955	5152	5105	8078	4846
change	+47093	+26405	+26991	+34039	+42437	+45772	+28946	+37431	+34806	+22205

Table 4. Horizontal Zonation: Number of colonies in all quadrats at each station.

		Station 1	2	3	4	5	6	7	8	9	10
Porites compressa	1983	54	59	39	66	42	75	40	61	46	40
	1973	57	44	42	37	37	17	24	20	45	25
	change	-3	+15	-3	+29	+5	+58	+16	+41	+1	+15
Montipora verrucosa	1983	3	9	2	6	15	8	4	2	7	3
	1973	12	4	11	10	6	3	4	0	2	1
	change	-9	+5	-9	-4	+9	+5	0	+2	+5	+2
Pocillopora damicornis	1983	6	8	2	15	8	3	1	1	7	16
	1973	9	9	4	8	12	9	2	4	3	10
	change	-3	-1	-2	-7	-4	-6	-1	-3	+4	+6
Cyphastrea ocellina	1983	1	1	1	10	2	2	0	10	1	11
	1973	0	1	0	0	1	3	0	0	1	0
	change	+1	0	+1	+10	+1	-1	0	+10	0	+11
Other[1]	1983	0	0	0	1	0	0	0	0	3	1
	1973	0	0	0	0	0	0	0	0	0	0
	change	0	0	0	+1	0	0	0	0	+3	+1
TOTAL	1983	64	77	44	98	67	88	45	74	64	71
	1973	78	58	57	55	58	32	30	24	51	36
	change	-14	+19	-13	+43	+11	+56	+15	+50	+13	+35

[1]Montipora patula, Porites lichen.

Table 5. Vertical Zonation: Mean coral cover (cm^2) per m^2 quadrat.

	Distance (m) down reef slope from crest 0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10
Porites compressa										
1983	2696	8349	7165	6652	5026	2196	1548	1243	852	81
1973	97	762	2807	1426	191	6	0	0	0	0
change	+2599	+7587	+4358	+5226	+4835	+2190	+1548	+1243	+852	+81
Montipora verrucosa										
1983	81	585	70	1270	968	362	364	6	187	27
1973	0	33	137	439	18	0	0	0	0	0
change	+81	+552	-67	+831	+950	+362	+364	+6	+187	+27
Pocillopora damicornis										
1983	48	233	25	71	4	2	0	4	0	0
1973	21	53	61	56	2	0	0	0	0	0
change	+27	+180	-36	+15	+2	+2	0	+4	0	0
Cyphastrea ocellina										
1983	15	10	11	3	0	0	0	0	0	0
1973	1	0	10	4	0	0	0	0	0	0
change	+14	+10	+1	-1	0	0	0	0	0	0
Other (Montipora patula, Porites lichen)										
1983	205	0	0	0	0	0	0	374	0	0
1973	0	0	0	0	0	0	0	0	0	0
change	+205	0	0	0	0	0	0	+374	0	0
TOTAL										
1983	3045	9177	7271	7996	5998	2560	1912	1627	1039	108
1973	119	848	3015	1925	211	6	0	0	0	0
change	+2926	+8329	+4256	+6071	+5787	+2554	+1912	+1627	+1039	+108

Table 6. Vertical zonation: Mean number of coral colonies per m² quadrat.

	Distance (m) down reef slope from crest									
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10
Porites compressa										
1983	8.4	12.3	8.2	8.7	5.4	2.6	2.2	2.9	1.2	0.3
1973	4.8	9.1	12.9	6.5	1.2	0.3	0.0	0.0	0.0	0.0
change	+3.6	+3.2	-4.7	+2.2	+4.2	+2.3	+2.2	+2.9	+1.2	+0.3
Montipora verrucosa										
1983	0.5	0.9	0.5	1.0	1.1	0.5	0.6	0.4	0.5	0.0
1973	0.0	0.6	1.5	3.4	0.1	0.0	0.0	0.0	0.0	0.0
change	+0.5	+0.3	-1.0	-2.4	+1.0	+0.5	+0.6	+0.4	+0.5	0.0
Pocillopora damicornis										
1983	1.3	1.7	1.4	1.1	0.7	0.1	0.0	0.4	0.0	0.0
1973	1.5	2.9	1.4	1.2	0.1	0.0	0.0	0.0	0.0	0.0
change	-0.2	-1.2	0.0	-0.1	+0.6	+0.1	0.0	+0.4	0.0	0.0
Cyphastrea ocellina										
1983	1.5	1.1	0.8	0.5	0.0	0.0	0.0	0.0	0.0	0.0
1973	0.2	0.0	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0
change	+1.3	+1.1	+0.6	+0.3	0.0	0.0	0.0	0.0	0.0	0.0
Other (*Montipora patula*, *Porites lichen*)										
1983	0.1	0.2	0.1	0.0	0.0	0.0	0.0	0.0	0.1	0.0
1973	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
change	+0.1	+0.2	+0.1	0.0	0.0	0.0	0.0	0.0	+0.1	0.0
TOTAL										
1983	11.7	16.2	10.6	11.3	7.2	3.2	2.8	3.7	1.7	0.3
1973	6.5	12.6	16.0	11.3	1.4	0.3	0.0	0.0	0.0	0.0
change	+4.2	+3.6	-5.4	0.0	+5.8	+2.9	+2.8	+3.7	+1.7	+0.3

Table 7. Maximum coral growth rates for each species. Based on average of largest 5 colony diameters (cm).

	1965	1973	1983	18 yr. rate(cm/yr)
Porites compressa	0	27.0	79.2	4.1
Montipora verrucosa	0	19.6	65.6	3.6
Pocillopora damicornis	0	13.6	22.4	1.2
Cyphastrea ocellina	0	5.8	6.4	0.4

Table 8. Comparison of number of colonies and mean coverage for the two surveys.

	Mean no. of colonies per m² quadrat		Mean cover (cm²) per m² quadrat	
	1973	1983	1973	1983
Porites compressa	7.6	6.4	1149.6	4420.6
Montipora verrucosa	1.2	0.7	136.1	483.9
Pocillopora damicornis	1.5	0.8	42.7	54.7
Cyphastrea ocellina	0.1	0.5	3.3	4.9
Others[1]	0.0	0.1	0.0	71.5
Total	10.8	8.5	1331.7	5035.6

[1]*Montipora patula*, *Porites lichen*.

low speciation within genera (Maragos, 1977). The occurrence of 30 coral species in the Kaneohe Bay area waters was studied by Maragos (1972), who found about half of these to be commonly distributed in the lagoon reefs. Grigg and Maragos (1974) proposed a pattern of reef coral succession after examining coral community composition, distribution, and structure on a series known-age submerged lava flows and on reference reefs adjacent to the flows on the island of Hawaii. The number of coral species present, density, per cent cover, and diversity were studied in relation to age of the substrate and degree of exposure to sea and swell at each station. Although all of these sites were more exposed to destructive physical disturbances than Kahaluu patch reef inside Kaneohe Bay, similarities of coral assemblage development are evident.

At the most sheltered stations, Grigg and Maragos found that coral cover is high and that the amount of cover is negatively related to exposure. Further, where coral cover is high, diversity is low, indicating dominance since the number of species present was relatively constant. In less exposed situations, where physical processes are not constantly interrupting succession, diversity rises initially as more and more corals colonize the available substrate. As space becomes limiting and interspecific interactions increase, the competitively successful species become dominant and diversity decreases. In the sheltered environment of Kaneohe Bay, this pattern of less interrupted succession is apparent. The amount of coral cover continues to increase while the number of colonies per unit area decreases. One species, Porites compressa, assumes an increasing dominance in the reef slope community as diversity gradually decreases. Grigg (1983) considers this coral to be competitively superior and that it will eventually dominate a community where wave stress is not an important factor.

In a detailed study on the island of Hawaii, Maragos (1983) systematically followed the development of coral communities after the construction of Honokohau Harbor in 1970. Although the protected harbor environment was much more favorable to coral colonization and growth, successional patterns similar to those on lava flows were found. The more rapid coral community development in the harbor is thought to be due to greater protection from wave exposure and the stability and suitability of the substrate, conditions comparable to the situation at Kahaluu. In Honokohau Harbor, the mean frequency of coral colony numbers reached a plateau six years after the substrate became available while coral abundance, as estimated from per cent coverage, continues to rise eleven years after construction. Presumably, colony numbers would begin to decline in the near future as space becomes limiting, similar to what is occurring in the eighteen year old recovering reef community at Kahaluu. An encrusting species, Porites lobata became more and more dominant over time on the boat harbor substrates.

Growth rate information is similar from both the Honokohau and Kahaluu situations. Common species of the genera Porites and Montipora show initial and continued fast growth. Small encrusting corals such as Cyphastrea ocellina exhibit persistent slow growth. The dominance of Porites in terms of size, frequency, and surface coverage becomes established at advanced stages of community succession in both study areas. In the lava flow and Honokohau studies, the low community diversity of early stages rises rapidly to an intermediate peak as more corals become established and continue to grow. However, with the increasing dominance of Porites, community diversity at Honokohau decreases markedly seven years following the creation of the available habitat. The lack of intermediate time period data from Kahaluu prevents determining whether the same pattern emerged as explicitly from this study.

However, as in other cases documented on Hawaii, diversity of the coral community at Kahaluu is seen to be decreasing due to increased dominance of Porites. In both the lava flow and Honokohau studies, Pocillopora meandrina is a major component of the community. Pocillopora meandrina is absent from areas other than the high wave energy regions of Kaneohe Bay (Maragos, 1973). The recovery of the reef slope community at Kahaluu probably also has been influenced by effects of sewage which was discharged into Kaneohe Bay until 1978 (see Evans et al., this publication).

There are many variables in the factors governing the recovery of coral reef communities. Pearson (1981) discusses three important areas of contention which cloud the issue. First, it is not clear what constitutes a climax community. It might differ from one locality to the next. Also, the question of time scale

is involved. Secondly, external disturbances may alter succession, preventing the attainment of any form of a climax community. Thirdly, coral settlement is modified by both the successional process and any disturbance, as are the factors influencing coral settlement and survival. Loya (1976) concludes that the difference between man-made polluting activities and natural catastrophes on coral reefs is the possibility that the human perturbed environment will not return to its former configuration, while reconstitution of reef areas denuded by natural disturbances is mainly a function of time. Grigg and Maragos (1974) estimate complete recovery of reef corals on lava flows off the island of Hawaii may occur within 15 to 50 years depending on environmental factors. The results from previous surveys in Kaneohe Bay by Maragos (1974) indicate that protected environmental conditions and other factors may result in complete reef slope recolonization within 30 years.

The present study suggests that the patch reef at Kahaluu is not fully recovered eighteen years after destruction. Coral community succession appears to be proceeding rapidly in a pattern suggested by previous investigations in Hawaii. Because of the length of time required for complete coral reef recovery, future studies should continue to follow the reestablishment of coral communities in these types of situations where initial surveys have been made after major disturbances.

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Reef corals in Kaneohe Bay. Six years before and after termination of sewage discharges (Oahu, Hawaiian Archipelago)

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Abstract

Watersheds surrounding Kaneohe Bay were dominated by rural and agricultural use before 1939. Reef coral communities flourished on lagoon reef slopes and were protected from the open ocean by a large barrier reef. After 1939, military dredging and filling, residential development, and population growth occurred, especially in and around the confined southeast bay. As population grew, sewage discharges into the lagoon increased, culminating in the construction of large sewage outfalls in the southeast bay by 1963.

After 1965, the scientific community, including Maragos (1972), began to study changes in the lagoon. It was speculated that eutrophication and sedimentation, as a result of urbanization and construction, were the cause of an observed decline in lagoon coral communities in the south lagoon and explosive growth of the green algae Dictyosphaeria cavernosa, which was smothering coral, in the middle lagoon. Reef corals in the bay's northwest lagoon remained abundant and appeared unaffected.

Pressure from the public and scientific community compelled the local government and military to terminate large sewage discharges in the southeast lagoon by 1978. Now only a minor amount of sewage is discharged in the northwest lagoon.

In 1983 we re-surveyed the lagoon and coral transects sites of Maragos (1972) using the same methods. These surveys revealed a remarkable recovery of corals, especially Porites compressa and Montipora verrucosa, in the southern and middle lagoon and continued high coral abundance in the northern lagoon. Minor coral species, Pocillopora damicornis and Cyphastrea ocellina, also were more abundant in the lagoon. In contrast, Dictyosphaeria declined greatly except for a minor increase in the northern lagoon.

This study and other recent investigations corroborate that sewage was a major stress to lagoon corals and a stimulant to Dictyosphaeria growth. In addition, these studies indicate that the detrimental effects of sewage on corals are generally magnified in combined embayments with restricted circulation.

Introduction

This study documents the response of lagoon reef coral populations in Kaneohe Bay to the reduction of sewage discharge into Kaneohe Bay by comparing the abundance and distribution of corals before and after the sewage removal. The original data were collected in 1970-71 at 14 lagoon stations by Maragos (1972) and at one station by Jokiel (unpublished). In late 1977 to mid 1978, the two major point sources of sewage discharge into the lagoon were eliminated. In 1983 we resurveyed coral populations at the same 15 lagoon stations using the same techniques.

Kaneohe Bay, located on the windward northeast coast of Oahu, is Hawaii's largest embayment, stretching 13 km along the coast and 4 km offshore. A large 4 km-long barrier reef occurs 1-2 km offshore from the center of the bay. The barrier and adjacent fringing reefs protect the lagoon from heavy wave action and restrict water circulation and exchange, especially in the isolated southern end of the lagoon (Fig. 1). The barrier reef is deeper in the north end of the bay, contributing to more vigorous wave action and water circulation there. As a consequence the lagoon can be divided into three physiographic sectors: the northwest semi-exposed, the central, and the isolated southeast sectors. The whole system of lagoon waters and associated reefs in the bay is unique to Hawaii. Kaneohe Bay has been extensively studied because of the presence of the Hawaii Institute of Marine Biology since 1951 at Coconut Island in the southern lagoon. Prolific coral communities have developed in the protected lagoon environment of the bay, especially on the steep lagoon slopes and shallow outer margins of the barrier, patch and fringing reefs. Although most reef coral species reported from Hawaii are found in Kaneohe Bay, only a few species dominate lagoon habitats, with the finger coral Porites compressa comprising over 80% of the total live coral cover (Maragos, 1972). The only other abundant species is Montipora verrucosa. Other common species include Pocillopora damicornis, Montipora verrucosa. Other common species include Pocillopora damicornis, Pavona varians, Cyphastrea ocellina, Fungia scutaria, and Montipora patula. About a dozen other coral species have been reported from the lagoon, including a soft coral Zoanthus pacifica and the ahermatypic coral Tubastrea coccinea.

Historical Background

Prior to western contact, the Hawaiian population in the Kaneohe watershed was principally involved with taro and fish culture (Devaney et al., 1976). The bay waters were regularly fished, and over 30 rock-walled fishponds managed along the inner reef and mud flats. The 19th century saw the decline of the Hawaiian culture and the development of ranching and large-scale agriculture in the bay, including rice, pineapple and sugarcane. However, by the end of the century, much of the bay watershed had reverted back to small scale farming, rangeland, and rural use.

Beginning in 1938, the bay underwent major changes to accommodate military and residential development, especially in the south. A major decade long military dredging and filling operation, concentrating on lagoon reefs, resulted in expansion of land area and the construction of a military air station at the southern headland of the bay (Mokapu); clearing of reefs and other hazards in the south lagoon to establish a seaplane runway; and dredging of a ship navigation channel from the south lagoon to the north end of the bay. Dredged materials not used for landfilling were dumped back into the lagoon. The 1940's ushered in a era of major residential development in the southern bay with rural lands cleared and many fishponds filled for housing tracts. The land disturbance caused soil erosion and sedimentation in the lagoon from stream runoff during periods of heavy rainfall. Much of the sediment settled in the deep lagoon (Roy, 1970). Between 1920 and 1980, the population of the bay grew from less than 5,000 to over 60,000.

Sewage discharges into the lagoon increased in response to population growth. The Marine Corps Air Station at Mokapu began to discharge sewage into the south lagoon in 1951 (Site "A", Fig. 1). Between 1951-1972, that sewage was subjected only to brief settling of the major solids. Afterwards an additional step of biological decomposition was added to the treatment process. In 1963 a large City and County municipal outfall began discharging secondary treated sewage into the south lagoon (Site "B", Fig. 1). A smaller secondary sewage treatment plant and outfall was established at Ahuimanu in 1970 to service the light rural and residential population of the north bay (Site "C", Fig. 1). This sewage entered Ahuimanu Stream and eventually the northern lagoon waters of the bay. By 1977 the combined effluents of the three sewage plants and outfalls totalled over 7.5 million gallons per day (20,000 m^3/day), with 95% being discharged into the south lagoon (Smith et al., 1981).

In the late 1960's, marine scientists became alarmed at the deteriorating condition of the lagoon's coral communities and suspected dredging and filling, sewage pollution, and sedimentation from urbanization to be the major causes (Roy, 1970; Banner and Bailey, 1970; Maragos, 1972; Smith et al. (eds), 1973; Maragos, 1974; Banner, 1968, 1974; Devaney et al., 1976; and Hollett, 1977). In 1968, Maragos initiated coral growth and mortality studies using transplanted corals to monitor response to bay environmental conditions. At each of 25 transplant stations, many of which were in the lagoon, he also conducted tran-

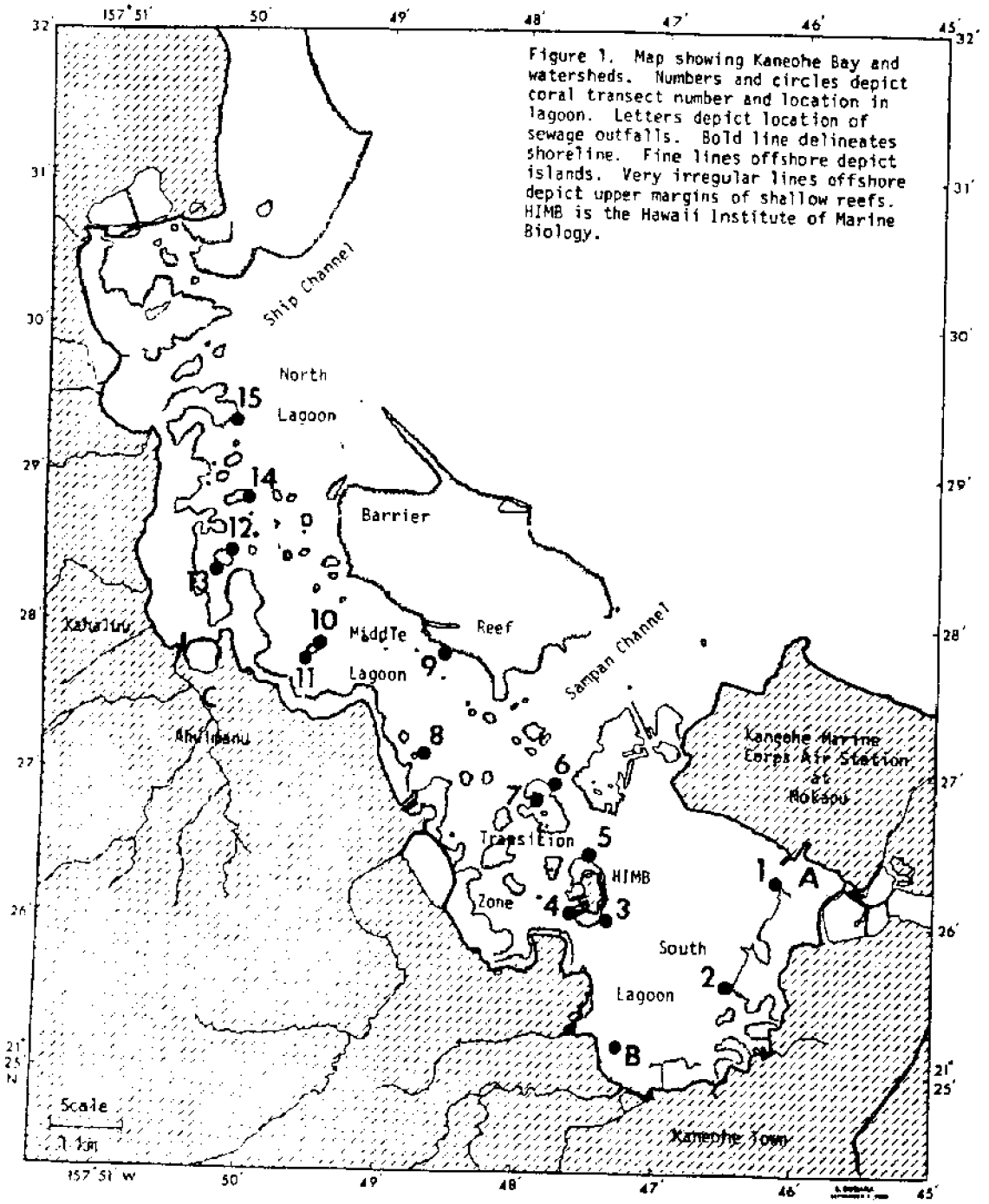

Figure 1. Map showing Kaneohe Bay and watersheds. Numbers and circles depict coral transect number and location in lagoon. Letters depict location of sewage outfalls. Bold line delineates shoreline. Fine lines offshore depict islands. Very irregular lines offshore depict upper margins of shallow reefs. HIMB is the Hawaii Institute of Marine Biology.

sect quadrat surveys in 1971 to estimate abundance and distribution of reef coral populations. The scientific community collectively blamed the decline of corals in the south bay on pollution from dredging and urbanization, and implicated sewage as stimulating the growth of a green alga (Dictyosphaeria) that was smothering corals in other parts of the lagoon. However, there were never any adequate baseline surveys of reef coral populations in the lagoon prior to bay dredging and filling operations, sedimentation, and sewage pollution. Hence the decline of coral populations was never really documented historically nor the causative factors clearly deliniated.

Nevertheless, considerable scientific and public concern over the welfare of the bay led the county and federal governments to remove sewage discharges from the south lagoon, and by mid 1978 both major sources were completely diverted to a deep ocean outfall outside the bay. Smith et al. (1981), anticipating the diversion project, studied and monitored bay ecosystem response by measuring physical, chemical, geological and biological characteristics before and after actual sewage diversion. Although this study succeeded in documenting the short term bay response to sewage diversion, it was not specifically designed to monitor reef coral populations and the one year post-diversion phase of the study was insufficient to document the post-diversion response of lagoon reef coral populations. Corals typically respond more slowly than other organisms.

In 1983, a summer course on coral reefs was held at the Hawaii Institute of Marine Biology and allowed us to collaborate on a resurvey of the lagoon transect sites of Maragos (1972). Since our resurvey was 5-6 years after diversion of sewage from the south lagoon, we felt this interval was sufficient to document changes, if any, to reef coral populations attributed to reduction of sewage. Hence we used the same techniques and sites of the earlier study to document the more recent condition of reef corals and to compare the results to the earlier survey results accomplished at the same sites 6 years before sewage diversion.

Methods

The 14 transect surveys accomplished by Maragos in 1971 in the lagoon were resurveyed by us (Fig. 1). An additional station (#8 on Fig. 1) located in the middle lagoon and originally surveyed by Paul Jokiel in late 1970 was also resurveyed because Jokiel accomplished the survey using the same techniques. During the earlier study, notes on locations were recorded. Also markers were left at the Maragos transects, which consisted of the original coral transplant platforms. Once over each site, Maragos used snorkeling gear to relocate the platforms and properly position the transect lines.

At several sites the original platforms could not be located because they had moved (#5), become overgrown with live coral (#6), were buried under natural accumulations of reef sediment (#7) or were not present (#8, #10). However, from memory and notes, Maragos was able to position all but one of the resurvey sites to within one to five meters of the original alignments. At only one site (#6 on Fig. 1), the original survey site could not be accurately relocated because coral growth within the 12-year interval was so prolific as to obliterate previous bathymetric features and the 'seascape' as it was remembered. We estimate that the resurveyed site was still within 50 m of the original survey site. In any case it was not possible to exactly replicate the earlier transect studies at any of the stations.

In addition to data variation attributed to changes in the coral populations over time, the inability of replicating the earlier alignments introduces data variation attributed to spatial changes in abundance and distribution of corals over small distance on a reef. To estimate the magnitude of this variation (or "error") and compare that to the magnitude of variation attributed to the time factor, we accomplished two transects at each of the 15 stations during our 1983 resurveys. The transects were aligned parallel to one another separated by a distance of 3-5 m. Data obtained from the "replicate" transects at each station were later compared to one another in addition to the comparisons between stations.

The survey data were collected using the contiguous quadrat method originally followed by Maragos (1972). At each station, SCUBA assisted divers laid out a 25 m long transect line from the top to the bottom of the reef slope, perpendicular to the depth contours. At all stations except #6, the line was long enough

to encompass the entire coral community on the reef slope with the deep end of the line on the muddy lagoon floor (devoid of coral) and the shallow end on the reef flat where coral growth is normally less developed. At station number six, 29 quadrats were required, and at least 20 quadrats were accomplished at all stations.

A one meter square quadrat frame divided with wires into a grid of 100 square of equal area (measuring 10 cm on a side) was laid and centered over the bottom end of the transect line. The diver then recorded on underwater writing tablets the coral species, other bottom types (sand, mud, rubble, dead coral, coralline algae), or selected algae (Dictyosphaeria cavernosa, Eucheuma sp.) under each square. The minimum "resolution" of this technique was half a grid square (50 cm^2). Species less than this size were noted as being "present". Data on depth and slope angle were also recorded for each quadrat. After completing the census for the first quadrat position on the line, the quadrat frame was then flipped over to the next position up the slope, on the line, and the census repeated until the quadrat survey reached the top of the line. This approach enabled a top-to-bottom profile of the reef slope one meter wide to be surveyed for each transect.

The raw data from the transects were later transcribed and converted to percent cover estimates for each species of coral or algae enumerated in the quadrat. Later the quadrat data were pooled to give percent live cover and distribution estimates for each species reported on the transect.

Results

The raw data from the 1971-72 and 1983 surveys are presented in Table 1 for each transect of the 15 stations. Transect data on total live coral and Dictyosphaeria coverage plotted against depth are summarized by region (north, middle, and south bay) in Fig. 2. A transition zone region was added as a subdivision of the middle bay region which includes the four mid bay transect stations closest to the south region. The transition "zone" encompasses the lagoon sector immediately south of the barrier reef but within the influence of enhanced water circulation near Sampan Channel and also within the influence of south lagoon waters moving north past Coconut Island. Transect Stations 1-3 constituted the south bay sites, Stations 4-7 the transition zone sites, Stations 8-11 the mid bay sites, and Stations 12-15 the north bay sites. A fourth south bay station was also surveyed (located adjacent to Kaneohe Municipal outfall "A" on Fig. 1) but no living corals or Dictyosphaeria were reported during either the 1971 or 1983 survey. Table 2 presents distributional data for individual species of corals encountered during the surveys, and Fig. 3 summarizes for the bay as a whole the changes in vertical abundance of Dictyosphaeria and live corals between the earlier and later surveys.

Space did not permit the presentation of replicate transect data plots for each of the 15 stations. However, data in Table 1 show that the variation between replicate transect data was in most cases much less than the variation between the 1971 and 1983 transect data at the same stations. This is strongly evident for plots of total live coral cover vs. depth at all except most north bay stations and Stations 4 and 6 in the transition zone. This is also evident for plots of Dictyosphaeria cover vs. depth at all except the south bay stations and Stations 12 and 13 in the transition zone. These results suggest that overall coral coverage in the north lagoon did not increase by 1983. Coral coverage was already high at 3 of 4 stations. Increases in coral coverage at Station 13, and to a lesser extent Station 12, were attributed to rapid recovery from a freshwater coral kill in 1965 (see Holthus, this volume). A slight decrease in coral coverage at Station 15 may have been the result of recent encroachment by Dictyosphaeria which increased dramatically at the site since 1971.

Dictyosphaeria was nearly absent in both the 1971 and 1983 surveys in the south bay presumably because conditions were still unfavorable for the algae. As noted earlier, coral surveys in 1983 at Station 6 probably involved a different population compared to the 1971 survey, and the bathymetry at the 1983 site was much different from the 1971 site. This could explain the anomalous minor "decline" in coral coverage at Station 6. Although coral coverage in shallow depth at Station 4 did not increase over time, the deep water populations did increase markedly in coverage.

Notwithstanding the north bay exception, total live coral coverage in the lagoon as a whole increased dramatically between 1971 and 1983, almost doubling in

Table 1. Raw data on live coral and Dictyosphaeria coverage, expressed in percentage of total bottom coverage, at one meter depth intervals on each transect and for all stations. Blanks indicate the transect did not extend to that depth. A dash indicates absence (zero abundance). A "P" indicates presence, but in very low amounts.

LIVE CORALS

Station #

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Depth															
1 meter															
1971	-	3.5	1	46	12		1.1	27	14	13	9.0	-	0.3		
1983a	3.3	-	100	30	77		15	36	8.7	52	44	69	55	42	
1983b	1.6	0.1	28	53	74		12	76	11	40	51	57	45	42	
2 meters															
1971	0.1	-	6.5	20	3.5	66	2.7	42	10	9.3	61	54	4.5	72	33
1983a	7.6	-	45	2	52	34	20	68	17	67	62	81	98	48	12
1983b	8.3	P	44	7	37	55	28	65	10	55	67	98	92	94	43
3 meters															
1971	-	-	0.5	1.5	1	63	-	18	1	4	50	70	11	100	93
1983a	6	P	33	4	42	46	48	51	27	64	76	67	57	96	27
1983b	5.5	5.5	40	1	22	30	48	76	14	73	43	93	12	100	49
4 meters															
1971	-	-	1	-	1	42	-	18	7	1	4	89	-	99	79
1983a	3	0.4	21	2	25	26	37	60	22	45	64	78	22	90	20
1983b	2	4	44	2	43	16	66	56	14	86	40	54	1.5	98	54
5 meters															
1971	-	-	3	10	0.5	15	0.5	13	-	0.5	10	22	-	68	60
1983a	16	7.7	10	11	28	17	39	62	12	50	52	60	17	78	28
1983b	6	0.6	29	7	10	4.3	59	62	14	46	55	10	2.1	64	32
6 meters															
1971	-	-	1	1	1	3	1	5	10	-	0.5	-	-	44	33
1983a	0.5		12	15	6	8	42	58	35	37	23	2.5	0.7	73	21
1983b	1	2	26	5	2	4	59	73	15	57	21	-	-	41	29
7 meters															
1971	-	-	1	2	-	-	-	2	6	-	3	-		26	13
1983a	-		34	12	2	29	38	28	46	18	12			56	15
1983b	P	3.5	26	1	32	3	25	70	8	20	16	-		32	26
8 meters															
1971	-	-	-	1	-	-	-	-	1	3.5	2			1	2
1983a	-		3	7.5	1	8	10	10	29	11	72			10	11
1983b	0.5	6	6	1	1	P	20	59	22	2	33			15	6.5
9 meters															
1971	-	-	1	0.5	-				2	5	22			-	0.5
1983a	-		4.5	13	5.5	5	0.3	4	13	1	46			2	5
1983b	2	1	0.2	1.3	9.3	0.5	-	28	12	22	37			10	1
10 meters															
1971			-	-	-					1.5	4			-	
1983a			0.5	4	2	6		2		4	3			-	
1983b			1	2	1	0.5		4.5	5.7	10	26			5	
11 meters															
1971			-	-	-					-	0.5			-	
1983a			6	-	0.5	-				2	2				
1983b			0.8	1	1	P			-	8	-				
12 meters															
1971			-	-	-										
1983a			2.3	-	1.5	-				1	-				
1983b			-	P	-						-				

Table 1. (continued)

Dictyosphaeria

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1 meter															
1971	-	-	-	12	14		51	8.9	41	18	11	0.4	-		
1983a	0.3	-	-	11	4.3		4.2	14	5	9.7	14	0.5	27	5	
1983b	0.6	-	0.5	4.2	21		7.8	8.8	4.3	9	5	0.4	8.8	14	
2 meters															
1971	-	-	-	40	26	18	77	10	52	35	32	0.2	-	4.2	16
1983a	0.2	-	0.3	5.7	22	2.6	4.5	26	2.2	13	-	4	P	2.2	29
1983b	-	-	-	3.5	20	5.9	3.5	27	5	38	-	-	P	-	30
3 meters															
1971	-	-	-	73	9	15	61	74	55	15	-	-	-	-	5
1983a	-	-	-	3	2	3.5	11	19	4	14	-	2	-	-	35
1983b	-	-	-	-	2.5	3	8	11	25	21	4	-	-	-	29
4 meters															
1971	-	-	-	48	19	12	61	1.5	85	69	40	-	-	-	10
1983a	-	-	-	2.5	-	3.3	11	4	6	-	0.5	-	-	-	28
1983b	-	-	-	-	-	-	6	15	13	4	-	-	-	1	36
5 meters															
1971	-	-	-	-	2	47	40	3.5	92	98	37	-	-	-	0.5
1983a	-	-	-	1.5	-	-	6	6	-	6.5	1.5	-	-	-	20
1983b	-	-	-	-	-	-	3.7	15	1	1	-	-	-	1	18
6 meters															
1971	-	-	-	4	27	-	5	0.5	65	90	86	-	-	-	-
1983a	-	-	-	-	-	-	1	3.5	6	14	-	-	-	-	-
1983b	-	-	-	-	-	-	3	6.5	-	0.5	-	-	-	-	2
7 meters															
1971	-	-	-	3.5	28	-	-	-	35	85	82	-	-	-	-
1983a	-	-	-	-	-	-	4	-	1.8	0.5	-	-	-	-	-
1983b	-	-	-	-	-	-	-	20	1.5	-	-	-	-	-	-
8 meters															
1971	-	-	-	-	26	-	-	-	-	18	98			-	-
1983a	-		-	-	-	1.5	-	-	-	-	-			-	-
1983b	-	-	-	-	-	-	-	10	2.5	-	-			-	-
9 meters															
1971	-	-	-	-	8				5.5	-	6			-	-
1983a	-		-	-	-	-	-	-	-	-	-			-	-
1983b	-	-	-	-	-	-	-	-	-	-	-			-	-
10 meters															
1971			-	-	7.5										
1983a			-	-	-	-				-	9			-	
1983b			-	-	-	-		-		-	-			-	
								-	-	-	-			-	
11 meters															
1971			-	-	18										
1983a			-	-	-	-				-	-			-	
1983b			-	-	-	-				-	-				
									-	-	-				
12 meters															
1971			-	-	11										
1983a			-	-	-	-									
1983b			-	-	-					-	-				
											-				
13 meters															
1971					10										
1983a					-	-									
1983b					-										

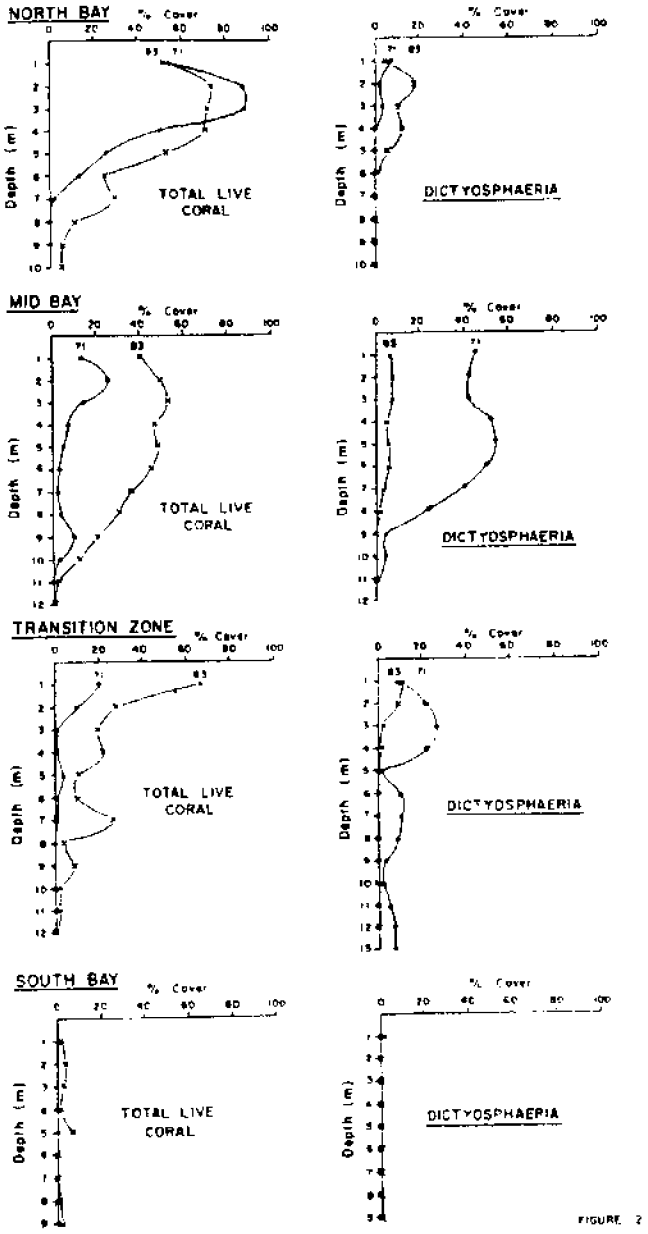

Fig. 2. Live coverage of coral and Dictyosphaeria in 1971 and 1983 plotted against depth for four regions in Kaneohe lagoon. Data from all stations within each region pooled. The dots represent 1971 data and the "X's" represent 1983 data.

Table 2. Distribution data for species of reef corals and Dictyosphaeria encountered during the 1971 and 1983 transect surveys at the 15 lagoon stations. Numbers indicate total number of times each species was encountered in the squares of the quadrat along each transect. The 1983 numbers represent the means of the replicate transect data at each station. A dash indicates the species was not present on the transect. MP - Montipora patula, PM - Pocillopora meandrina, and PS - Psammocora stellata.

	LOCATION														
	South Bay			Transition Zone				Middle Bay					North Bay			TOTALS
	Station No.															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Porites compressa																
1971	--	7	16	237	50	943	15	365	129	114	376	612	29	711	564	4168
1983	19	8	313	220	351	374	438	1006	353	730	620	872	504	922	424	7154
Montipora verrucosa																
1971	3	--	10	43	7	259	--	13	7	3	10	1	7	158	67	588
1983	58	22	208	78	172	138	26	19	29	26	172	4	57	18	1	1028
Pocillopora damicornis																
1971	--	--	--	--	1	1	3	2	6	3	3	8	4	2	8	41
1983	6	6	8	12	18	30	20	32	12	34	10	100	27	9	4	328
Cyphastrea ocellina																
1971	--	--	--	--	--	--	--	1	--	1	--	--	--	--	1	3
1983	2	--	--	--	2	2	8	6	9	10	4	6	5	2	5	61
Fungia scutaria																
1971	--	--	1	--	1	--	--	14	1	12	11	14	3	3	9	69
1983	--	--	2	--	2	--	6	4	4	14	6	1	--	4	1	44
Pavona varians																
1971	--	--	--	--	--	--	--	1	1	4	--	--	--	--	--	6
1983	--	--	--	--	--	2	--	1	1	--	32	--	--	--	--	36
Other Corals																
1971	--	--	--	--	--	3MP	--	--	2MP	--	3MP	3MP	--	5MP	1PS	17
1983	--	--	--	--	--	1PM	--	1PS	--	--	2MP	--	--	--	1PS	5
Dictyosphaeria cavernosa																
1971	--	--	--	520	327	448	907	240	991	610	630	3	--	25	134	4835
1983	3	--	1	51	84	48	76	225	74	160	40	10	118	30	326	1246

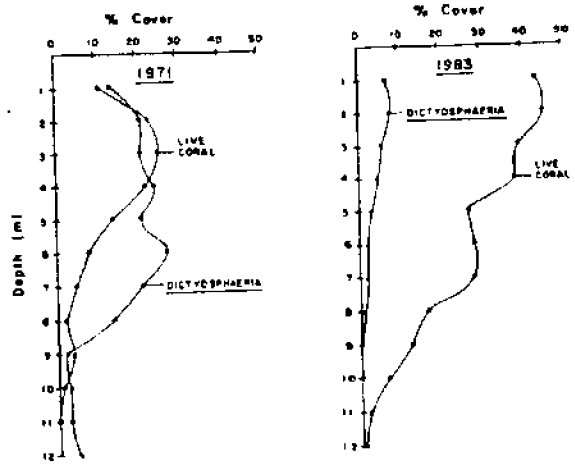

Fig. 3. Live coverage of coral and Dictyosphaeria in 1971 and 1993 plotted against depth. Data from all stations pooled.

abundance (Table 2; Fig. 3). Live coral coverage was substantially higher in 1983 at all depths at south, transition, and middle bay regions compared to 1971 levels. The abundance of coral in 1983 at the mid bay stations had nearly approached the highest levels in the lagoon reported in the north lagoon. The transition zone and particularly the south lagoon coral populations did not yet reach the high abundance levels reported more to the north. Despite spectacular increases in south lagoon coral communities by 1983, overall abundance is still only a fraction of those of other regions and it may take decades for the communities to recover completely (Fig. 2). Notable coral recovery on old dredged surfaces was also reported at Station 2 and observed elsewhere in the south lagoon. In contrast, coral recovery on deteriorated reef surfaces covered with sediment had not yet begun at one south bay station possibly due to non-suitability of the substrate for coral settlement.

In 1971, Dictyosphaeria was more common in the lagoon than any single coral species and its abundance was equivalent to all coral species combined (Table 2). However, by 1983 Dictyosphaeria showed dramatic declines in coverage at most bay stations with its recent overall level being only 25% of its earlier level (Table 2; Fig. 3). Spectacular decreases were reported at all transition and mid bay stations where Dictyosphaeria had earlier exhibited its peak abundance in the bay (Fig. 2). Dictyospaheria declines in deeper water appeared to be larger than those of shallow water although declines were generally substantial at all depths (Figs. 2,3; Table 1). Although Dictyosphaeria continues to be nearly absent in the south bay, it showed a moderate increase in most north bay stations (Table 1,2; Fig. 2) in 1983 compared to 1971 levels. Interestingly, the alga showed a dramatic increase at Station 13, the north bay station closest to the Ahuimanu Sewage outfall which was still discharging sewage at the time of the 1983 survey.

Dramatic increases in the abundance and distribution of individual species of corals were also reported (Table 2). The most abundant species Porites compressa nearly doubled its abundance since 1971 and recorded major increases at all stations except two (#8 and #15; Table 2). Porites was completely absent at Station 1 in 1971 but present in 1983. The growth of Porites was so impressive at some stations (10-13) that the platforms were heavily colonized and nearly hidden by coral growth. Up to 50 cm of growth was reported over the platform at Station 12 and the platform could not be relocated at all at Station 6 where coral growth was suspected to have covered it. Likewise Montipora verrucosa nearly doubled its overall abundance in the lagoon showing increases at 12 of the 15 stations (Table 2). The species was absent from Stations 2 and 7 in 1971 but present at those stations in 1983.

Several of the less common species reported at the stations showed remarkable increases in their distribution and abundance (Table 2). Although Pocillopora damicornis was absent from all south bay and one transition zone stations in 1971, it was present at all 15 stations and showed increased at 14 stations. A similar but more impressive trend was recorded for Cyphastrea ocellina (Table 2). During the 1971 survey, the species was reported at only 3 stations (2 middle bay and one north bay station). By 1983 Cyphastrea was reported at 12 of the 15 lagoon stations and showed increased abundance at all of these stations. It was absent only at two south bay and one transition zone station. In contrast, the soft coral Zoanthus pacifica was observed to be present at all south bay, one transition and one mid bay station in 1971 but was absent at all stations during the 1983 survey. The other rarer species of corals were not encountered often enough during the transect surveys to demonstrate any trends over time.

Discussion

The study of Smith et al. (1981) is the only other to document ecological conditions in Kaneohe both before and after the cessation of sewage discharges in the south lagoon. They viewed the bay as a single nutrient subsidized ecosystem prior to diversion and placed emphasis on monitoring biomass and productivity of major organism groups rather than the progress of individual species. They documented a rapid decline in phytoplankton, zooplankton and benthos (primarily suspension feeders) in the south bay and a decline in Dictyosphaeria in the middle bay following diversion and the elimination of sewage nutrient subsidy. Nevertheless the study was not able to document recovery by reef corals. However, Brock and Smith (1983) monitored cryptofaunal communities on reefs before and after diversion and noted increased biomass of hard-bottomed cryptofaunal communities during sewage loading and declines after diversion.

In contrast, our study documented an essentially opposite pattern and rate of response by reef coral communities. Coral populations were at depressed levels in the south to middle lagoon before diversion. Although responding slowly at first to the termination of sewage, reef corals are now dramatically recovering their abundance, distribution, and diversity throughout all regions of the lagoon previously affected. Surprisingly these responses were not limited merely to south lagoon corals earlier affected directly by sewage or transition and middle bay coral populations, primarily Porites and Montipora, that were previously affected by massive growths of Dictyosphaeria. Even some less common coral species including Pocillopora and Cyphastrea showed substantial increases in abundance and distribution throughout the entire lagoon with the six year period following sewage diversion. Although it is difficult to explain how the termination of sewage discharges could stimulate measurable coral recovery to to 10 km to the north, the exhibited patterns of coral recovery cannot be dismissed as a coincidence nor are other explanations for the recovery plausible. Indeed if there is a relationship, then some of the coral species responding to the reduction of sewage stress may serve as extremely sensitive indicators of sewage pollution.

Our 1983 documentation of Dictyosphaeria declines are consistent with the earlier measurements of Smith et. al (1981). We determined that the algae declined to one fifth of its prediversion abundance overall and noted major population collapses at seven out of the eight stations in the transition and middle lagoon regions. The rapid decline following diversion suggests that Dictyosphaeria was previously stimulated by nutrient subsidies from the sewage. Furthermore, Smith et. al (1981) explained the northern shift of Dictyosphaeria populations between 1970-1977 to be the consequences of increased sewage discharges over the period. Additionally, the initiation of sewage discharges in the north bay from the Ahuimanu Sewage Treatment Plant in 1970 could explain both this shift as well as the moderate increases in Dictyosphaeria coverage we observed at the north bay transects.

The continued absence of Dictyosphaeria from the south lagoon is more difficult to explain. Smith et. al (1981) concluded that the algae's growth was limited by light due to reduced light penetration in the water column from suspended particulates. Although light must be limiting to some degree, it does not appear to be the sole explanation for its absence in the south lagoon. Maragos (1972) reported huge populations of the algae in deeper water (to 9-11 m) during the mid bay and transition zone transect surveys in 1971 and during qualitative observations in the bay between 1970-1974. Furthermore, he was constantly removing growths of the algae from his deeper platforms to prevent the algae from smothering the coral transplants. Our 1983 surveys show that most of the Dictyosphaeria decline occurred on the deeper portion of the reef slope (see Figs. 2,3) during a time interval when light penetration was expected to increase. Clearly light was not limiting the algae on mid lagoon reef slopes and other factors may be responsible for its continued absence in the south lagoon. Substratum instability on the steeper deteriorated reef slopes (see Kinsey, 1979) and residual toxicity of the bottom sediments in the south lagoon from previous sewage discharges may render bottom habitats there inhospitable to Dictyosphaeria colonization and growth. Perhaps the inhibitory factors are simply the same as those which have discouraged development of other typical reef benthos including corals in the south lagoon over many years.

Until now it has been difficult to differentiate the net contribution of early major dredge and fill operations from that of later sewage discharges to the destruction of reef coral populations in the south lagoon. Our 1983 south bay transect results appear to support the hypothesis that sewage discharges had prevented or inhibited the recolonization of corals on dredged surfaces in the south lagoon. Our recent studies indicate corals have begun to rapidly recolonize dredged surfaces there now that sewage has been diverted. Furthermore, Maragos (1972, 1974) earlier observed greater coral recovery on dredged surfaces outside of the south lagoon. The more recent estimates of military dredging and filling (see Devaney et al., 1976) indicate that 280 acres of reefs were filled at Mokapu and over 15,000,000 cubic yards of reef material was dredged between 1938 and 1945, most of this in the south lagoon. Dredged materials not used for fill were discharged into the lagoon adjacent to the reefs. Although the documentation of the effects of this activity on coral reef communities was not accomplished at the time, it is certain that dredging and filling had a catastrophic impact on south lagoon corals. However, Maragos (1972) also indicated that transplanted corals, especially Porites and Pocillopora survived and grew

poorly in the south lagoon during the period of active sewage discharge. Hence, coral populations in the south lagoon may have been destined for major damage and destruction by sewage stress, even in the absence of the earlier massive dredge and fill operations.

In retrospect, the earlier decision to eliminate sewage discharges from the south lagoon resulted in major benefit to reef coral populations in Kaneohe lagoon. A similar diversion of the Ahuimanu sewage should result in additional recovery of reef corals and benefit to the reef ecosystem in the bay. Equally important is the fact that the diversion of this sewage to a deep ocean outfall offshore from Mokapu Peninsula and outside the bay has not resulted in noticeable adverse impact to the exposed reef communities adjacent ot the outfall. In fact, reef fish populations are much greater in the vicinity of the outfall plumes.

At first it may pose as an enigma that the same amount of sewage that caused catastrophic damage to corals inside the bay would have only negligible impact to reefs outside the bay. The ocean outfall site is exposed to strong currents, waves, and water circulation and water residence times measured on the order of weeks (see Smith et. al, 1981). The rapid turnover of waters outside the lagoon prevents a buildup of nutrients, greater biomass of phytoplankton and the eutrophic waters that characterized the south lagoon during the period of sewage discharge. In retrospect, the location of the outfalls in the south lagoon was perhaps the worst of all alternatives and points to the need to site sewage outfalls in well flushed waters to avoid adverse effects to coral reefs.

Conclusions

The results of ecological studies completed after diversion of sewage from the lagoon of Kaneohe Bay enable us to reconstruct more accurately the recent history of corals and major ecosystems in the bay. Reef corals which normally flourish on the reef slopes in the lagoon of Kaneohe Bay were subjected to dredging and filling and urban pollution after 1938. Dredge and fill operations were concentrated in the south lagoon and destroyed or degraded many reefs. Sedimentation from dredged material disposal and from land sources led to two meters of deposition and shoaling of the lagoon floor which buried coral habitat at the base of the reef slopes. A freshwater flood in 1965, probably a natural event, led to mass mortality and injury to shallow water corals and other reef life above depths of 2 meters.

Between 1950 and 1978, sewage discharge into the isolated southern lagoon provided nutrients which subsidized high levels of plankton biomass in the waters and large populations of benthic suspension feeders in the south bay. Coral communities, dominated by a single species sensitive to sewage (Porites compressa), declined in the south bay or were displaced by the suspension feeders. In the middle lagoon, the sewage nutrients stimulated the growth of a benthic alga, Dictyosphaeria cavernosa which overgrew and smothered many corals on the reef slopes. Even some rare species of corals up to 10 km away from the outfalls exhibited decreased levels during the period of sewage discharge. In 1970 additional sewage began to be discharged into the northern lagoon, resulting in moderate growth of Dictyosphaeria there and possible displacement of some coral.

Termination of the southern lagoon sewage discharges reversed the earlier trend towards eutrophication and led to rapid declines of plankton, south bay suspension feeders, reef cryptofauna, and mid bay Dictyosphaeria populations. Corals took longer to respond but are now beginning to recolonize all previously degraded lagoon coral habitats. Although coral recovery appears to be nearing completion in the middle lagoon, at least one and two decades respectively may be required for recovery to peak the transition and south lagoon. The planned diversion of the remaining sewage discharges from the north lagoon should accelerate coral recovery and reverse the spread and growth of Dictyosphaeria there.

The diversion of the sewage to a deep open ocean outfall outside the bay, apparently has not resulted in major adverse impacts to coral reefs. Rapid flushing of ocean waters prevent present levels of sewage discharge from leading to eutrophication and associated adverse effects. In retrospect, the previous discharge of sewage into the poorly flushed south lagoon magnified adverse effects on corals in both the south and middle lagoons. Experience with Kaneohe Bay suggests that, in general, sewage outfalls should not be placed in protected coral lagoons and embayments with restricted water exchange.

The response of reef corals to the introduction and then the elimination of lagoon sewage effluents did not correspond to those of the dominant ecological components of the water column, and particularly components directly or indirectly subsidized by the sewage nutrients. Coral reefs achieve their greatest development in clear, (nutrient poor) waters and are not subsidized by large external sources of nutrients. This plus the fact that coral reefs are able to grow and flourish in wave exposed environments, creating its own habitat in the process, are two principal reasons why coral reefs succeed and have a competitive edge in some tropical marine environments otherwise unfavorable to major development by other kinds of ecosystems. In the case of Kaneohe Bay, the introduction of large external sources of sewage nutrient into the reef system enabled other communities to compete successfully against and eventually displace corals. In this respect corals serve as useful indicators of sewage pollution, and several species studied by us appear to be extremely sensitive to pollution.

Systems approaches and models primarily emphasizing the transfer of nutrients and energy through systems may not be as accurate in predicting the responses of coral reef ecosystems to perturbations. As the Kaneohe Bay example has shown us, the coral responses to sewage fluxes were different, slower, less predictable, and more complicated than the gross responses of the other major ecosystem components. Factors such as substrate suitability, ecological succession, taxonomic variability, physiological stress, and competition for space probably had major influences on the responses of corals.

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A comparison of coral community structure on reef flats in Kaneohe Bay, Hawaii

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Abstract

Coral colony size-frequency distribution, species composition and total coral coverage was estimated for various reef flat stations. These data provide additional evidence that reef recovery had proceeded rapidly in the five years following termination of sewage discharge into Kaneohe Bay. Proximity to stream mouths is an important factor controlling reef coral community structure, suggesting that occasional "fresh water kills" are an important factor in this region.

Introduction

The characteristics of coral community structure can provide insights into some aspects of past environmental conditions. Loya (1972) and Weinberg (1981) suggested that size distribution patterns of the coral populations could reflect age and growth modes. Size measurements can be useful in discerning patterns and overall dynamics of a community. The use of size measurements (e.g. diameter or length) has limitations in determining absolute age due to complications such as colony regeneration (fragmentation) and fusion. The usefulness of the "size-frequency" approach has been demonstrated by Grigg and Maragos (1974) in their study of coral colonization on Hawaiian lava flows. Dodge and Vaisnys (1977) employed coral age and size class population patterns using x-radiology as a measure of coral responses to sedimentation and turbidity associated with dredging. Connell's (1978) assessment of tropical rain forests and coral reefs also showed the importance of the relative age composition of the dominant species in "climax" communities so as to infer the relevance of diversity in relation to pertubations.

Results of studies on coral reef destruction and recovery have been reviewed by Johannes (1975), Endean (1976) and Pearson (1981). In Kaneohe Bay, initial studies by Banner (1968) documented some aspects of a coral community "kill" caused by freshwater runoff. His studies were later extended and related to urban pollution (Banner and Bailey, 1973; Banner, 1974). More extensive and detailed work was later conducted by Maragos (1972), with emphasis on coral community structure. Integrated approaches relating to both the structural and functional aspects of the Kaneohe Bay ecosystem have been made by Smith (1977) and Smith et al. (1973 and 1981). These studies were specifically related to the effects of increased nutrient loading (nitrogen and phosphorus) accompanying sewage discharged into the bay. Smith's (1977) delineation of the bay into the Northwest, Central, and Southeast Sectors is relevant to this study. Sewage was diverted from the bay in 1978. Smith et al. (1981) pointed out that the benthic compositional response was slow and could not be ascertained at that time. Comparison of patterns of coral community structure from reef flats throughout the three regions together with other studies (e.g. Evans et al., this volume) would broaden the data base in assessing the impact of these events on coral reefs. It may be possible to deduce stages of serial succession by taking into consideration the theoretical concepts of Connell (1978) and Grigg (1983).

Material and Methods

The reef flats sampled were in the Southeast, the Central and Northwest Sectors of the lagoon area at Kaneohe Bay (see Fig. 1). These sites were selected so that depth, distance from edge of reef flat, proximity to stream months, orientation to tradewind induced waves (water circulation and turbulence) and other factors were similar for each series of 3 stations.

Sampling Methods

Two 4 m^2 plots were sampled at each station. These were at a distance of 30 m from each other. Each sample was situated approximately two to three m shore-

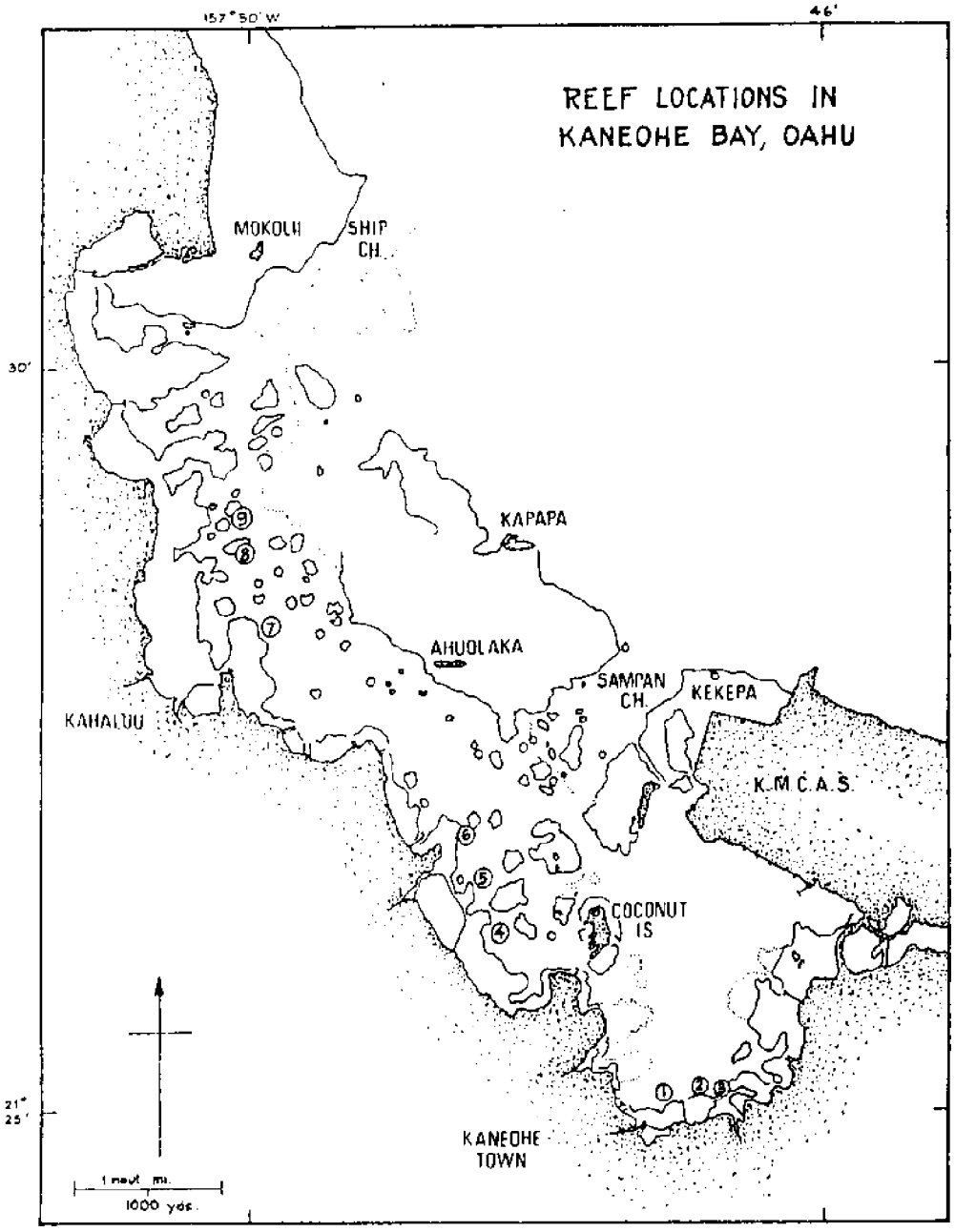

Fig. 1. Location map of sampling stations at Kaneohe Bay. Stations 1-3 for the Southeast Region; Stations 4-6 for the Center Region; and Stations 7-9 for the Northwestern Region. Adapted from the U.S.C & G.S. Chart 4134 and aerial photographs.

word from the reef edge. The 2 m x 2 m square plots (4 m²) were subdivided into 1 m² areas and measured using a 1 m² quadrat frame strung with line into 100 subdivisions (each 10 cm x 10 cm). Subsamples proved to be relatively homogenous at each station and were combined. This gave a sample size of 8 m² per station (two samples of 4 m² located 30 m from each other). All were in water depths of 1 to 1.3 m. In these sample areas, the maximum diameter lengths of all the scleractinian corals present were measured with a meterstick to the nearest cm. The data gathered were used to plot a size frequency distribution of the coral species in the area (see Figs. 2-4). Estimates of live coral cover are based on an assumed circular bottom cover estimate($A = 3.14\ r^2$). Relative bottom cover estimates of substrate types present were made based on the number of grids (10 x 10 cm) covered within the 1 m² quadrat. The estimates of cover and numbers of individuals were used to calculate Shannon-Weiner index of diversity H' and equitability J'.

Results

There were discernible patterns of differences and similarities in the coral community structure of the reef flats studied. "Average colony size" (total live coral cover/total no. of colonies) and total coral coverage increased from the Southeast Sector to the Northwest study stations (see Table 1). Though the idea of "average colony size" may not necessarily have direct biological meaning, there were particular compositional and size range distributional patterns at each station (see Figs. 2 to 4).

Table 1. Data summary for the 9 stations.

	Station								
	1	2	3	4	5	6	7	8	9
Montipora verrucosa									
Total Cover (cm²)	0.10	1.89	3.07	3.59	5.17	5.94	1.12	0.84	0
No. of Colonies	28	142	89	33	31	22	14	8	0
Porites compressa									
Total Cover (cm²)	0	0.89	0.47	7.52	14.9	19.7	25.8	40.0	64.6
No. of Colonies	9	25	12	66	63	54	101	136	81
Pocillopora damicornis									
Total Cover (cm²)	0.11	1.88	5.98	5.06	7.26	9.43	6.39	6.43	0.19
No. of Colonies	14	109	154	69	86	169	112	95	3
Cyphastrea ocellina									
Total Cover (cm²)	0	0.12	0.59	0.33	0.12	0.20	1.05	0.57	0.50
No. of Colonies	0	21	52	25	9	18	49	19	13
Fungia scutaria									
Total Cover (cm²)	0	0	0	0	0	0	1.25	1.25	0.46
No. of Colonies	0	0	0	0	0	0	14	14	5
Total Coral									
Total Cover (cm²)	0.26	4.69	10.1	16.3	27.5	35.2	35.6	58.0	85.7
No. of Colonies	51	297	307	192	189	263	293	272	102
Dictyosphaeria cavernosa									
Total Cover (cm²)	0	0	2.12	3.37	1.25	19.2	3.37	0.25	7.87
Coralline algae									
Total Cover (cm²)	0	0	0	1.37	0	18.7	16.2	6.50	16.0
Hc'	1.06	1.14	0.98	1.13	1.02	1.01	0.87	0.72	0.08
Hn'	0.99	1.12	1.13	1.30	1.17	1.00	1.92	1.16	0.70
Jc'	2.37	1.89	1.63	1.88	1.70	1.67	1.25	1.02	0.14
Jn'	2.21	1.85	1.88	2.16	1.94	1.66	1.89	1.65	1.16
Average Colony Area									
cm² Colony⁻¹	0.01	0.02	0.03	0.08	0.14	0.14	0.12	0.21	0.84

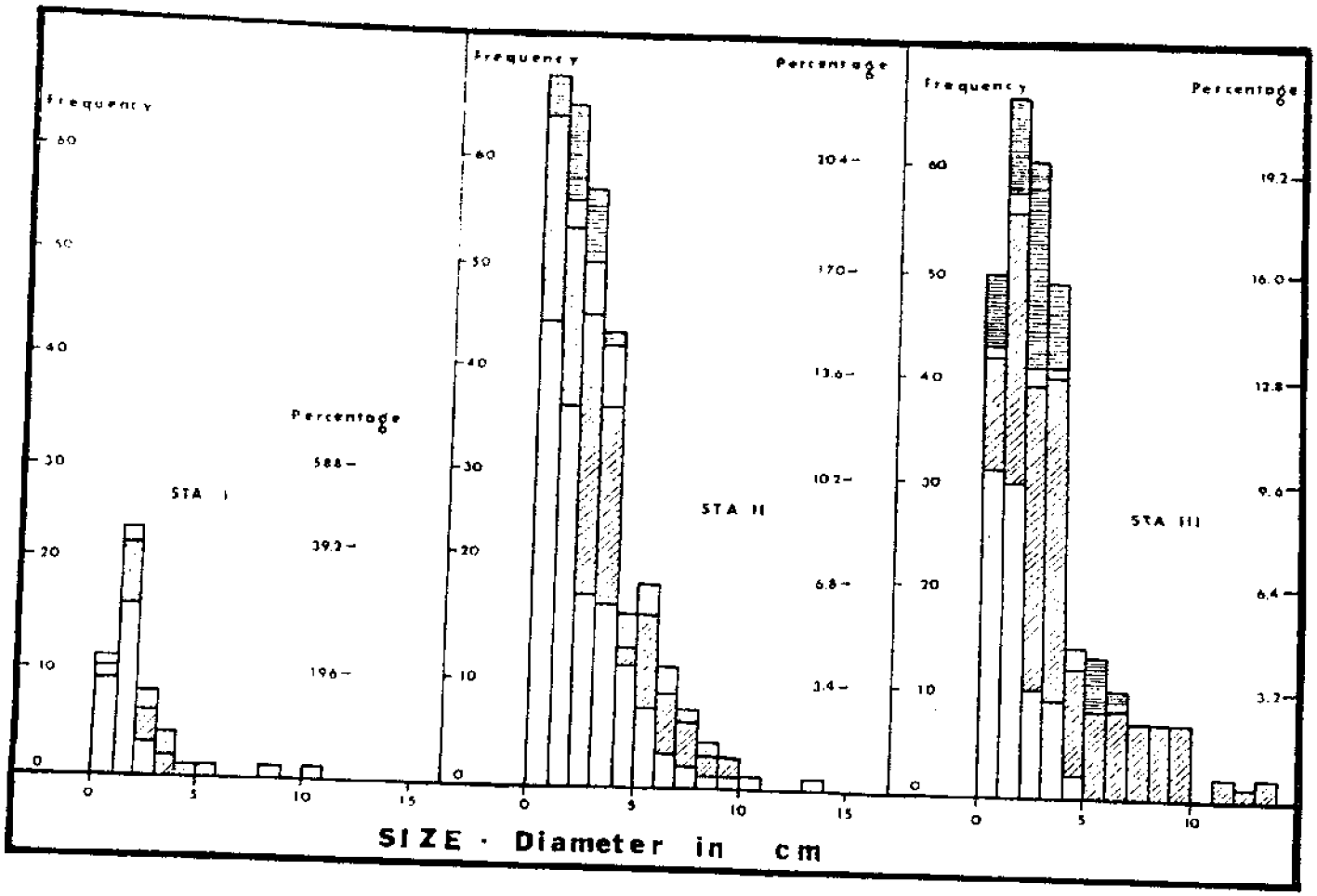

Fig. 2. Size-Frequency distributions of corals in the Southeast Sector (stations 1 to 3).

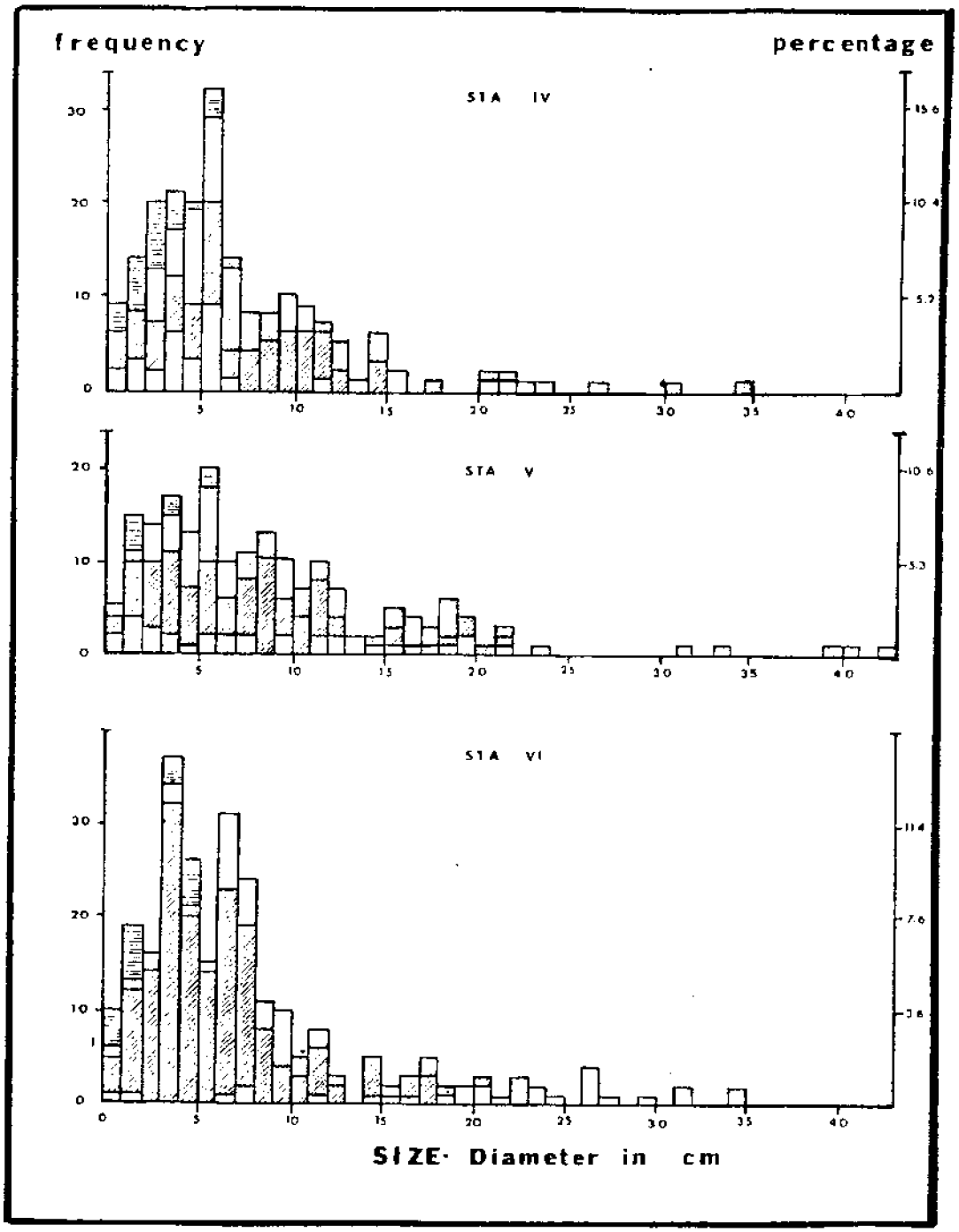

Fig. 3. Size-Frequency distributions of corals in the Central Sector (Stations 4 to 6).

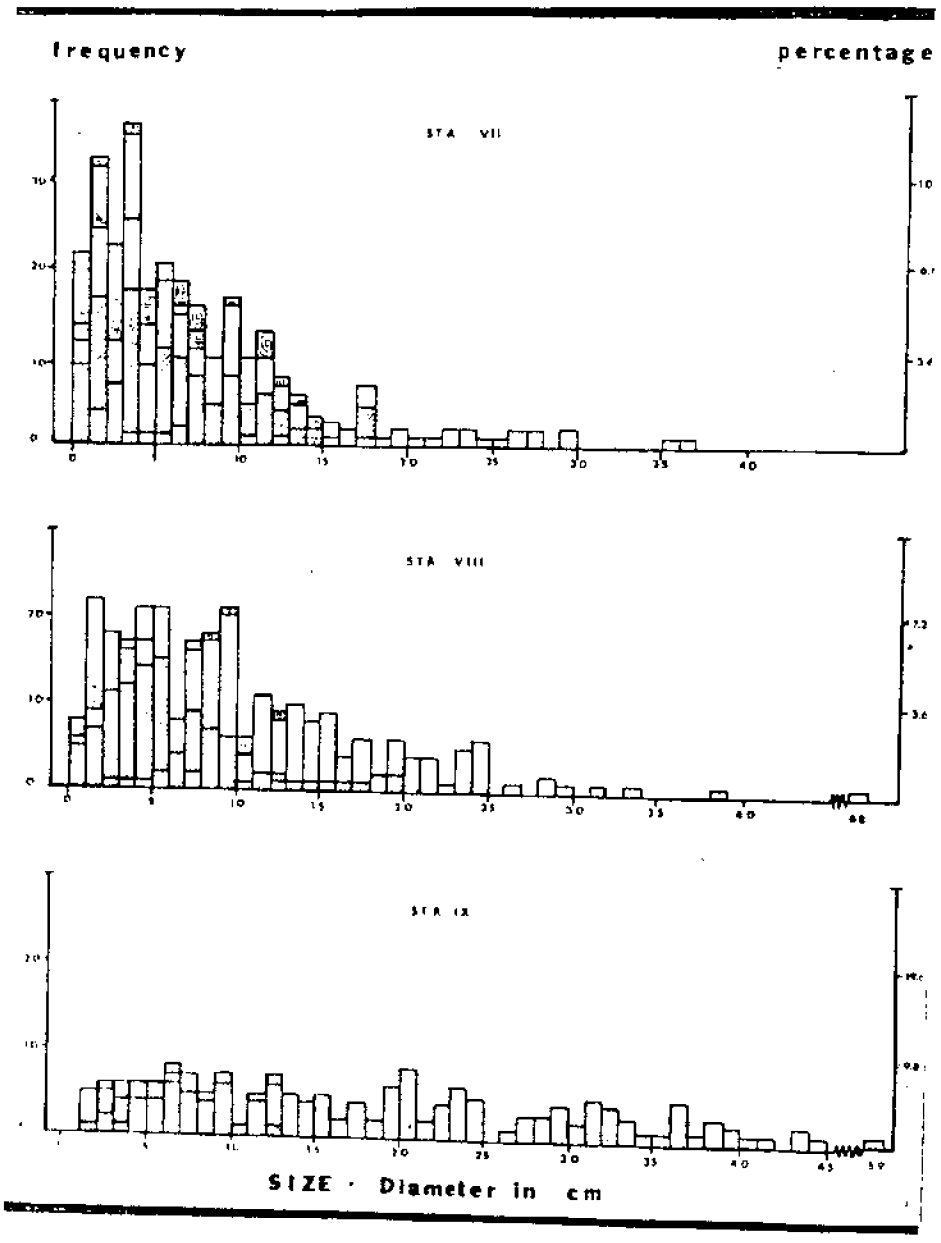

Fig. 4. Size-Frequency distributions of corals in the Northwest Sector (stations 7 to 9).

In the Southeast Sector (Stations 1 to 3) the "size" of Montipora verrucosa (see Fig. 2) was obviously skewed with a maximum in the 0 to 5 cm range. Most of these colonies seemed to have originated from planula settlement with only about 3 to 5% being derived from fragmentation (based on gross morophology and x-radiography as decribed by Esguivel (this volume). An increasing abundance of Porites Pocillopora damicornis in coverage and number of colonies was observed. Porites compressa and Cyphastrea ocellina were less common and occupied a smaller portion of bottom cover. This sector had the highest proportion of sand with silt substratum (coral rubble estimated at approximately 30 to 50%).

The Central Sector near Heeia (stations 4 to 6) appeared to have been influenced by exposure at extreme low tide and/or freshwater runoff as evidenced by dead upper portions of coral colonies and presences of terrigenous silt. This region shows a less skewed size pattern. Porites compressa had the broadest range, followed by Pocillopora damicornis, Montipora verrucosa and Cyphastrea ocellina, in order of decreasing size. Porites compressa occupied the greatest coral cover (7 to 19%) in all the stations with an increasing bottom cover from Stations 4 to 6. Pocillopora damicornis showed the highest number of colonies in this region though its coverage (5 to 9%) was relatively less than P. compressa. M. verrucosa had only 3 to 6% cover and C. ocellina had the lowest bottom cover and number of colonies. This region had a more developed reef frame than the southeast region and the presence of coralline algae was more noticeable.

The Northwest region (Stations 7 to 9) was characterized by the increasing abundance of P. compressa and the appearance of Fungia scutaria. The size range of P. compressa tended to be less skewed towards the North with the greatest kurtosis at the northernmost station. P. damicornis and M. verrucosa seemed to have a decreasing abundance towards the northern stations. C. ocellina had a relatively high cover (0.5 to 1.0%) as compared to the other sectors. Though M. verrucosa was not present in the sample quadrats, a few colonies were sighted outside the sample plots. The reef framework in this sector was relatively more developed and coralline algae were more abundant (6 to 16%).

From three to five species of scleractinian corals were observed in the reef flat stations. The lowest number of species (3) was in Station 1 and the highest was in Station 6 of the Central Sector and Station 7 of the Northwest Sector. Shannon-Weiner Index (H') and equitability (J') for each station showed some varying patterns. There does not seem to be much difference in average H'c for the Southeast (1.06 ± 0.07) but a sudden decrease was seen in the Northwest region (0.56 ± 0.45) even with the added presence P. scutaria. H'n for all the regions were quite variable. The sudden decrease in diversity is also seen in the average equitability values; with the Northwest region having the lowest equitability (Jn = 1.57 ± 0.38 and Jc = 0.81 ± 0.59) reflecting the strong dominance of P. compressa in the region.

Discussion

Characteristics of coral communities are usually studied by comparing differences in space and/or time. The high variance encountered in some coral reef measurements does not necessarily exclude the presence of patterns. Patterns can be discerned to suggest commonality of their positions in a certain dimension. To prioritize the variables in a particular framework is usually the goal for the student assessing community structure. In this study the southeast to northwest sampling of some leeward reef flats in Kaneohe Bay show patterns which could be attributed to water circulation, substrate composition, proximity to stream mouths, and their stage in seral succession.

The area near Station 1 had no previous significant coral population (Maragos 1972). Smith et al. (1981) implied that this area was possibly undergoing "decalcification" and bioerosion due to sewage and siltation. This area was of particular interest because it showed distinct signs of recovery as evidenced by the skewed distribution and a large number of new corals in the size class between 1 to 5 cm. This recruitment could have occurred only recently. Most of the new colonies were less than 3 years of age based on Polacheck's (1978) growth data for M. verrucosa and P. damicornis. Apparently new recruitment did not occur for the first few years following sewage diversion (Smith et al., 1981). This is not surprising because the reef was covered with organic mud and the substrate was unsuitable for coral settlement. In time, the muds were winnowed from the flats exposing hard substrate which was later colonized.

The high recruitment of M. verrucosa and P. damicornis is comparable to what Grigg and Maragos (1974) and Maragos (cited by Jokiel et al., 1983) considered as fugitive species. Also this sector is the most protected (Bathen 1968) and thus as Jokiel (1978) has suggested M. verrucosa and P. damicornis may be more adapted for this condition. It is also interesting to note that the composition of most of the colonies were of planular settlement and only 3 to 5% were from fragments. This seems to coincide with what Jokiel et al. (1983) reports; that asexual reproduction was less important in M. verrucosa (being only 5%) than M. dilitata based on graft compatibility. The wide spaces between coral colonies and soft sediments does not yet seem to limit the expansion of the species present. Only a few species of fish in low abundance were observed (only six species were reported by Smith et al., 1981). This does not represent a high predation pressure at the present time. Predators such as Chaetodon spp. (see Cox, this volume) were not seen in this area though some scarids were observed. Small scarids in Hawaii normally do not graze live coral.

Only four species of corals were encountered in the central region, but high H' and J' were obtained due to the even distribution of the species. The absence of P. scutaria may be the result of sampling limitations. Usually this species is found near the margins of reefs in this region (Maragos, 1972). Even though there is a relatively well developed reef framework, low tide exposure compounded by freshwater runoff and siltation could have limited coral growth in this Central sector as compared to the Northwest sector (Banner 1968, and Banner and Bailey 1973).

The Northwest Sector which is supposedly the least influenced by disturbances had the lowest diversity, the largest colonies, and the highest coral cover reflecting a long period of undisturbed growth. P. compressa seems to outcompete M. verrucosa and P. damicornis. This could be related to the relative competitive ability of P. compressa to this environment compared to P. damicornis which is more adapted to exploit environments that are disturbed occasionally. The higher frequency of P. scutaria in the samples suggests that this area has a stronger water movement to which this species is more adapted (Jokiel and Coudin, 1976).

Even though there are varying degrees of differences in environmental regimes (i.e. previous exposure to pollution, runoff, siltation, etc.) in the three sectors, successional patterns similar to those suggested by Grigg (1983) and Connell (1978) can be inferred. That is, that degrees of disturbances attributed to freshwater runoff and siltation, complicated by sewage could be responsible for the level of diversity of these reefs. In the most northern region there are evidences of competetive exclusion by P. compressa which are comparable to the "climax" Cynometra forests of Connell (1978) and Grigg's (1983) Porites lobata dominance in Hawaii.

Acknowledgements

I would like to thank Paul Jokiel and Jim Maragos for their challenge, guidance and advice in the process of this study. I am indebted to Chris Evans, Paul Holthus, and Peg Bartlett who assisted in field work, and to all my friends in the summer course of 1983 at Coconut Island who have made my stay in Hawaii port memorable.

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Growth of the Reef Coral Porites compressa on the Coconut Island Reef, Kaneohe Bay.

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Abstract

Direct measurement of growth in the reef coral Porites compressa over a four year growth interval between 1979 and 1983 yielded the following values for branch elongation: 1.5 cm yr^{-1} in a shallow backwater lagoon, 2.4 cm yr^{-1} on the windward reef crest, 3.5 cm yr^{-1} at a depth of 3 m on the reef slope and 2.8 cm yr^{-1} at a depth of 7 m. This translates into a maximum theoretical skeletal carbonate accretion rate of 25 kg m^{-2} yr^{-1} for the skeletal reef framework. However, this value can be doubled if we add infilling of the reef margin framework with sediment derived from the adjacent reef flat and other locations. During this study Hurricane Iwa damaged sections of the reef and revealed the presence of a weakened layer of reef framework that was laid down during the period of sewage pollution circa 1960 to 1978.

Introduction

The "finger coral" Porites compressa is the dominant reef-forming coral in Kaneohe Bay, Oahu, Hawaii. This species accounts for most of the living coral within the bay. P. compressa often covers from 80% to 100% of the substrate on the reef margins in the bay (Holthus, 1985; Holthus et al., 1985; Evans et al., 1985). Living tissue covers only the outermost few cm of the branches. These branches, however, extend without interruption for many meters into the reef. Colony cross sections can be inspected in areas of the reef that have been dredged or where slumping occurs on reef margins.

The branched framework is secondarily infilled with sediments as the coral grows away from the substratum. Hence the skeletal network of the coral forms a natural sediment trap or "sink". In deeper environments, the coral can survive smothering only if its growth rate equals or exceeds rate of sediment deposition between the branches. Measurement of the rate of linear growth in this species provides an estimate of the theoretical maximum rate of reef framework growth. Such data on growth rate of this species was lacking. Also, there was little information on the rate of recovery of reefs that were damaged by sewage discharge that occurred in the bay between circa 1960 and 1978. Therefore, this study was undertaken to measure growth rate in various environments on Coconut Island reef following the termination of sewage discharge into Kaneohe Bay in 1979.

Materials and Methods

Growth Experiment

A single large (2 m diameter) colony of Porites compressa was carefully subdivided into smaller colonies of 10 cm diameter. These were allowed to heal for several weeks in situ and then carefully moved into large continuous flow laboratory aquaria for staining with Alizarin Red-S (Lamberts, 1974). On 20 May 1979 the flow of water was stopped and Alizarin stain was added in sufficient quantity to bring the concentration to 20 ppm. Skeletal staining was allowed to continue from 0800 h to 1700 h under full sunlight in heavily aerated water. Flow of water was then resumed. On the following day, the corals were carefully transported in pails of water onto the reef. Eight colonies were attached with vinyl-covered wire to vinyl-coated steel mesh platforms at each of four stations.

The stations were located along a horizontal transect running directly northeast from the Hawaii Institute of Marine Biology through several reef zones on the windward Coconut Island Reef (Fig. 1). Station 1 was located on a coral knoll in the sheltered channel adjacent to the laboratory. Depth of this site was 0.5 m below MLLW. Station 2 was located 100 m seaward on the outer windward reef flat margin at a point that nearly uncovers at extreme low tide. Station 3 was located on the reef face at a depth of 3 m in an area of high coral cover.

Station 4 was located at 7 m which appeared to be the lower limit of coral growth on the reef face. The stations were visually monitored over a period of 4 years.

On 11 June 1983 the frames were removed and brought back into the laboratory, the corals were dried and cut longitudinally with a diamond saw. The original red stain band, as well as the new white carbonate material that had been deposited in the succeeding 4 years, was evident.

Linear branch extension, branch thickness and branch spacing (distance between centers of adjacent branches) was measured. These data were used to estimate the maximum potential mass accretion and amount of open space created between the branches. The open space between branches is a site for possible sediment accumulation. Also, several branches were imbedded in polyester resin and cut into longitudinal thin sections. These sections were analyzed using x-radiographic technique (Knutson et al., 1972), in order to determine growth increments and annual changes in branch diameter.

During the summer of 1983 visual surveys were made around Coconut Island and throughout the bay. Damage caused by Hurricane Iwa shifted and split large colonies. This allowed examination of old skeleton laid down during the period of extensive pollution in the bay (circa early 1960's to 1978).

Results

Physical and biological conditions at the various growth sites during the period of growth were quite dissimilar. Station 1 was characterized by restricted circulation, high nutrient loading from land runoff, large amounts of fine sediment, high temperature fluctuations and occasional low salinity stress from runoff during storm conditions. Station 1 was within 20 m of a stand of mangroves and was also influenced by high nutrient effluent from an experimental aquaculture operation. Corals were continually subjected to partial overgrowth by the algae Dictyosphaeria cavernosa and experienced adverse growth conditions. Station 2 was located on the windward margin of the Coconut Island reef flat and nearly uncovered at low tide. This shallow site was subjected to heavy wave action during high winds and low salinity during heavy rains. Solar radiation was very intense. The station experienced rapid temperature fluctuations due to the influence of water flowing off the reef flat at falling tide. Station 3 was located at a depth of 3 m and therefore was not influenced by surface fluctuations in water quality. Solar radiation was not as severe. Station 4 was at a depth of 7 m near the lower limit of coral growth. Little water motion occurs at this depth in Kaneohe Bay so the environment is characterized by extremely heavy deposition of fine sediments. Irradiance was relatively low. Growth rates and relative irradiance are reported in Table 1.

The amount of open space within the skeletal framework between the branches of the colony was calculated. An equilateral triangle with each leg being equal to the mean branch spacing was drawn. Circles having a radius of half the mean branch diameter were drawn with centers at each vertex of the triangle. It was then a simple geometrical exercise to calculate the percentage of the triangle area covered by skeletal framework and the percentage that is open space between the branches (Table 2). Skeletal carbonate mass accretion rate was calculated using a mean density of 1.5 g cm^{-3} (Jokiel and Cowdin, 1976).

Branch thickness is inversely related to depth, but branch spacing is directly related to depth (Table 2). In other words, branches become thinner and more widely spaced with increasing depth. Linear growth was lowest at the reef flat station, with maximum growth rate at 3 m, but decreasing at 7 m. As a result, skeletal carbonate accretion rate shows a maximum (24 kg m^{-2} yr^{-1}) at 3 m but drops to half that value at 7 m. However, rate of creation of space between the branches is about the same at both depths (Table 2).

The x-radiographs revealed 4 annular cycles of branch diameter between 1979 and 1983 (Fig. 3). It appears that branches become very thin in Dec.-Jan. when light and temperature are at the annual minimum. Sub-annual (monthly?) bands are evident. Branching occurs at the onset of spring growth.

Observations

Influence of Pollution

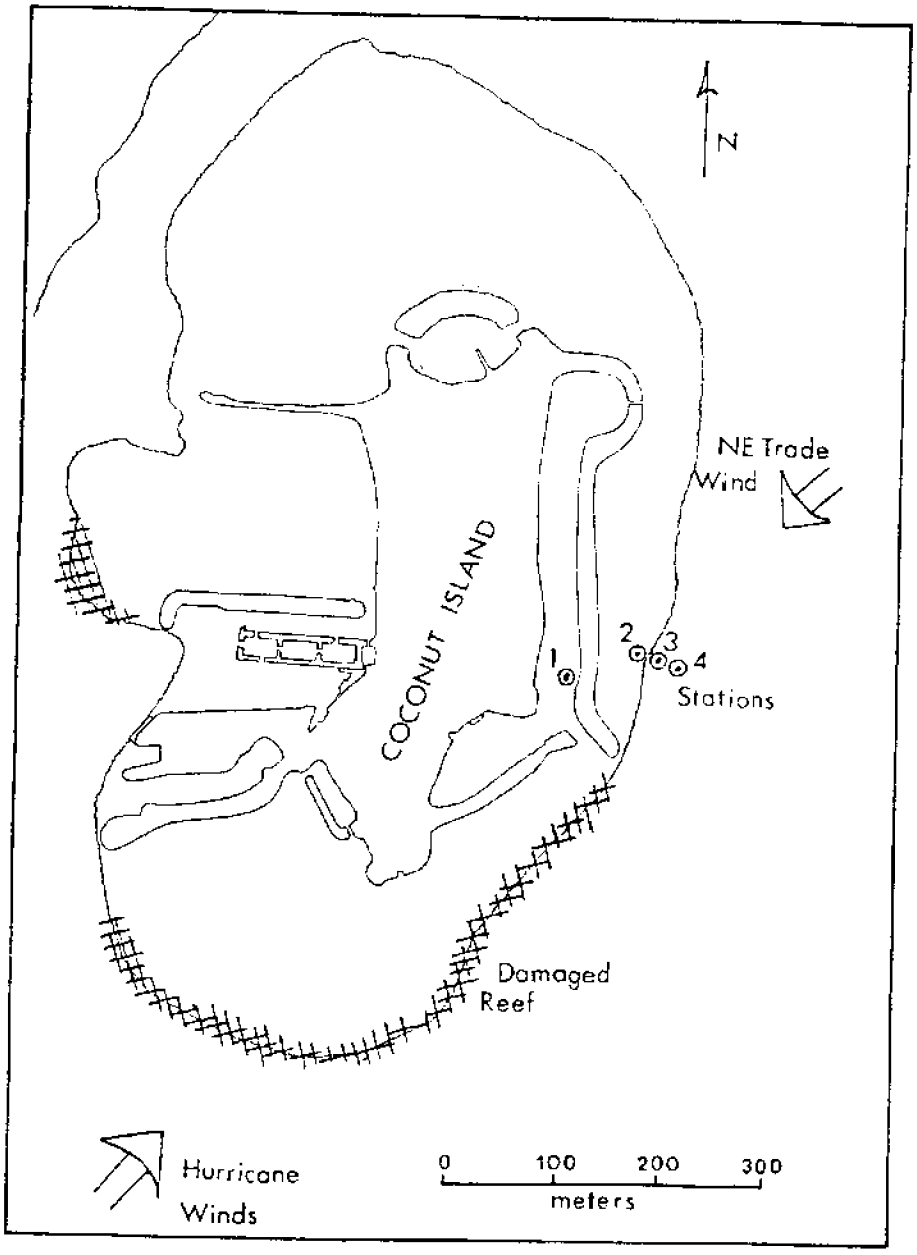

Fig. 1. Map of the Coconut Island Reef showing Stations 1-4, direction of winds generated by Hurricane Iwa and areas where Porites compressa colonies were dislodged and transported downslope as a result of the storm.

Table 1. Linear growth of the reef coral Porites compressa on the Coconut Island reef in various environments over the 4 year growth period (1979-1983). Relative irradiance was calculated from light extinction data taken in Kaneohe Bay after termination of sewage discharge (Smith et al., 1981).

Station	Location	Depth (m)	Mean Total Growth (cm) ±S.D.	n	Total Mortality (%)	Mean Annual Growth (cm yr^{-1})	Relative Irradiance (% Surface)
1	Protected Channel	0.5	5.9±2.4	16	80	1.5	87
2	Windward Reef Crest	0.5	9.7±1.4	18	50	2.4	87
3	Windward Reef Slope	3.0	13.8±1.6	32	0	3.5	42
4	Windward Reef Slope	7.0	11.2±2.7	52	0	2.8	13

Table 2. Growth and maximum accretion rates of skeletal framework and accumulated sediment within framework of reef coral Porites compressa on the windward Coconut Island Reef. Value for skeletal density of coral = 1.5 g cm^{-3}, density of sediment = 1.3 g cm^{-3}.

	Depth (m) 0.5	3.0	7.0
Branch diameter (cm) ±S.D.	1.2±0.4	1.1±0.2	1.1±0.4
Branch spacing (cm) ±S.D. (distance between branch centers)	1.7±0.3	1.7±0.4	1.9±0.6
Open space in framework (%)	46	55	72
Mean annual growth (cm)	2.4	3.5	2.8
Skeletal carbonate accretion rate (kg m^{-2} yr^{-1})	19	24	12
Space being added between branches (cm^3 m^{-2} yr^{-1})	11,000	19,300	20,200
Sediment accommodation potential thickness (cm yr^{-1})	1.1	1.9	2.0
mass (kg m^{-2} yr^{-1})	14	25	26
Maximum potential accretion rate of skeletal framework plus sediment (kg m^{-2} yr^{-1})	33	49	38

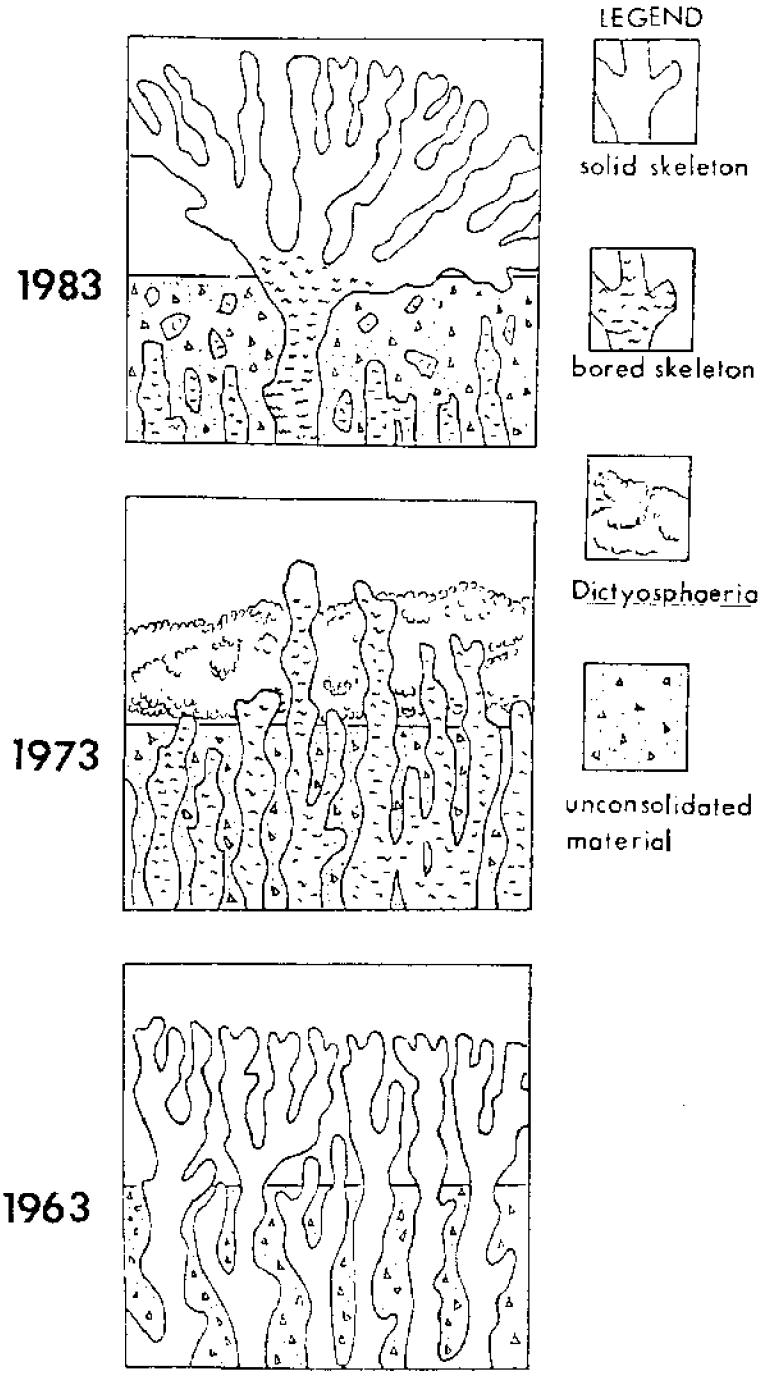

Fig. 2. Sketches of colonies of Porites compressa living along the reef margins of Coconut Island. Diagrams represent condition of corals in pre-pollution period (1963), during time of pollution (1973) and during recovery (1983).

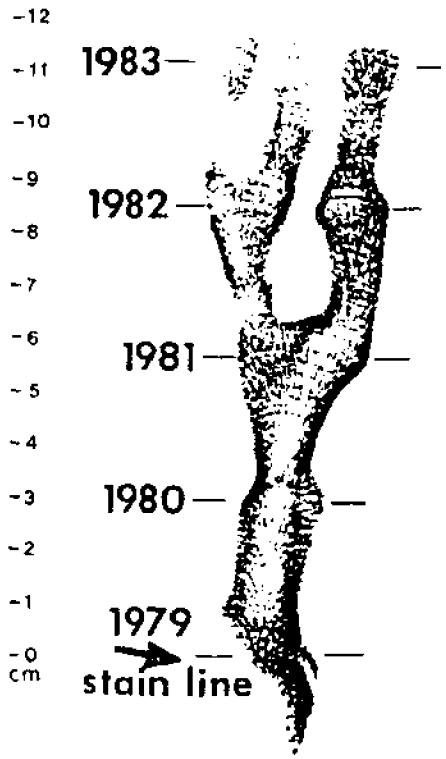

Fig. 4. X-radiograph of a coral branch from a colony used in the growth study (7 m depth). Location of the original alizarin stain line (1979) and subsequent annual changes (1980-1983) for newly deposited skeleton are shown.

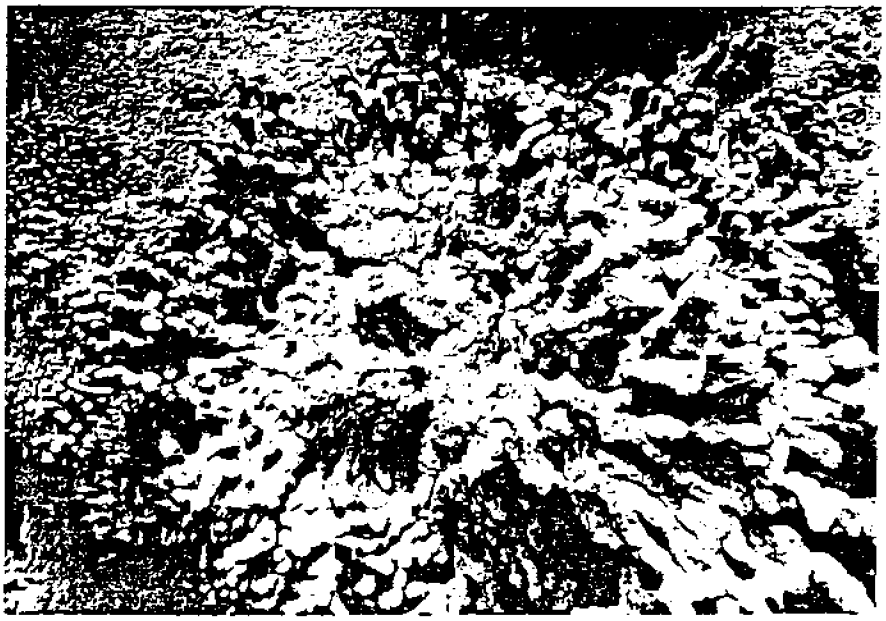

Fig. 4. Photograph of corals overturned by Hurricane Iva. Original central stalk of the coral is badly weakened by boring organisms and covered with encrusting barnacles and bivalves. Such massive encrustation and boring of skeletal material ceased upon termination of sewage discharge in 1979. Note that coral branches have begun to grow upward along the edges in the 6 months between the time when the storm passed and the time that the photograph was taken. The coral head is approximately 1 m in diameter.

Water transparency was very high prior to the onset of sewage discharge. Visibility was generally 10 to 15 m. The steeply-sloping reef faces that fringe Coconut Island were covered with healthy stands of the reef coral Porites compressa to depths of 10 m (S. J. Townsley, L. Zukeran, E. Van Heukelem, personal communication). Skeletal material laid down in this period can still be observed to be relatively free of boring and encrusting organisms (Fig. 2), as shown by retrospective analysis of freshly split colonies exposed by Hurricane Iwa. During the survey of 1983, the old skeletal material in the branches more than 50 cm from the growing tips was found to be free from boring and encrustations. Material between 10 cm and 50 cm (period of pollution) was severely bored. Severly bored material was too crumbly to section with a rock saw, even when the branch was imbedded in polyester resin. Comparative samples taken from unpolluted reefs in the northern portion of Kaneohe Bay did not show the bored and encrusted band between 10 and 50 cm from the growing tips. Effects of pollution in the bay have been previously documented (e.g. Banner and Bailey, 1970; Maragos, 1972; Banner, 1974; Smith et al., 1981). Eutrophication of Kaneohe Bay between 1960 and 1979 had a severe impact on the Porites compressa community. Phytoplankton and benthic plants were stimulated by the higher availability of nutrients. Increased particulate concentration in the water decreased light penetration. Rapid growth by the green "bubble algae" Dictyosphaerea cavernosa choked out corals (Fig. 2), although a few coral "nubbins" survived in most areas. Organic material accumulated and sediments became anoxic (Guinther and Bartlett, 1985). The increase in suspended particulate organic matter led to a great increase in standing crop of filter feeders. Barnacles, oysters, bryozoans, vermetids, serpulid worms and other encrusting organisms quickly colonized all available hard substratum. Even the benthic alga Dictyosphaeria cavernosa was extensively colonized by filter-feeding epifaunal communities. Recruitment of new coral colonies was seldom observed during the period of pollution, but has become extremely common since pollution abatement. Boring molluscs, sponges and polychaetes riddled and weakened coral skeletons. The colonies became so soft that we could not walk or stand on coral heads without having them shatter under our weight. After pollution abatement, the surviving branches rapidly grew into new colonies with hard skeletons that can support the weight of a man (Fig. 2).

Influence of Hurricane Iwa

On November 23, 1982, Hurricane Iwa moved across the western portion of the Hawaiian Archipelago along a northeasterly path and passed close to the island of Kauai. The island of Oahu caught the eastern edge of the storm. On the island of Oahu, winds came from the southwest as the hurricane approached, but gradually shifted to the southeast as the storm increased in intensity. This is opposite to the prevailing direction of the Trade Winds. Waves generated by the storm struck the normally protected "leeward" side of Oahu. Reefs in this area were severely damaged (Pfeffer and Tribble, in press).

Similar phenomena occurred in Kaneohe Bay. The bay is protected from large ocean swell by a large barrier reef. Reefs within the bay normally do not receive severe wave stress. The northeast margins of reefs receive moderate wave stress generated by the prevailing NE Trade Winds, but the back-side of these reefs are highly protected and calm. The normally protected southeast edge of the Coconut Island Reef received the brunt of the storm wave energy induced by Hurricane Iwa, with wind speeds gusting up to over 80 miles per hour (Fig. 1).

Coconut Island Reef was struck at low tide. The reef crest, dominated by large heads of the coral Porites compressa was covered with less than 0.5 m of water when the storm struck. Behind the reef crest is a broad, sandy reef flat that extends 50 to 100 m to the island shore. Seaward of the reef crest the reef slopes at a steep angle (approximately 60°) to the flat lagoon floor (depth approximately 10 m). During the storm large heads of Porites compressa were dislodged from the reef crest (Figs. 1 and 4). Nearly all of the large colonies broke off at the weak area of skeleton located 10 cm from the branch tips. The weakness in the coral was a result from the period of pollution as described above. Several colonies in diameter were dislodged and tumbled down the reef slope into deep water. My visual estimate is that an average of about 2 cubic meters of reef material from the shallow margins and reef flat shifted downslope along each meter of damaged reef margin for a distance of 1 km. An estimated total of 2000 cubic meters of coral was removed and transported into deeper water by the storm.

Eight months after the storm, it was apparent that abundant coral fragments broken by the storm were regenerating and growing into new colonies (e.g. Esquivel, 1985). Many of the large overturned heads had reoriented the growth axis of the branches in an upward direction (fig. 4). Different "morphs" of this species can be identified by color and branch size (Hunter and Kehoe, 1985). This allows one to recognize material broken from parent colonies. Fragments of readily identifiable morphs were strewn as much as 20m to 30m downstream of the parent colony during the storm. Storm waves washed the fine sediments from the outer reef flat, thereby creating a suitable hard substrate that promoted fragment survival and cementation. Subsequent regrowth and fusion of cloned colonies derived from fragments led to a fairly rapid recovery of areas damaged during the storm. Storm damage was no longer obvious by 1985.

Discussion

Branched corals such as Porites compressa adapt to life in deeper water by decreasing their branch diameter and increasing the space between branches. Such morphological changes can be viewed as as an adaptation to reduction in light, reduction in water motion and higher sediment accumulation rate. Corals growing in deeper water receive less light. Increased branch spacing allows more of the limited available light to penetrate between the branches of the colony and reach the zooxanthellae located in tissues on the sides of the branches. Water motion is generally reduced in deeper water. Wider spacing of branches allows greater circulation of water through the colony. Thickening of the branches in shallow water is advantageous because greater structural strength is required in turbulent, shallow conditions. Thus, morphological changes that are beneficial as hydromechanical and photobiological adaptations in the environment can also be viewed as an adaptation to accommodate the higher sediment accumulation rates experienced in areas where water motion and light are low.

The estimated maximum calcification rate of 24 kg m^{-2} yr^{-1} for solid stands of Porites is in agreement with maximum accretion rate reported for others (e.g. Chave et al., 1972). Infilling of the spaces between the branches with sediment derived from the reef flat could increase local maximum potential accretion rate to 50 kg m^{-2} yr^{-1}. This value is an order of magnitude larger than the mean reef flat calcification values previously reported, and certainly will only apply to a narrow zone at the edge of the reef. The edge zone is, however, the area that is growing outward, so it is of great interest in terms of understanding maximum horizontal extension of patch reefs in Kaneohe Bay. Patch reefs and fringing reef margins in Kaneohe Bay often show 80% to 100% coverage by this species (e.g. Holthus, 1985).

Some of the patch reefs at the north end of the bay do not emerge at extreme low tide and are completely covered by this species (Hunter and Kehoe, 1985). Such reefs probably are calcifying near the upper end of the range (10 to 15 kg m^{-2} yr^{-1}) and probably can continue an average upward growth of at least 1 cm yr^{-1}. Again, this value applies to localized areas and disregards the fact that some of the material is eroded and transported into deep water by storms. Furthermore, this value applies only to reefs that are highly protected from ocean swell and large storm waves. Regeneration of coral populations in Kaneohe Bay since the termination of sewage discharge in 1978-79 has been dramatic (e.g. Evans et al., 1985; Holthus et al., 1985), but a record of the period exists in the reef framework. This strata of weakened and encrusted skeletal material is rapidly being infilled and overgrown by strong new skeletal framework. Material laid down during the period of pollution will be increasingly difficult to detect in future years.

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A note on comparative quadrat sampling for infaunal and epifaunal invertebrates, 1968-71 and 1983, on the Coconut Island Reef Flat, Kaneohe Bay, Oahu, Hawaii

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Abstract

Dramatic changes occurred in the Coconut Island reef flat infauna and epifauna following the termination of sewage disposal in the bay in 1978. Comparison of samples taken in 1968-71 with samples taken in 1983 revealed a sharp reduction in number of crabs, bivalves and various filter-feeding invertebrates. Sewage abatement apparently reduced the amount of food available to these species. On the other hand, sea cucumbers increased in number. These organisms are deposit feeders. The substrate was highly anoxic in 1968-71 due to eutrophication. Perhaps the anoxic sediments were an unsuitable food source for the sea cucumbers.

Introduction

The shallow marine biotopes on the extensive fringing and patch reefs in Kaneohe Bay (windward coast of the Island of Oahu, Hawaii) have undergone substantial changes in species composition during the last half century. These changes have been most obvious in the southern part of the Bay where water circulation is more restricted and where urbanization of the adjacent watershed has been most pronounced. The reef structures of Kaneohe Bay were built by, and (on their outer fringe and frontal slopes at least) were at one time mostly populated by, corals and coralline algae - forms which have become increasingly rare or altogether absent in the south part of the Bay.

Degradation of the coral/coralline algae reef community has been attributed to a combination of factors related to urbanization (including dredging) mostly since the 1940's (see Banner and Bailey, 1970; Caperon, et al., 1971; Banner, 1974). Primary among these factors appears to have been the discharge of municipal sewage from the Kaneohe Wastewater Treatment Plant into the southern basin (Smith, 1977). Although impacts of urbanization generally became a subject of intense inquiry during the 1960's and 1970's (see Ziemann, 1970; Maragos, 1972; Krasnick, 1973; Grovhoug, 1976; Bastetter and Cooke, 1979), very little quantitative data exists pertaining to the biological communities extant prior to urbanization of the watershed and eutrophication of the south Bay waters. Thus, "degradative" changes in the biota of the Bay can be documented only be reference to anecdotal material (e.g., the "coral gardens" of the south Bay) or by studying spatial and/or temporal changes as expressions of a eutrophication gradient.

In 1978 the discharge of sewage was diverted from Kaneohe Bay to a deep ocean outfall outside the Bay. A subsequent change in the quality of Kaneohe Bay water was carefully monitored and documented by Smith, et al. (1981). A corresponding decline in the abundance of readily observed benthic filter-feeders such as sponges, soft corals, bryozoans, and tunicates was noted (Dr. Paul Jokiel, Dr. Richard Brock, personal communications). Infaunal populations of clams also appeared to be declining (see Guinther, 1984). Changes in the biomass of the cryptofauna (specifically, the endolithic fauna) have been reported by Brock and Smith (1983).

Materials and Methods

Between December 1968 and May 1973, years representative of the period of eutrophication in south Kaneohe Bay, one of the authors (Guinther) undertook a series of benthic samples on the fringing reef of Coconut Island (Moku o Loe), located in the southern part of Kaneohe Bay between 2 and 2.5 km from the sewage

outfall. Sample locations were initially established according to a "stratified random" pattern - that is, placement of the sampling device was determined randomly from grids established for designated reef sectors representing different exposures to wind, waves, and probably water quality. Samples were taken in shallow, reef flat environments, dominated in most cases by loose sedimentary material (sand, gravel, cobble). Depths varied from sites representative of the lower littoral or upper sublittoral zone to perhaps -50 cm relative to MLLW. Primary differences in physical attributes within this depth range are in the relative proportions of hard and soft bottom types to be found in any given quadrat.

Initially, ony molluscs were quantified in the quadrats: later, the scope was expanded to include crustaceans, and still later, all macroinvertebrates (generally excluding spreading, colonial forms such as sponges, bryozoans, and corals, which were recorded as present but not quantified in these samples). The project for which the samples were collected was eventually abandoned before sufficient numbers of samples were collected from any given sector or reef zone to enable a rigorous statistical analysis of the data. Nonetheless, in view of the documented changes in water quality which occurred between 1978 and 1983, and the evidence that certain invertebrate populations in the south Bay were declining, a resampling of the shallow reef flat environment held the promise of providing interesting comparative data. M. L. Bartlett undertook this additional sampling as a student project in the summer of 1983.

The original samples were collected by forcing a 1/4 square meter (actual dimensions were 50 x 50 x 17 cm), stainless steel box frame into the substratum and removing all sand and coral rock to a depth of approximately 15 cm. The material, removed by hand, was placed in containers and transported back to the Hawaii Institute of Marine Biology laboratory (located on Coconut Island) for sorting and washing over brass sieves (1, 2 and 4 mm mesh openings). Macroinvertebrates were removed and counted.

The 1983 samples (Fig. 1) were collected in an identical manner using the same box frame (being constructed of welded, stainless steel, it had survived in excellent condition). Because there was insufficient time to undertake a random sampling program valid for the relatively complex reef flat environment, it was decided that samples would be collected from the same locations as those sampled a decade before. An additional program - expending a greater effort in resampling than had been done initially would not have contributed to the validity of the comparisons. Although a sample by sample comparison is not strictly possible, the results of the resampling proved to be dramatically different from the 1968-1973 results. Indeed, after the first several samples were collected in 1983, the low organism counts prompted a thorough review of the collection and sorting process by Gunther to confirm that the methods being followed by Bartlett were indeed the same as those used between 1968 and 1973. Indeed, there was a dramatic change.

Results

The results of the two sampling programs are presented in Table 1 (summarized in Table 2), with the 1968-73 sample counts arranged in the left column and the 1983 counts listed in the right column. The data have been arranged to match 1983 samples with the earlier sample sites, at least to the extent possible. Where it states in Table 1 that there was "no comparable sample", it is meant that no sample from the particular series could be matched with a sample from the other series collected in the same immediate area.

Although larger polychaetes found in the samples were removed and counted, a significant number of these forms can be expected to pass through the finest (1 mm mesh opening) sieve. Thus, counts for this taxon would not be representative.

Discussion

The results of this study are admittedly preliminary. The number of samples is small. However, evidence from other studies (most particularly Brock and Smith, 1983) have demonstrated that a decline in benthic biomass followed diversion of sewage inputs from the Bay, and our results extend these findings to the larger invertebrates of the shallow reef flat environment. The reduction in biomass can be attributed to a decrease in organic loading: prior to diversion,

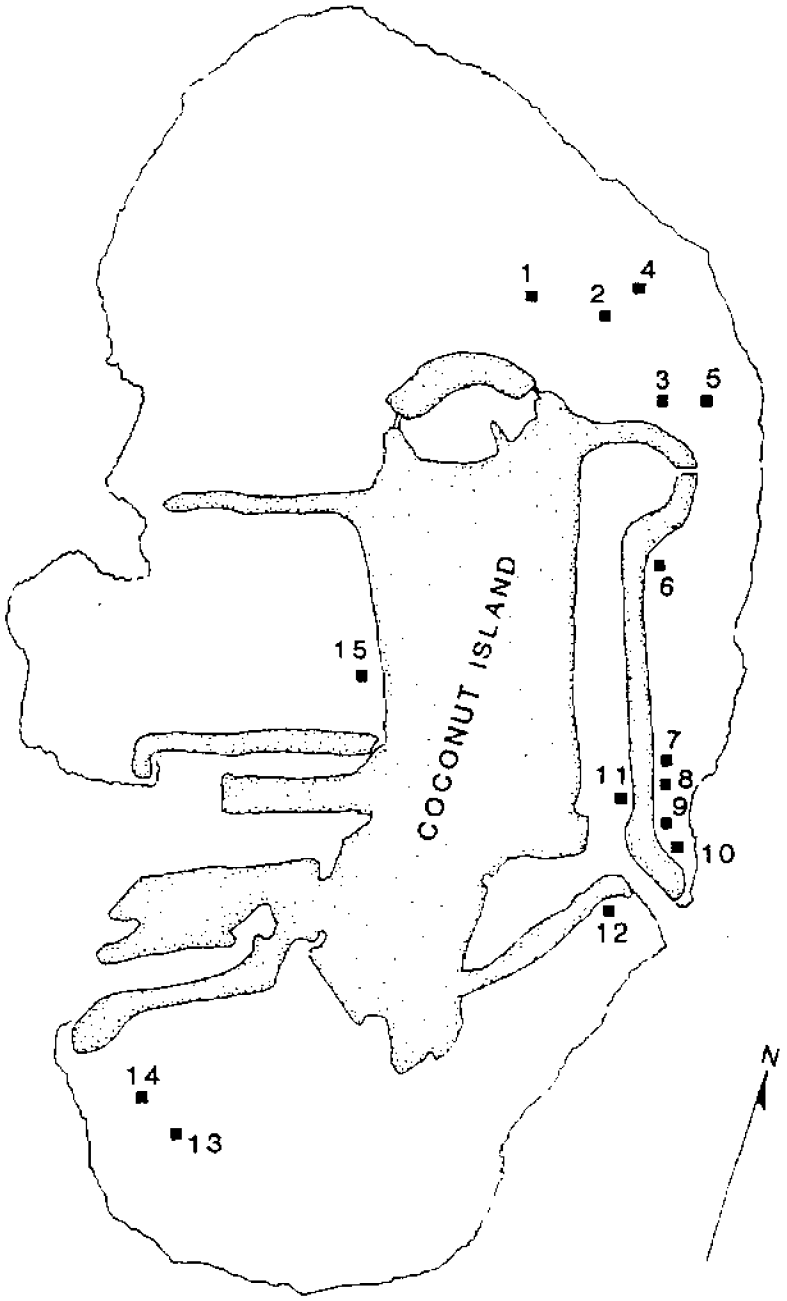

Fig. 1. Approximate quadrat sample locations for M. L. Bartlett's 1983 samples.

TABLE 1. Quadrat counts (Number of individuals per 1/4 m^2), for the Coconut Island (Moku o Loe) reef flat, comparing samples taken from 1969 to 1973 and samples taken in 1983.

1969-73		1983	
SAMPLE: 6 (NW41-85-04)** DATE: 1/05/69		SAMPLE: 1 DATE: 08/07/83	
		misc. polychaetes	18
Muricodrupa funiculus	1		
Isognomon perna	1		
Ctena bella	22		
Tellina palatam	35		
Etisus electra	1		
Etisus sp.	2		
Leptodius sanguineus	2		
Thalamita admete	1		
		Chirodota rigida	17
SAMPLE: 9 (NW64-95-09)* DATE: 05/02/69		SAMPLE: 2 DATE: 07/07/83	
		misc. polychaetes	7
Crucibulum spinosum	24	Crucibulum spinosum	1
Bittium zebrum	3		
Ctena bella	12		
other molluscs	3		
Lingula reevii	1	Lingula reevii	2
SAMPLE: 11 (NE2-24-9)* DATE: 07/16/69		SAMPLE: 3 DATE: 06/23/83	
		misc. polychaetes	5
vermetids	p		
Ctena bella	41		
Tellina robusta	1		
		Holothuria monocaria	3
SAMPLE: 8* DATE: 03/28/69		SAMPLE: 4 DATE: 08/07/83	
		Zoanthus pacificus	14
		misc. polychaetes	25
Diodora octagona	10		
Bittium zebrum	20		
Natica gualteriana	1		
Muricodrupa funiculus	1		
Peristernia chlorostoma	5		
Ischnochiton octaloides	3		
Isognomon perna	2		
Ctena bella	106		
Macoma obliquilineata	1		
Tellina palatam	8		
other molluscs	5		
		Alpheidae	1
		Holothuria monocaria	13

1969-73		1983	
SAMPLE: 3 (NE41-09-08)* DATE: 12/07/68		SAMPLE: 5 DATE: 08/18/83	
		misc. polychaetes	6
		uniden.	2
Plakobranchus ocellatus	1		
Ctena bella	3		
Tellina robusta	4		
Macoma obliquilineata	1		
		Chirodota rigida	21
SAMPLE: 7 (SE41-16-03)* DATE: 03/11/69		<SAMPLE: 5 (above)>	
Ctena bella	5		
Tellina robusta	3		
Macoma obliquilineata	2		
SAMPLE: 10 (SE64-77-07)* DATE: 07/10/69		<no comparable sample>	
Ctena bella	8		
Tellina robusta	1		
Macoma obliquilineata	2		
SAMPLE: 38 DATE: 06/23/71		SAMPLE: 6 DATE: 08/18/83	
Bunodeopsis medusoides	7		
		Edwardsia sp.	2
		Anthopleura sp.	31
		misc. polychaetes	6
		Ctena bella	2
Tellina palatam	1	Tellina palatam	8
		Holothuria monocaria	7
SAMPLE: 35 DATE: 04/29/71		SAMPLE: 7 DATE: 06/11/83	
Aiptasia pulchella	11		
Anthopleura sp.	4		
Anthopleura nigrescens	195		
Bunodeopsis medusoides	17		
other anemones	4		
		Edwardsia sp.	2
		Palythoa sp.	1
Pomatoleios kraussii	3		
		misc. polychaetes	11
Crucibulum spinosum	1		
Bittium zebrum	1		
Natica gualteriana	1		
Isognomon perna	1		
Ostrea hanleyana	2		
Brachidontes crebristriatus	1		
Tellina palatam	3		
		Macoma obliquilineata	3
Etisus electra	13		
		Gonodactylus guerini	1
Chirodota rigida	1	Chirodota rigida	1
Holothuria monocaria	5	Holthuria monocaria	1

1969-73		1983	
<no comparable sample>		SAMPLE: 8 DATE: 06/11/83	
		misc. polychaetes	17
		Tellina palatam	2
SAMPLE: 34 DATE: 04/27/71		SAMPLE: 9 DATE: 06/09/83	
Aiptasia pulchella	97		
anemone	2699	anemone	1
Porites compressa	p		
Pomatoleios kraussii	1		
Eurythoe complanata	2		
Ischnochiton petaloides	2	misc. polychaetes	36
		Ischnochiton petaloides	1
Isognomon perna	12	Hipponix sp.	1
Ctena bella	1		
Tellina robusta	1		
other molluscs	2		
Etisus laevimanus	4		
Etisus electra	18	Etisus electra	4
Calcinus latens	1		
other crustacea	1		
Chirodota rigida	6		
Holothuria monocaria	2		
SAMPLE: 33 DATE: 04/26/71		SAMPLE: 10 DATE: 06/13/83	
Aiptasia pulchella	3		
other anemones	82		
Eurythoe complanata	4	Montipora verrucosa	p
other polychaetes	1	other polycheates	71
Diodora octagona	2		
Peristernia chlorostoma	5		
Natica gualteriana	1		
Ostrea hanleyana	1	Ischnochiton petaloides	4
Ostrea sandvicensis	1		
Isognomon perna	19		
Ctena bella	21	Ctena bella	2
other molluscs	18		
Etisus laevimanus	1		
Etisus electra	22	Etisus electra	16
Calcinus latens	4		
other crustacea	5	Portunidae	1
		Xanthidae	2
		Holothuria monocaria	1
		Ophiactis savignyi	4

1969-73		1983	
SAMPLE: 39 DATE: 06/24/71		SAMPLE: 11 DATE: 08/24/83	
Aiptasia pulchella	101		
Edwardsia sp.	4		
other anemones	14		
		Palythoa sp.	9
Eurythoe complanata	15		
misc. polychaetes	2	misc. polychaetes	36
Ischnochiton petaloides	2		
		Hipponix sp.	1
Ctena bella	14	Ctena bella	3
Tellina palatam	15		
		uniden. shrimp	1
Panopeus pacificus	1		
SAMPLE: 31 (042171H-0022) DATE: 04/23/71		SAMPLE: 12 DATE: 06/09/83	
Aiptasia pulchella	6		
Anthopleura sp.	6		
other anemones	184	other anemones	1
		Palythoa psammophilia	2
Pomatoleios kraussii	379	Pomatoleios kraussii	5
Eurythoe complanata	1		
Ischnochiton petaloides	2	Ischnochiton petaloides	1
Diodora octagona	6		
		Hipponix sp.	1
Bittium zebrum	3		
Isognomon perna	13		
Ctena bella	44		
Tellina palatam	3		
		Macoma obliquilineata	2
other molluscs	12		
Etisus electra	4	Etisus electra	4
Metopograpsus thukuhar	1		
Leptodius sanguineus	7		
Pachygrapsus sp.	2		
other crustacea	30		
		Holothuria monocaria	3
<no comparable sample>		SAMPLE: 13 DATE: 08/08/83	
		Chirodota rigida	53
		Holothuria monocaria	1
SAMPLE: 16 (101270-0392) DATE: 10/12/70		SAMPLE: 14 DATE: 06/24/83	
Aiptasia pulchella	3		
Anthopleura sp.	1		
misc. polychaetes	5	misc. polychaetes	6
Ctena bella	4		
Tellina robusta	4		
Macoma obliquilineata	1		
		Alphaeidae	1
Chirodota rigida	3	Chirodota rigida	8
Holothuria monocaria	4	Holothuria monocaria	1

1969-73		1983	
<no comparable sample>		SAMPLE: 15 DATE: 08/24/85	
		misc. polychaetes	17
		Hipponix sp.	4
SAMPLE: (DI)57.5.3 DATE: 05/28/73		<no comparable sample>	
anemone	4		
Ctena bella	7		
Chirodota rigida	11		
Lingula reevii	3		
Ptychodera flava	6		
SAMPLE: 32 (0421714H-S2) DATE: 04/23/71		<no comparable sample>	
Aiptasia pulchella	2		
Anthopleura nigrescens	13		
other anemones	30		
Pomatoleios kraussii	530		
Siphonaria normalis	8		
Bittium zebrum	18		
Peristernia chlorostoma	3		
Uxricodrupa funiculus	2		
Isognomon perna	7		
Ostrea banleyana	3		
Ostrea sandvicensis	2		
Drachidontes crebristriatus	2		
Ctena bella	19		
other molluscs	20		
Etisus electra	2		
Pachygrapsus sp.	4		
Leptodius sanguineus	5		
Calcinus latens	1		
Xanthidae	6		
other crustaceans	66		
Chirodota rigida	1		
Holothuria monocaria	2		

* Only molluscs (and brachiopods) enumerated in sample
** Only molluscs, brachiopods, and crustaceans enumerated in sample

Table 2. Taxonomic summary. Counts normalized to number/m^2 based on all samples sorted for the phylum.

	1969-73		1983	
CNIDARIA (COELENTERATA)				
ACTINARIA				
Aiptasia pulchella	99			
Anthopleura nigrescens	92			
Anthopleura sp.	5		8	
Bunodeopsis medusoides	11			
Edwardsia sp.	2		1	
--- all anemones, incl. misc.[1]	1550			10
SCLERACTINIA				
Porites compressa	p			
Montipora verrucosa			p	
ZOANTHINIARIA[2]				
Palythoa psammophilia			3	
Zoanthus pacificus			4	
POLYCHAETA				
Eurythoe complanata	10			
Pomatoleios krausii	406		1	
--- all polychaetes, inc. misc.	183			71
MOLLUSCA				
GASTROPODA				
Bittium zebrum	11			
Crucibulum spinosum	6		<1	
Diodora octagona	4			
Hipponix pilosus			2	
Muricodrupa funiculus	1			
Natica gualteriana	1			
Peristernia chlorostoma	3			
Plakobranchus ocellatus	<1			
Siphonaria normalis	2			
Vermetidae	p			
BIVALVIA				
Brachidontes crebristriatus	1			
Ctena bella	77		2	
Isognomon perna	14			
Macoma obliquilineata	2		1	
Ostrea hanleyana	2			
Ostrea sandvicensis	1			
Tellina palatam	16		3	
Tellina robusta	4			
POLYPLACOPHORA				
Ischnochiton petaloides	2		2	
--- all molluscs, incl. misc.	164			10

ARTHROPODA, CRUSTACEA		
DECAPODA		
Alpheidae[3]		
Calcinus latens	2	<1
Etisus electra	18	6
Etisus laevimanus	2	
Etisus sp.	1	
Leptodius sanguineus	4	
Metopograpsus thukuhar	<1	
Pachygrapsus sp.	<1	
Panopeus pacificus	<1	
Portunidae, uniden.		<1
shrimp, uniden.		<1
Thalamita admete	<1	
Xanthidae, uniden.	2	1
STOMATOPODA		
Gonodactylus guerini		<1
-- all crustacea, incl. misc.	63	8
BRACHIOPODA		
Lingula reevii	1	1
ECHINODERMATA		
OPHIUROIDEA		
Ophiactis savignyi		<1
HOLOTHUROIDEA		
Chiridota rigida	5	27
Holothuria monocaria	6	8
--- all echinoderms	14	36
HEMICHORDATA		
ENTEROPNEUSTA		
Ptychodera flava	3	

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1 - The majority of "other" anemones are probably the small form of Aiptasia pulchella.

2 - Several species of zoanthids were very common on the Coconut Island reef during the 1968-1973 sampling. However, their distribution only poorly coincided with the locations of the samples reported herein.

3 - Sampling to a depth greater than 15 cm below the substratum surface would be required to obtain a representative sample of the alpheid shrimp.

the concentration of particulate organic carbon varied between 20-40 mmoles/m^3 in the south part of Kaneohe Bay (Smith, et al., 1981); after diversion, particulate organic carbon dropped to 15 mmoles/m^3.

Our results are of interest in view of the conclusions expressed by Brock and Smith (1983) that the soft bottom cryptofauna (as opposed to the hardbottom cryptofauna) displayed neither a large biomass response to nutrient loading, nor a great decline following termination of nutrient inputs. We would suggest that this conclusion is somewhat method dependent. That is, by sampling a greater volume of sediment and concentrating on the larger organisms, the mobile infaunal and epifaunal organisms of the reef flat can be shown to have increased during nutrient loading and declined after termination of nutrient loading.

Potentially, other factors may have influenced the small change in soft bottom infauna recorded by Brock and Smith. In our study, one group of organisms, the holothurians, appears to have actually increased in abundance between 1973 and 1983. Of all the infaunal species recorded, only the holothurians (particularly Chiridota rigida) feed directly on organic particulates within the sediment. All of the other soft bottom species (e.g., the bivalves, Ctena bella and Tellina palatam), although found within the substratum along with C. rigida, feed on detritus and/or phytoplankton from off the bottom or out of the water column (the bivalves extend a siphon out of the substratum). A decline in the richness of organic particles within the sediment would lag behind that in the water column and on the bottom surface. Further, if during the period of eutrophication the sediment environment were overloaded by the accumulation of organic matter, the resulting tendency toward anoxic conditions could become detrimental to species with no or minimal direct contact with the overlying water column, depressing the populations of these species.

The data provide little information on changes in the species composition (see Table 2). The 1968-73 samples (bearing in mind that not all groups were looked at in all samples) are on the whole more diverse than the 1983 samples. A number of species collected during the period prior to diversion of sewage from the Bay were not collected in the post-diversion samples. However, given the apparent densities of most species enumerated in 1983, considerably more samples would need be collected to reasonably expect to encounter all of the species recorded earlier. In the Brock and Smith (1983) study it was noted that no taxa were eliminated following sewage diversion: the decrease in biomass was primarily due to a reduction in the numbers of individuals. Our data suggest the same may be true for the groups of organisms studied here. The 1983 results give no clear indication that the species composition of the cryptic macroinvertebrate assemblage on the shallow reef flat at Coconut Island changed radically following diversion of the sewage from Kaneohe Bay, although some species may have disappeared from the habitat.

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Genetic structure of two species of Montipora on a patch reef: conflicting results from electrophoresis and histocompatibility.

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Abstract

The genetic structure in populations of two species of the coral Montipora was investigated using histocompatibility and electrophoretic techniques. Patterns of graft acceptance and rejection were different for each species. Electrophoretically distinct tissues were capable of fusing, indicating that clonal identity is not necessarily inferred by graft acceptance. A greater understanding of the genetics of invertebrate immunology is required before histocompatibility criteria can be used independently to assess population genetic structure with confidence.

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Patchwork patchreefs: The clonal diversity of the coral Porites compressa in Kaneohe Bay, Hawaii

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Abstract

Morphological charcteristics were used in conjunction with an immunocompatibility assay to examine the genetic diversity of a patch reef population of Porites compressa. Visually identical colonies which exhibited tissue graft fusion were identified at distances of from 0.2 m to 100 m across the reef. In a 2 m X 10 m transect of the reef, 99% of the 291 colonies of P. compressa were identified as belonging to 8 morphologically distinct and immunocompatible groups. Three of these morphotypes alone comprised 40% of the total P. compressa cover within the transect, but were not found on nearby patch reefs where other morphotypes were predominant. The clonal structure of each patch reef is apparently unique. Sexual recruitment and the genetic diversity of P. compressa on mature reefs appear to be low, while asexual reproduction by the establishment of clones derived from fragments appears to be a significant factor resulting in a population dominated by a small number of individual clonal types.

Introduction

Decades of research have resulted in the tenet that the basis of evolutionary theory lies in the identification of the genetic variation within populations. In most species, each individual has a unique genetic identity. However, for species in which asexual reproduction results in physically separate, but genetically identical ramets or clonemates, demographic data will be confused when identical clones are construed to be genetically different individuals. Likewise, evolutionary or ecological questions dealing with gene flow, natural selection, life history patterns, or competition hinge on the precise identification of individual genotypes and their distributions in a population (Harper, 1981; Parker, 1979; Hinkevich and Loya, 1983; Cook, 1983).

For most clonal species - corals, sponges, strawberries, aspens, tunicates, or even lizards and fish - it is difficult to distinguish clonemates from other genotypes by morphological differences alone. Two methods which have been utilized to distinguish genotypic variants are the traditional electrophoretic enzyme analysis and the more recently developed technique of histocompatibility testing by tissue grafting. Clonal genetic identity has been determined by tissue grafting in fish (Kallman, 1970; Angus and Schultz, 1979); lizards (Cuellar, 1977); tunicates (Watanabe and Taneda, 1982); corals (Neigel and Avise, 1983a; Jokiel et al., 1983; Heyward, this volume); and sponges (Curtis et al., 1982; Jokiel et al., 1982; Neigel and Avise, 1983b). In this study, we used the technique of tissue grafting to identify and differentiate individuals of the scleractinian coral Porites compressa. In addition, we found that clonemates of individuals of this species can be identified consistently in the field based on a small set of morphological characters and that these identifications correspond directly to the results of the genotypic analysis allowed by the tissue grafts. To our knowledge, this is the first plant or animal species in which clonemates in natural populations may be distinguished from other genetically non-identical members of the species based on visual markers. We utilized this singular feature of P. compressa to estimate the number of genotypically unique individuals in a clonal coral population on a patchreef in Kaneohe Bay, Oahu, Hawaii.

Materials and Methods

The study area, a patch reef (#43, Roy, 1970) approximately 200 x 120 m in size is located at the northern end of Kaneohe Bay. Depth of the reef at low tide varies from 1 m to 2 m near the center and 4 m to 5 m at the edge of the slope. A channel approximately 10-12 m deep surrounds the reef, separating it from the nearest patch reef by approximately 20 m.

A 2 m x 10 m transect was established on the northwest (leeward) edge of the reef, in an east to west direction, and extending to within about 20 m of the reef edge. This area of the reef was chosen because of its uniformity in depth, and thus, presumably, in wave exposure, water motion, and light intensity. The transect was permanently marked at four corners with iron stakes, and at 1 m intervals with surveying tape. A 1 m quadrat with a 10 cm grid was used to map each coral colony within the transect. The area of each colony was estimated from the mapping data with a Summagraphics XY digitizer program. Photographs of each quadrat were made with a Nikonos camera mounted on a 1 m frame. All underwater work was done with SCUBA.

Eight large Porites compressa heads within the transect were designated as donor colonies. Three to 24 branches (minimum length 2 cm) were removed from each colony and securely attached with prelabeled cable ties to branches of other colonies judged to be morphologically identical to the donor. Colony color, branch size and shape, compactness of branches within the colony, and the states of polyp expansion or contraction during daylight observations were used as visual markers for distinguishing different morphological types. Some morphotypes had more visually distinctive characteristics and were easily recognized, while others had subtle differences and were more difficult to distinguish. Our ability to identify clonemates and to distinguish between morphotypes increased with familiarity and with observation of grafting results.

Branches chosen for grafting were relatively straight and symmetrical in circumference to facilitate contact between donor and recipient tissue. Care was taken not to abrade coral tissues during the grafting procedure. Autografts (branches retied to original heads) were made for each donor colony. All grafts were done in the field to avoid the additional stress of transport and maintenance in the laboratory. Two sets of grafts were scored at 20 d, 47 d and 62 d after grafting; two sets at 14 d, 41 d and 51 d after grafting; and three sets at 15 d and 30 d after grafting.

The extent of clonal dispersal, and our ability to consistently identify isogeneic colonies were tested by tying three additional sets of grafts on the leeward half of the patch reef. Each centered on one of 3 donor colonies of P. compressa and radiated from that colony in all directions. Grafts from morphotype P6 were also expanded to colonies outside of the 2 X 10 transect. From 7 to 23 grafts were made from each donor head to recipient colonies which were judged to be morphologically identical and ranged from 0.2 m to 100 m away from the donor colonies. These grafts were scored after 56 d, except for one set which was scored after 23 d.

Grafts were judged as fusions, rejections, or technical losses (loose or broken). A total of 120 grafts were made, with 7 losses. A number of grafts (fusions and rejections) were returned to the lab, photographed, and soaked in commercial bleach to remove tissue to ascertain to what extent skeletal growth and/or fusion had occurred.

The patch reef (#42) closest in proximity to the study reef and a patch reef in southern Kaneohe Bay (#8) were surveyed for the presence of P. compressa colonies which were identical in morphotype to two common morphotypes found on the study reef. No identical colonies were found but five grafts from each donor type were tied to colonies of similar color and morphology found at approximately the same depth on reef #42.

Results

Porites compressa colonies occupied 86% of the total coral cover within the 2 m x 10 m transect of the patch reef (Table 1). Montipora verrucosa (9%), Pocillopora damicornis and Porites lobata (<1%) and sand or rubble areas (5%) comprised the remainder of the 20 m^2. Colonies totaling 61% of the total P. compressa cover could be determined as one of 8 morphotypes, based on morphological characteristics (color, branch length and width, and compactness of branches within the colony) and the grafting results (Table 2). Three morphotypes (P3, P6, and P9) dominated the transect, together comprising approximately 40% of the total P. compressa cover. The eight morphotypes were represented by 47%, or 136 out of 291, of the P. compressa colonies within the transect. Mean colony size ranged from 406 cm^2 to 1523 cm^2. There were no significant differences (ANOVA, Duncan's Multiple Range Test, $p>0.05$) in mean colony size between the eight morphotypes or between quadrats through the length of the transect.

Table 1. Morphological characteristics, number, mean size, and percent of total Porites compressa cover within the 2 X 10 m transect. Total percent cover of Montipora verrucosa and bare substratum are included. Compactness Index (C.I.): 1=distance between branches < width of branches, 2=distance between branches= branch width, 3=distance between branches > branch width, 4=areas with closely packed branches separated by areas without branches.

Morphotype	Color	Branch Length/Width	C.I.	Polyp State (day)	Number Colonies/ 20m²	Mean Colony Size cm² ±s.d.	% Cover
P1	white	short/med	4	in	21	920 ±1099	11.39
P4	yellow-green	short/med	1	out	16	803 ±543	7.61
P5	caramel	short/med	4	out	15	804 ±839	7.11
P6	yellow-green	long/wide	3	out	31	712 ±731	13.03
P7	white	short/narrow	2	in	7	406 ±265	1.68
P8	tan	long/med	3	out	1	1523 ---	0.90
P9	brown	med/wide	2	out	30	692 ±715	15.51
P24	purple	long/wide	3	out	7	993 ±892	4.06
Unidentified P. compressa colonies					149	391 ±398	25.04
Montipora verrucosa					29		9.00
Bare Substratum							4.67

Table 2. Results of tissue grafts within 2 X 10 transect (P3-P24) and scatter plots (P6, P11, P12, P14). Location coordinates indicate quadrat number within transect, with each meter numbered from 1 to 10 from seaward to leeward across the reef, and each of the two meters of the transect width designated A or B (i.e. 1A = the most seaward quadrat on the north side of the transect).

Donor Colony	Distance Between Donor & Recipient	No. Fusions/ Total No. Grafts	Location of Donor Colony
P3	1.6-4.6	8/8	5B
P4	1.0-5.1	3/4	2B
P5	0.2-9.3	5/14	1A
P6	0.1-100.0	23/24	7B
P7	0.2-4.4	6/17	6A
P8	0.8-5.5	0/15	5B
P9	1.0-5.2	6/8	9B
P24	1.0-5.5	3/3	8B
P11	0.8-5.0	7/7	reef edge
P12	2.7-6.0	6/6	reef crest
P14	0.2-5.3	10/13	reef flat

Grafts scored as fusions (isografts) were characterized by both confluent coenenchyme and skeletal tissue. Soft tissue fusion was evident for some grafts after 7 d, but a minimum of 30 d was found to be necessary for strong skeletal fusion (as judged by our inability to separate the grafted branches with a moderately gentle tug). Some morphotypes (P3, P6, P9 and P24) fused as isografts more rapidly than others (7 d compared to 20 d). At least one immunocompatible colony was found for each of the donor colonies within the 2 x 10 m transect, with the exception of P8, for which none of the 15 grafts resulted in fusion (Table 2). Fusions (indicative of genetic identity) occurred at distances from 0.1 to 100 m from the donor colonies. All autografts resulted in fusions.

Graft rejections (allografts) were characterized by an initial bleaching of the tissues in the contact zone, followed by subsequent tissue death, which resulted in a band of exposed skeleton 2-3 mm wide separating the tissues of the grafted branches. After several weeks, this band usually became pink in color, possibly due to bacterial invasion, and then slowly became a shallow groove between the two branches as a result of growth of tissue on either side of the scar. Partial overgrowth (3-4 mm) of the donor recipient branches was noted after 2 months. After 6 months, some graft interfaces were almost totally overgrown by the recipient colony, except in three instances in which the donor branch overgrew the branch to which it was grafted. A thin, flat skeletal ridge separating rejecting branches was observed in some of the allografts. Pink or white bands devoid of coral tissue and elevated calluses were evident in contact zones between natural allografts of contiguous colonies in the field.

The results of the scatter plots grafts of morphotypes P6, P11, P12 and P14, which tested our ability to identify isogeneic colonies based on morphological characteristics and gave an indication of the extent of clonal dispersal, are presented in Table 2. Three morphotypes were highly recognizable (100% fusions) and distributed in all directions to distances of up to 100 m over the reef. Colonies of one of these clonal types (closest to the reef crest) were separated by large areas of dead and encrusted P. compressa and may represent relicts of one or a few large colonies. One morphotype was mistakenly identified in three out of 12 grafts (85% fusions) to colonies which were later recognized as being subtly distinguishable in morphology from the donor head.

All of the between-reef grafts were rejections; no colonies histocompatible to the two morphotypes common on the study reef could be found on either the nearest patch reef or the patch reef in the southern end of the bay.

Discussion

Porites compressa is the most abundant coral species on Oahu (Dollar, 1982; Grigg, 1983), and is competitively dominant in the shallow, calm waters of Kaneohe Bay where it comprises approximately 85% of the total coral cover. It forms thickets of adjacent but not interconnected colonies producing a patchwork of various colors, shapes and sizes (Maragos, 1972).

The life history pattern of P. compressa is very different from that of the "r-strategists" of Pocillopora damicornis and Stylophora pistillata as described by Loya (1976). This species is dioecious (colonies with all male or all female polyps), and broadcasts gametes through the summer months on a biweekly cycle (Stimson, 1978 and personal observations.) Sexual recruitment of P. compressa to patch reefs is apparently low (Polacheck, 1978) and no colonies smaller than 30 cm^2 were seen in our transect, although colonization of bare substratum by planulae of this species is evident in the more southern parts of the bay (Jokiel et al., 1983). Mortality rates for P. compressa have been estimated as less than ten percent over a twelve-month interval (Polacheck, 1978). The smallest and largest heads within our transect had geometric mean radii of approximately 4.8 cm and 27.1 cm, respectively. Given an annual growth rate of 2.47 cm yr^{-1} (Polacheck, 1978), these colonies may be approximately 2 years old and 11 years old, if derived from planula settlement, although estimation of age from colony size is not a strictly dependable measure (Hughes and Jackson, 1980). Large colonies on the seaward reef edge with radii of 150 cm or more may be as much as 60 years old or older or may be the result of fusions of separate isogeneic heads.

The ecological significance of different intraspecific variants in corals is poorly understood. Vaughan (1907) divided Porites compressa from Hawaii into 16 formae and 2 subformae based primarily on calical structure. These formae also exhibit diversity in gross colony morphology, but whether morphotypes which we

have distinguished correspond to any of Vaughan's formae was not determined. Variation in colony color may be due to differences in animal or plant pigments (Kawaguti, 1944). Colonies with different branch length or width may be differentially susceptible to breakage due to waves or storms. The state of polyp expansion or contraction of colonies, found to be consistent within clones of each morphotype in this study, is indicative of a dichotomy between colonies which feed during the day or at night (Lasker, 1976). Potts (1976) suggested that different physiological or morphological variants of Acropora palifera were the results of different selective pressures in different habitats on a reef. However, the habitat-selected characters of fusion, infilling, or overgrowth (Potts, 1976, 1978) between adjacent branches were also observed in natural and experimental interactions between colonies of P. compressa within the homogeneous reef flat environment of our transect and probably do not reflect differences in adaptive response.

Fragmentation is an important method of reproduction in scleractinian corals (Highsmith, 1982). In general, the bigger the fragment size, the better the chance of survival of the fragment to establish a new colony (Highsmith, 1982; Heyward, 1982). Large heads of P. compressa which have broken from their bases and fallen over on their sides frequently slide down slopes at the edges of reefs (Bartlett, this volume). Coral planulae or fragments may then colonize the available space on the newly-bared dead bases of these toppled heads; this process may result in the gradual peripheral expansion of reefs. Fragments generated by waves would be carried in a leeward or southwesterly direction across patch reefs in Kaneohe Bay. This may have resulted in the observed patch work of isogeneic, clonally derived colonies of P. compressa making up these patch reefs. Heyward (1982) found that the isogeneity of Montipora ramosa increased from seaward (40%) to leeward (74%) across the Great Barrier Reef in Australia. There is no apparent pattern in isogeneity, size, or number of P. compressa colonies in the very limited distance of our transect. However, colonies tend to be larger (up to 3 m in diameter) on the extreme seaward edge of the reef, and are more numerous per unit area and smaller (less than 1 m in diameter) on the leeward side.

There is a great deal more bare, hard substratum on the seaward edge and crest of the reef than on the leeward side. These areas appear to be the dead skeletal remains of P. compressa colonies and are encrusted with coralline algae and an occasional small colony of Pocillopora damicornis. Dictyosphaera cavernosa, a green bubble alga, is often found on these patches of dead coral skeletons and overgrowth by this alga may have been a determining factor in the death of the original coral colonies (Smith et al., 1973). Clumped within patches of such spaces are small (5-10 cm diameter) living heads of P. compressa. Grafts between these small colonies were not attempted, but every head in each small area appears to be morphotypically identical to its neighbors; thus, these colonies may represent either isolated remnants of a single large head or mass settlement of genotypically related planulae. However, no obviously recently settled small colonies were found in areas of bare substratum on the patch reef. Sexual recruitment of P. compressa may be low due to the small size of eggs (120 um; Stimson, 1976) and larvae, or unsuccessful fertilization due to unbalanced sex ratios as was found by Kojis and Quinn (1982) in other species of Porites.

Neigel and Avise (1983a) provide operational properties requisite for self-recognition systems based on their work with Acropora cervicornis. Their criteria of (1) multiple simultaneous modes of interactions, (2) reproducible responses, and (3) fusion of autografts were met by P. compressa in Kaneohe Bay and were observed under both natural and experimental conditions. The observation that colonies separated by large distances (600 m, Neigel and Avise, 1983a) do not exhibit tissue compatibility was further supported by our inability to find colonies on an adjacent patch reef which were identical to common morphotypes on the study reef. Some colonies on the study reef were apparently unique (i.e., P8); that is, no other morphologically identical colonies were found. Neigel and Avise (1983a) also suggest that, if gene flow is restricted (i.e., resulting in local settlement of sexually produced daughter colonies), then grafts between related allogeneic colonies might potentially exhibit fusions if the alleles for self-recognition were identical. It seems unlikely, in our study, that fusions between morphotypically identical colonies represent sibling and not clonally derived colonies, unless genes for these morphological characters are strongly linked to those controlling self-recognition responses.

Tissue grafting appears to be a valuable tool in assessing genetic diversity and population structures of many groups which produce clonally derived offspring by parthenogenesis or fragmentation (Neigel and Avise, 1983a, b). However, it is important that some caveats be applied if graft results are interpreted without substantiating evidence from morphological, electrophoretic, or other assessments of genotype (Curtis et al., 1982). Heyward (this volume) has found enzyme allelic variation in colonies of Montipora verrucosa which fused when grafted together.

For many organisms the recognition of clonal types requires bioassays involving grafting, electrophoresis, or other techniques requiring a considerable period of time. We have demonstrated that clones of Porites compressa are recognizable by a small set of morphological characteristics which can allow immediate identification of clonemates in the field. Identification of individual morphotypes has been substantiated by tissue grafting. This system presents unique opportunities for future studies which will address questions concerning intraspecific competition between clonal genotypes of P. compressa. Differential fitness and competitive abilities of these genotypes may be assessed by measurements of growth rate, survivability of fragments, and reproductive output within and between clones.

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Biochemical genetics of Pocillopora damicornis in Kaneohe Bay, Oahu, Hawaii.

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Abstract

Within- and between-reef patterns of biochemical genetic variation were assessed for Pocillopora damicornis from eight sites in Kaneohe Bay, Oahu, Hawaii. Electrophoretic banding patterns observed for a number of enzymes confirm the exact inheritance of adult allozymes by planulae and suggest that polyploidy may be involved. Phenotypic diversity was low on reefs, which were usually dominated by a single clone comprising 30-60% of individuals, and may be reduced on some reefs as a consequence of past disturbance events. There was some geographic differentiation among reefs within the bay, with respect to the identity of clones present on a particular reef. This seems to be due to dispersal factors rather than selection on parts of the genotype. Some concordance of morphotypes, reported to planulate asynchronously, with certain electrophoretic clones was seen. But there is considerable overlap of clones and phenotypes of single loci assigned to either morphotype, so that there is little apparent biochemical differentiation associated with asynchronous planulation.

Introduction

The present lack of data relating to gene flow between geographically isolated populations of coral species prevents both the resolution of controversies on the zoogeographic origin of coral faunas (Dana, 1975; Heck and McCoy, 1978) and an adequate understanding of the initial stages of reef recolonization processes (Pearson, 1981). While it has been suggested that the larvae of some corals may be effectively dispersed over considerable distances (Dana, 1975; Richmond, 1981), the extent of genetic differentiation of coral populations remains largely untested. A necessary precursor in the interpretation of between-population variation and a primary indicator of population boundaries is the within-population genetical structure. Additionally, this structure may be used as an indication of the types of reproductive processes producing recruits for that population.

Few studies of corals address the question of within-population genetical structure. Those which do suggest that for Montipora dilitata (Jokiel et al., 1983; Heyward and Stoddart, this volume), Acropora cervicornis (Neigel and Avise, 1983) and Pocillopora damicornis (Stoddart, 1983a), populations may be comprised of a limited number of clones and that the spatial extent of these clones may be quite narrow. This suggests that asexual reproduction (fragmentation for M. dilitata and A. cervicornis and fragmentation and asexual planulation for P. damicornis) provides a greater proportion of these populations' recruits than sexual processes and that recruitment is relatively localized. The only coral population reported with a genetical structure consistent with predominantly sexual reproduction is one of Montipora verrucosa (Jokiel et al., 1983; Heyward and Stoddart, this volume).

Presently, these studies of coral genetics use two analytical techniques, electrophoresis and self-recognition, which have dissimilar analytical properties. The self-recognition method may be more sensitive in detecting clones than an electrophoretic study using only a few loci (Neigel and Avise, 1983), but it is largely inappropriate to assessing between-population differentiation as a) the same clone rarely appears in more than one population, b) it provides only a relative and dichotomous result, i.e. different or not different, and c) the extensive number of graft comparisons needed to adequately compare a number of populations. Electrophoretic data are well suited to comparisons of populations and an extensive literature of such comparisons and their interpretation exists for non-corals. Its only such use in corals to date is limited to a comparison of three populations of P. damicornis (Stoddart, 1983a) which suggested

that corals at sites separated by less than 10 km could be extensively differentiated.

Genetic differentiation may result from either, or both, differing local selective forces or separate origins of recruits. The above-mentioned study of P. damicornis was conducted in a series of small embayments around Rottnest Island, Western Australia (32°S, 115°30'E) and it may be that both physical distance and disjunct circulation of water between bays contribute to this genetic differentiation by restricting gene flow. The proximity of these sites and the apparent similarity of the habitat at each suggests that restricted gene flow may be more important than differential selection in promoting population differentiation here. The present study uses the biochemical genetics of eight populations of Pocillopora damicornis situated in Kaneohe Bay, Oahu, Hawaii (21°28'N, 147°48'W) to investigate gene flow properties for this species. Although these sites are separated by distances comparable to those of the Rottnest Island sites, their location within a single embayment may emphasize the effects of distance per se as opposed to the discrete circulation of adjacent bays and in addition, minimize the potential for differential selection.

Materials and Methods

Samples

Reefs were sampled throughout the Bay (Fig. 1) using a line transect technique. A 40 m tape was laid in a straight line across the reef-flat with one end of the tape at the edge of the reef and the other end at a point away from the edge. Branch tips (≈ 5 cm length) were broken from heads at 1 m intervals along the transect; the head selected being the nearest to the tape at the start of each m. The 40 samples were then placed, with seawater, into a large bucket and transferred to the laboratory where the growing tips of branches (≈ 1 cm to 5 cm length) were excised and homogenized. Tips were homogenized with equal volumes of indicator-extractant (0.1 ml mercaptoethanol, 10 g sucrose, 0.1 g bromphenol blue, 25mg NADP per 100ml distilled water) within 5 h of collection. Samples were then frozen at -20°C and electrophoresed the following day. Richmond and Jokiel (1984) describe the existence of "Y" and "B" type P. damicornis in Kaneohe Bay which have asynchronous periods of planulae shedding; they also list morphological criteria for identifying these forms.

On three Stations (No 4, No 6 and No 8) samples were assigned to morphotypes. Before samples were broken from colonies, the colony was assigned to a morphotype by an experienced observer. Observers were changed for each reef. Originally it was proposed to divide samples into "Y", "B" and "other" classes, but while observers were usually confident about "Y" assignments, "B" forms were less distinct causing the adoption of "Y" and "not-Y" classes.

Planulae were collected from aquaria containing single adult colonies. Twenty planulae from each of two colonies were electrophoresed individually.

Electrophoresis

Enzymes assayed for all reef samples were : leucyl-glycylglycine peptidase (LGG : EC 3.4.11/13), phosphoglucose isomerase (PGI : EC 5.3.1.9), mannosephosphate isomerase (MPI : EC 5.3.1.8) and malate dehydrogenase (MDH : EC 1.1.1.37). In addition, assays for phosphoglucomutase (PGM : EC 2.7.5.1), adenosine deaminase (ADA : EC 3.5.4.4), 6-phosphoglucose dehydrogenase (6PGD : EC 1.1.1.44), nucleoside phosphorylase (NP : EC 2.4.2.1), glutamate-oxaloacetate transaminase (GOT : EC 2.6.1.1), xanthine dehydrogenase (XDH : EC 1.2.1.37) superoxidase dismutase (SOD : EC 1.15.1.1) and leucyl-tyrosine peptidase (LT : EC 3.4.11/13) were carried out for some samples. Electrophoretic techniques are described in Stoddart (1983a) with the additions that PGM was run on the tris-EDTA-borate buffer, along with ADA. GOT and XDH, and 6PGD were run on the tris-citrate buffer. This previous study identified electrophoretic bands which were derived from zooxanthellae, although these only occurred for a few enzymes. Only bands shown to be derived from coral were used for the present study.

Statistics

Heterogeneity chi-squared tests were used to test phenotype frequencies for each reef against the pooled observations of the other reefs for each enzyme. To avoid low expected values, the rarer phenotypes for each enzyme were pooled. Diversity of multilocus phenotypes was calculated using a genotypic diversity

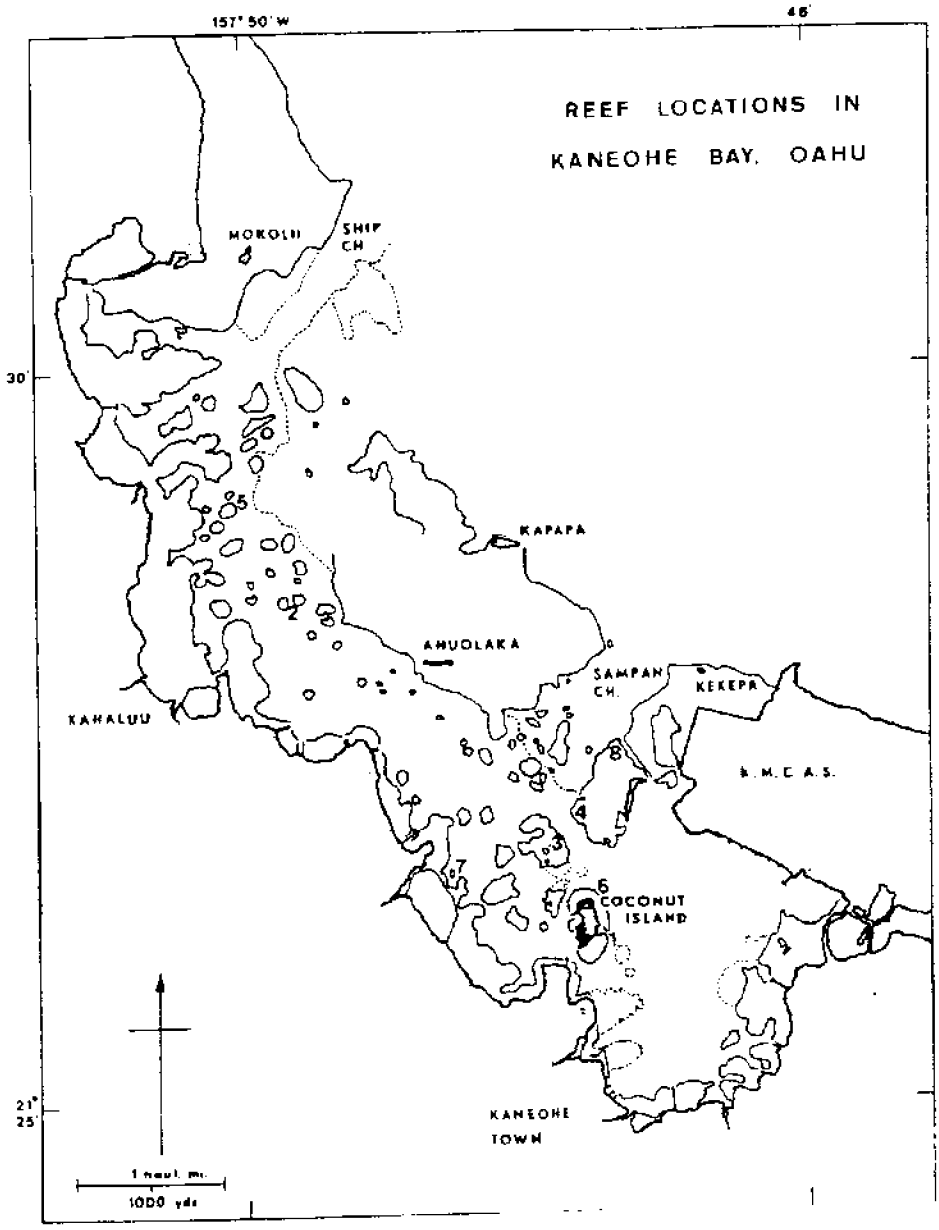

Fig. 1. Map showing locations of the eight reefs sampled in Kaneohe Bay.

index, GI (Stoddart, 1983b), where GI = 1/< gi2 when gi is the relative frequency of the ith genotype.

Clustering of populations used the UPGMA algorithm (Sneath and Sokal, 1973) with similarity calculated either as Manhattan distance, MD, of phenotype-frequency data for individuals or, clones, where $X_{y,i}$ = frequency of the ith phenotype in population Y.

$$MD = \sum_j |X_{Aji} - X_{Bji}|$$

or as the proportion of shared phenotypes, Ns

$$Ns = Na,b/(Na + Nb)$$

where Na,b is the number of multilocus phenotypes shared by reefs a and b and Na and Nt the total phenotypes in each.

Results

As in the case of P. damicornis previously assayed from Kaneohe Bay and elsewhere (Stoddart, 1983a), all planulae displayed electrophoretic banding patterns identical to those of their brooding parent. This precludes the testing of locus-allele models using inheritance. However, unlike the previous study, variation patterns between genotypes were not resolvable into a simple diploid system as a consequence of the number and pattern of bands, differential staining intensities and a marked excess of apparent heterozygotes.

As allele intetpretations were not available, banding patterns were scored as phenotypes and frequencies of these phenotypes used in place of allele frequencies to describe enzyme variation between reefs. On the assumption that zones of activity with different relative mobilities and which result from metabolism of different substrates are not derived from the same locus, composite phenotypes from the four enzymes routinely assayed were called multilocus phenotypes. The ratio of distance traversed by a protein "band" to distance traversed by the wave front (Rf) was determined.

Single-locus effects

LGG

Two distinct zones of activity were apparent, with the zone of greatest anodal mobility (Rf = 0.6) being the most intensely staining but not showing concise bands and having little apparent variation. The slower zone (Rf = 0.4) contained six discrete bands in varying combinations (Fig. 2a). The pattern of variation could be ascribed to a 7-allele, 2-locus model if a null allele (i.e. an allele coding for an unexpressed or non-functional enzyme) is postulated for locus 1 (bands A, B, E and null in locus 1 and C, D and F in locus 2). However, this would not explain the observed patterns of band intensity and excess heterozygosity and a one locus polyploid model, at least 4 n, may be more likely. As previously recorded (Stoddart, 1983a) for P. damicornis, LGG is a monomer.

Almost all phenotypes were multibanded (99% of individuals and 98% of multilocus phenotypes). Heterogeneity chi-squares with ABC, BD and pooled remainder classes, calculated from individuals, show Stations No 2, No 6 and No 4 to be significantly different. Stations No 2 and No 6 have similar patterns with excess ABC phenotypes and are different from Station No 4 which has a low ABC frequency.

PGI

Two zones of activity were apparent. Only the slower zone (Rf = 0.1) was scored as the more anodal zone (Rf = 0.15) was suspected of being derived from zooxanthellae by the results of a previous study (Stoddart, 1983a). A 2-allele 1-locus model, with PGI a dimer (Darnall and Klotz, 1975), adequately describes the banding sequences recorded (Fig. 2b). But again, the the patterns of banding intensity and the deficit of homozygotes suggest that a diploid model may be inappropriate.

For this enzyme, apparent heterozygosity comprised 85% of individuals and 81% of multilocus phenotypes. Chi-square tests of pooled AA and CC, homozygote, classes against ABC's show Stations No 2, No 8 and No 4 to be distinct. The former two with deficits of homozygotes, the latter with a surplus.

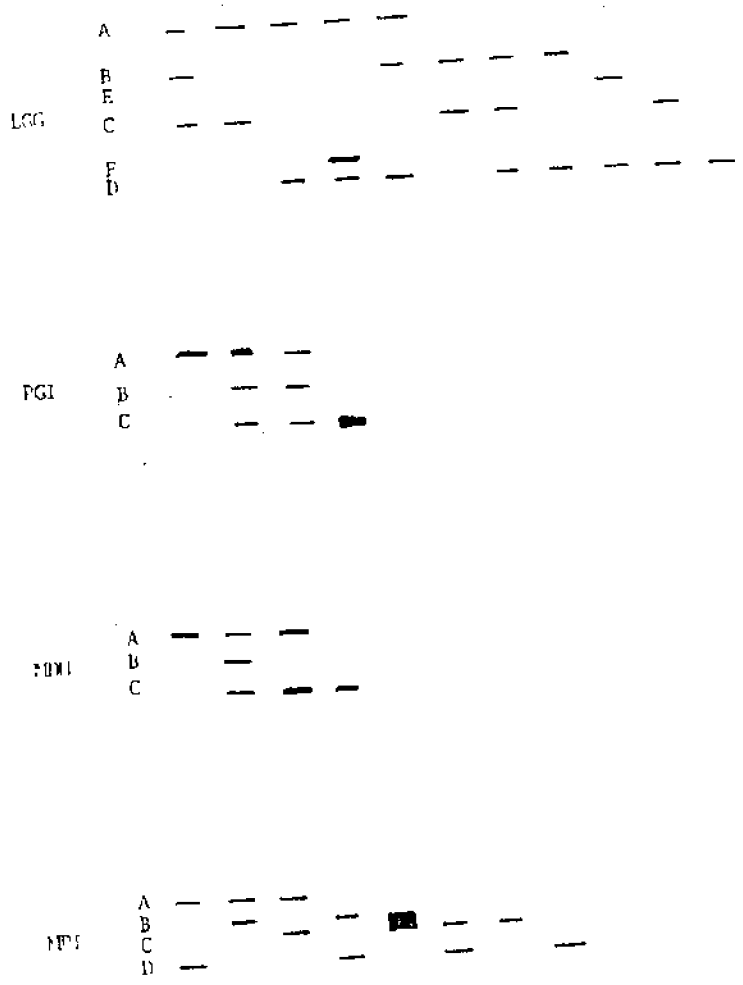

Fig. 2. Banding patterns for the four enzymes assayed for all populations. Bands represented for MDH and PGI show the actual patterns of intensity of the gels. Those for LGG and MPI show the positions, as variations in intensity were too numerous to depict.

MPI

Staining produced a single zone of activity (Rf = 0.3) with banding patterns suggesting a single locus with 4 alternative alleles (Fig. 2c). However, B and C bands had similar mobilities and it was at times difficult to distinguish between BC and CC interpretations. The latter was the only apparent homozygote observed for this enzyme, while all possible two-banded combinations were observed (93% of individuals and 88% of multilocus phenotypes) and more than one locus may be involved. Stations No 4 and No 6 were statistically distinct with a deficit and surplus, repectively, of the AC phenotype when chi-squared analyses were performed on AC, BD, CD and remainder classes.

MDH

Two zones of activity were present (Rf = 0.6, Rf = 0.5) of which the more anodal was polymorphic (Fig. 2d). With the exception of the AC phenotype, the results were similar to those of PGI. The apparent dimeric structure of this enzyme is consistent with MDH from other organisms (Harnall and Klotz, 1975; Hopkinson et al., 1976) but not with an AC phenotype. As the C band is intermediate in mobility between the A band and the lower zone of activity, an AC phenotype may be the result of a heterozygote of an A allele and a further allele whose mobility corresponds to the lower zone. This would yield an ACD phenotype with C the hybrid band and D being masked by the lower zone band. Even if this phenotype is disregarded, heterozygosity is still high (83% of individuals and 72% of multilocus phenotypes). Stations No 2 and No 4 are significantly distinct, using pooled AA and CC phenotypes versus pooled ABC and AC phenotypes. Station No 2 has a deficit of the former class while Station 4 has a surplus.

LTY

LTY was assayed for several reefs and always appeared polymorphic for the more cathodal two of the three zones of activity (Rf's = 0.6, 0.5 and 0.4). The most mobile zone was identical to that of LGG's faster zone. Although the intermediate zone of activity was highly variable, the alternate bands were too close together to be effectively scored. Apparent heterozygotes showed as a diffuse band, suggesting that they may be dimeric as described for this locus in other P. damicornis (Stoddart, 1983a).

NP

Low activity and diffuse banding patterns prevented scoring of NP. Variation seen on Stations No 3, No 5 and No 6 was similar to that reported by Stoddart (1983a) for NP, with banding between Rf's 0.1 to 0.3.

ADA

Assayed only for Station No 1, ADA exhibited a single zone of activity (Rf = 0.3), usually with two bands present but occasionally with one. While some bands were sharp on this buffer, others were streaked.

PGM

PGM banding patterns suggest the presence of two loci (Rf = 0.2, Rf = 0.3 with 2 to 3 alleles at each. Banding was concise and phenotypes were highly variable for corals from the two Stations assayed (No 1 and No 8).

GOT

GOT appeared variable when assayed for Station No 6, but banding was not scoreable as staining intensity was low and bands were streaked.

SOD

While SOD was largely monomorphic (Rf = 0.1), phenotypes for multilocus phenotype P1 (see below) appeared to contain 2 bands. Staining intensity was inconsistent and often faint, with the best resolution on gels stained for MPI.

6PGD : XDH

Bands were concise with a single monomorphic band for each (Rf's = 0.15 and 0.3 respectively).

Multilocus Phenotypes

From a total of 320 individuals assayed, 43 distinct multilocus phenotypes were found (Tables 1 and 2). Diversity statistics for single reefs and for the pooled total are given (Table 3). The number of phenotypes per reef ranged from 7 to 16 and diversity on all reefs was similar. Reefs were characterised by a single dominant phenotype which comprised from 30 - 60% of sampled individuals, 3 to 6 additional phenotypes with an average of 10% of individuals for each and a number of other phenotypes represented only once. Phenotype P1 was the most abundant phenotype on six of the eight reefs and equally numerous with phenotype P2 on Station No 5. Only on Station No 4 was it displaced from this position by phenotype P13 which is abundant only at this site.

Three phenotypes (P1, P2 and P3) were found on every reef. These were usually among the most abundant on any reef (average rankings 1.75, 3.38 and 4.81, respectively). Of the remaining phenotypes, twenty six were restricted to single station, five occurred at two stations, four at three stations, three at four stations and two at five stations. There were no other obvious patterns in the spatial distribution or abundance of phenotypes.

Clustering

Similarity and distance measures for the eight reef stations are given in Tables 4a and 4b, with the resultant dendrograms appearing in Fig. 3. Each dendrogram is dissimilar to the other two and there are no identical clusters of subsets of the reefs. The only dendrogram showing a relationship to the geography of the reefs is that constructed from shared multilocus phenotypes. The order of clustering largely reflects the geographic distance between Stations, except in the case of Station No 5 which is placed closer to the Sampan Channel reefs (Fig. 1) than would be predicted. Neither of the two remaining dendrograms could be related to any apparent environmental pattern.

Morphotypes

The results of the association of biochemical phenotypes with morphologically identified "Y" and "not-Y" type P. damicornis are summarized (Table 5). Only three phenotypes are assigned to a single class in any quantity. These are phenotype P1 for "Y" and P7 and P10 for "not-Y". Others have either dual identity, although this may be biased towards one class (e.g. phenotypes P3 and P13) or are not highly replicated phenotypes. Neither is there any clear distinction if the analysis is reduced to the single-locus level.

Discussion

Pocillopora damicornis has been descibed as containing numerous ecomorphs which may have, in part, a genetic basis (Veron and Pichon, 1976) and the taxonomy of the genus Pocillopora contains some areas of uncertainty. For instance, P. meandrina which was until recently synonymized with P. verrucosa (Veron and Pichon, 1976) is now considered a distinct species (Veron and Pichon, 1982, pp. 133-135). The inclusion of more than one species in the present analyses would greatly confuse interpretation of patterns of variation. As a conservative measure to eliminate such errors, the more distinct ecomorphs, such as the danae type, were eliminated from the samples. This is likely to minimally effect this study as these forms occurred largely outside the sampled areas. Stations No 4 and No 8 were the only samples which would have included these forms and here they would only have been a small proportion of the sample.

Variation within reefs

The description of multilocus phenotypes as clones seems appropriate in light of the exact inheritance of adult enzymes by planulae discussed previously (Stoddart, 1983a) and reconfirmed here. In addition to the proliferation of clones through the asexual production of planulae, pieces of individual colonies may be propagated through fragmentation. Many of the P. damicornis heads on these reefs are attached to unconsolidated rubble and during periods of high wave energy fragmentation, similar to that described for this species in the Eastern Pacific (Highsmith, 1982), may result in a considerable increase in the number of colonies.

Table 1. The distribution of phenotypes for the four enzymes assayed for each station. Values for individuals are listed first, followed by data for multilocus phenotypes. Heterogeneity chi-squares are calculated from pooled data for individuals. Classes used for each enzyme are given in the Results section.

Station		1	2	3	4	5	6	7	8
Phenotype									
LGG	ABC	18: 2	22: 2	21: 4	2: 1	10: 2	25: 1	15: 2	15: 1
	ABD	-	1: 1	4: 4	1: 1	1: 1	-	-	-
	AC	-	-	-	-	1: 1	-	-	-
	AD	-	1: 1	1: 1	1: 1	1: 1	-	1: 1	-
	ABCD	-	1: .1	-	-	-	-	-	s
	AFD	-	-	-	-	-	-	-	2: 1
	BD	20: 6	9: 5	14: 7	30: 6	22: 6	12: 4	20: 5	17: 5
	BC	-	-	-	5: 3	4: 1	2: 1	-	1: 1
	BCD	-	5: 3	-	1: 1	1: 1	-	3: 1	2: 1
	CD	2: 2	-	-	-	-	1: 1	-	-
	DD	1: 1	-	-	-	-	-	1: 1	-
	ED	-	-	-	-	-	-	-	3: 2
Chi-square DF=2		2.8	7.9[2]	2.3	25.4[3]	3.4	8.3[2]	0.2	0.4
PGI	AA	5: 1	-	8: 2	12: 1	5: 3	7: 2	10: 3	1: 1
	AB	35: 9	40: 14	32: 14	28: 12	34: 9	33: 5	30: 7	39: 1
	BB					1: 1			
Chi-square DF=1		0.2	7.1[1]	0.2	5.3[1]	0.0	0.1	2.4	5.3[1]
MDH	AA			1: 1	3: 1	5: 2	1: 1	3: 1	1: 1
	ABC	34: 8	40: 14	33: 12	24: 10	32: 9	34: 5	31: 8	38: 9
	AC				1: 1	1: 1			
	CC	6: 2		6: 3	12: 1	2: 1	5: 1	6: 1	1: 1
Chi-square DF=1		0.0	7.8[2]	0.0	15.2[3]	0.0	0.0	0.8	0.8
MPI	AC	21: 2	37: 7	22: 5	5: 4	18: 5	30: 3	19: 4	29: 4
	AB			2: 1					
	AD	1: 1	2: 2	1: 1	6: 2	6: 3	1: 1	1: 1	2: 2
	BD	6: 2	2: 1	3: 3	7: 3	8: 1	1: 1	7: 1	4: 1
	DC	4: 1	1: 1		14: 2	2: 1	3: 1		2: 2
	CC	1: 1	2: 2	9: 3	7: 2				
	DD								2: 1
Chi-square DF=3		0.5	7.6	3.6	32.4[3]	2.6	7.9[1]	1.2	3.1

Table 2. Composition and distribution of the 43 multilocus phenotypes (clones) found in samples from eight Stations.

Clone	LGG	PGI	HPI	MDH	1	2	3	4	5	6	7	8	Total
P 1	ABC	ABC	AC	ABC	17	21	15	2	8	25	12	15	115
P 5	ABC	ABC	AC	AA		1	1						2
P15	ABC	ABC	CD	ABC	1								1
P24	ABC	ABC	AC	CC				4					4
P25	ABC	AB	BD	ABC			1						1
P38	ABC	AA	AC	ABC						2		3	5
P 6	ABD	ABC	AC	ABC			1	1	1	1			4
P26	ABD	ABC	BD	ABC			1						1
P27	ABD	AA	CC	ABC				1					1
P28	ABD	ABC	AB	ABC				1					1
P35	AC	CC	CD	ABC									
P 9	AD	ABC	CD	ABC			1	1	1		1		4
P19	AD	ABC	AC	ABC		1							1
P18	ABCD	ABC	AC	ABC		1							1
P38	APD	ABC	AC	ABC								2	2
P 2	BD	ABC	BD	ABC	5	2	1	5	8	1	7	4	33
P 3	BD	ABC	AC	ABC	4	3	2	1	6	3	1	10	30
P 4	BD	ABC	AD	ABC	1	1		3	1			1	7
P10	BD	ABC	BC	ABC	4			2		3		1	10
P11	BD	ABC	CC	CC	1		1				6		8
P12	BD	AA	CD	CC	5					5			10
P13	BD	AA	BC	CC				12	2			1	15
P20	BD	ABC	CC	ABC		1							1
P29	BD	AA	CC	ABC			7				1		8
P30	BD	ABC	CD	CC			1						1
P31	BD	ABC	AB	ABC			1						1
P36	BD	AA	AC	ABC					1				1
P 7	BD	ABC	CD	ABC		2	1	7	4		5		19
P 8	BCD	ABC	AC	ABC		3		1				2	6
P21	BCD	ABC	BC	ABC		1							1
P22	BCD	ABC	CC	ABC		1							1
P37	BCD	ABC	AD	AA					1				1
P41	BCD	ABC	AC	AA								3	3
P14	BC	ABC	AD	AA				3	4			1	8
P32	BC	ABC	BD	ABC				1					1
P33	BC	ABC	BD	AC				1					1
P39	BC	AA	AC	ABC						2			2
P16	CD	ABC	CD	ABC	1								1
P17	CD	ABC	BD	ABC	1								1
P40	CD	ABC	AD	AA						1			1
P23	DD	AD	ABC		1						1		2
P42	ED	ABC	DD	ABC								2	2
P43	ED	ABC	CD	ABC								1	1
													320

Table 3. Diversity statistics for the eight Station samples and the pooled total; including Nc=the number of phenotypes (clones) per sample; Oc=the number of phenotypes (clones) unique to each Station; Go=the phenotypic diversity; and Ic=the number of phenotypes represented by a single individual.

Station	Nc	Oc	Go	Ic	Most common clone (%)
1	10	3	4.26	5	P1(43)
2	14	5	3.36	9	P1(53)
3	16	6	5.21	12	P1(38)
4	13	2	6.40	6	P13(34)
5	13	3	7.62	6	P1-P2(20)
6	7	2	2.37	2	P1(63)
7	10	1	5.80	4	P1(30)
8	11	1	4.47	5	P1(38)
Mean	11.8	3	4.94	6.13	n.a.
S. D.	2.82	1.69	1.69	3.09	
	(2.82)	(1.69)	(1.69)	(3.09)	
Combined 1-8	43		6.26	21	P1(36)

Table 4a. Manhattan distances for pairwise combination of Stations, calculated from phenotypic frequencies of 1) individuals (below the diagonal) and 2) phenotypes (above the diagonal).

Stas.	1	2	3	4	5	6	7	8
1		.59	.36	.44	.55	.35	.43	.51
2	.45		.55	.49	.59	.61	.43	.50
3	.29	.43		.40	.37	.48	.45	.53
4	.65	.98	.79		.34	.38	.47	.30
5	.30	.55	.45	.50		.34	.34	.46
6	.26	.33	.28	.74	.45		.35	.42
7	.25	.44	.26	.58	.31	.40		.48
8	.34	.28	.44	.81	.41	.31	.46	

Table 4b. Similarity between Stations, expressed as the proportion of phenotypes (clones) shared by Station pairs.

Sta	1	2	3	4	5	6	7	8
1								
2	.17							
3	.15	.20						
4	.22	.26	.21					
5	.17	.22	.21	.35				
6	.29	.14	.13	.20	.15			
7	.25	.21	.27	.22	.26	.18		
8	.29	.20	.11	.33	.25	.22	.14	

Table 5. Biochemically detected phenotypes (clones) associated with "Y" and "not-Y" morphotypes from Stations 4,6, and 8. Values are the number of reefs on which each phenotype was assigned to a morphotype and the sum of individuals for each, in parentheses.

Phenotype	"Y"	"not-Y"
P 1	3(43)	
P 2	3(5)	2(5)
P 3	2(2)	2(12)
P 4		1(3)
P 6	1(1)	
P 7		1(10)
P 8	2(2)	1(1)
P 9	1(1)	
P10		3(6)
P12		1(5)
P13	1(10)	2(3)
P14	2(3)	1(1)
P32		1(1)
P33		1(1)
P38		1(2)
P39	1(1)	

As the multilocus phenotyps were distinguished on the basis of only four probable loci, the estimated number of clones in a sample will be conservative, since variation at other parts of the genome will be undetected. However, the amount of variation present at each locus, with regard to the number of phenotypes, provides the potential to discriminate over 1000 multilocus genotypes. As the total number of clones detected was only 43, the analysis is unlikely to be greatly influenced by this constraint. In spite of this, some multilocus genotypes would be more likely to occur through sexual processes than others, due to the high frequency of occurrence of their single-locus components, and these may be multiclonal associations.

The origin of asexual planulae and their relationship to the extensive gametic production of P. damicornis is controversial (Stoddart, 1983a; Martin Chavez, this volume). Although electrophoretic studies are unable to provide direct tests of reproductive mechanisms, as distinct from reproductive modes (i.e. sexual, asexual, etc.), the present inconsistency of banding patterns for LGG, PGI and MDH with diploid explanations may be significant. It is well known that polyploidy is often associated with asexual reproduction. This relationship may result from the cytological mechanisms associated with ameiotic processes, or as a consequence of an initial hybridization event producing a new ameiotically reproducing species (White, 1978) and it may be maintained in response to the functional properties of multiple alleles in buffering non-functional alleles (Lokki, 1976). Reports of asexually produced planulae in P. damicornis (Stoddart, 1983a) and other anthozoans (Black and Johnson, 1979) which make no mention of polyploidy suggest that any polyploidy must have arisen as a consequence, rather than a cause, of asexuality in the current instance. Gametogenesis, in particular spermatogenesis, often breaks down in polyploid animals, usually allopolyploids, as a result of non-disjunction of chromosome segments caused by abnormal chiasma during meiosis (White, 1978). Cases have been described in which spermatogenesis is non-functional but oogenesis proceeds in an essentially mitotic fashion (for example Jacob, 1957). In the present case, the investigation of the viability of gametes, the process of fertilization and the karyotype of this species should be priority research topics if the mechanism of reproduction is to be resolved.

Despite the identity of planulae with parent and the existence of clones, diversity of single and multilocus phenotypes is higher than expected for an obligately asexual organism and an alternate mode of reproduction may occur. There are no large shifts in diversity, measured either as number of clones or genotypic diversity (Table 3), between reefs which might indicate shifts in the prevailing reproductive mode producing recruits. There is some suggestion that the number of clones may be greater in reefs closer to the outer edge of the bay, or in the channels connecting the bay with the ocean. It is in these areas adjacent to the exterior of the bay, where P. damicornis is largely replaced by P. meandrina and the other synonyms or "growth forms" of P. damicornis (P. danae, P. bulbosa, etc.) occur. While diversity is intermediate on Station No 9, the most exterior reef, this reef is the only one containing unique alleles (C and E of LGG). This may result either from genes from P. damicornis outside the bay or, from genes from other Pocillopora, ecomorphs of damicornis or other species. Possible gene flow, or the lack of such, between members of the damicornis complex and P. meandrina would have important implications for the taxonomy of this genus and is a further fruitful area of research.

The small shifts in diversity observed between reefs may be related to past disturbance events or bottlenecks, which are diversity reducing phenomena (Soule', 1975). Historical events are notoriously difficult to test and despite the comprehensive documentation of recent disturbance events in Kaneohe Bay, other environmental considerations confuse interpretations. Banner (1968) records a mass mortality of corals in response to inundation by freshwater and sediment during a storm and a number of reefs are known to have been recently dredged (Devaney et al., 1982). The effects of this former event were particularly severe on Stations No 6 and No 7 causing almost total mortality of corals to a depth of 1 m and to a depth of 0.5 m on Station No 1. In terms of numbers of clones present, these three stations have the lowest diversity of all. Station No 8, which might be expected to be highly diverse from its position towards the bay's edge is situated next to a boat channel subjected to intensive dredging and is next lowest in number of clones.

Male Gonads

Spermatogenesis takes approximately 4 weeks and complete development does not always occur. During the course of this study only 2 spermaries were found with mature sperm; in all other cases, spermaries seemed to be reabsorbed (Fig. 5) before maturity was reached.

The earliest identifiable male gonads are small spermaries which bud from the mesenteries (Fig. 6). In this first stages of development, they are filled with spermatocytes with heads of approx. 3 to 4 microns in diameter. These testes consisted of sacs of various sizes and shapes (Fig. 6) that could reach sizes up to 150 microns once a lumen develops (Fig. 7).

After this stage, when the spermaries are presumably close to maturity, a reabsorption stage is observed (Fig. 5). The covering endoderm never was stretched thin as is common in other anthozoans when testes are mature (Jennison, 1979; Fadlallah, 1983). Spermary maturity coincides with the time of maximum oocyte diameter.

All male gonads of a colony sample are in approximately the same stage of development, but 3 different stages could be found on occasion.

Female Gonads

Ovogenesis takes approximately 5 weeks to reach completion. An overlapping of two gametogenic cycles has been observed to occur (Figs. 1-3).

Oocytes within polyps from the same colony were usually in the same stage of development, however, two different size populations of oocytes could occur (Figs. 1-3), with the small ones corresponding to the oocytes that would presumably mature one month later. The coexistence of these two oocyte populations indicates gametogenic cycles can overlap as a result of developmental times.

Ovaries were located in the same position along the mesenteries as the testes, but on separate ones, and usually consisted of only one oocyte. However, as many as four could be observed in the same endoderm when measuring about 20 microns. It is not clear if these multiple bodies were oogonia or primary oocytes. In the early stages, conspicuous yolky granules are present in the cell cytoplasm (Fig. 8). In later developmental stages, these granules become larger and evenly distributed throughout the cell (Figs. 9-10), which has a large nucleus and a prominent nucleolus (Fig. 10).

Like spermaries, ovaries are surrounded by mesoglea and endodermal tissue that lacks zooxanthellae in the first stages of development. In later stages, near the time when maximum size is attained by the oocytes (around 130 to 160 microns), zooxanthellae start appearing in the surrounding endoderm. This can be used as an indirect measure of female gonad maturity. Not a single oocyte was observed with algal symbionts inside at any stage of development.

Table 2 summarizes the results of the number of fertile polyps from the mid-part of branches, and the distribution of number of gonads per polyp.

Planulae Development

The planulae development takes about two weeks from the time the first embryos appear until the last mature larvae are shed. The first embryo-like structures were observed when the oocytes had reached their maximum size (Figs. 1-3). In this early stage of development, the planulae are linked to the mesentery by a stalk and are as much as twice the size of the mature oocytes (Fig. 11). By this time, scattered zooxanthellae are seen inside the embryo. The symbionts become more abundant during growth of the larvae, until complete development is reached, with fully developed mesenteries and abundant zooxanthellae. At the end of their growth period, when they measure between 600 to 800 microns, each planula fills the entire gastric cavity of the polyp and is ready to be shed (Fig. 12).

The proportion of polyps with planulae are summarized in Table 2. Considering only the planulae bearing polyps (90% of the total polyps examined), 67% had only one, 28% had two, and the rest, 4.5%, had three or more. These results differ from those reported by Harrigan (1972) who found that 97% of the planulae bearing polyps contained only one larva. This difference could be due to my use of histological methods that enable more precise measurements.

In addition to the above association of numbers of clones and disturbance events, other interpretations are possible due to confounding environmental variables. One factor which may be of considerable importance is the depth of the reef at the sample site. A tidal range of up to 1.1 m in Kaneohe Bay (Bathen, 1968) may lead to aerial exposure of coral heads on some reef areas. If this is coincident with rain storms or the hotter periods of the day, considerable mortality may result (P. Jokiel, personal communication). This may act as a disturbance event whose severity will vary according to reef depth. Although there was micro-scale variation, subjective estimates of reef depth at transect sites place Station No 4 as the deepest and Station No 2 as the shallowest. However, in some areas, due to a lack of corals on the center of the reef, transects sampled greater areas of edge than on reefs where coral distribution was more even. Thus to adequately test predictions of diversity based on disturbance estimates by comparative methods, microhabitat should be taken into account.

Differentiation within Kaneohe Bay

A basic precept of population genetics is the delimitation of the unit of measurement, i.e. the population. Many definitions merely use the occurrence of the same species in a given locality as their criteria, but others stress the potential for members to interbreed in a local population, or deme (see for instance Mayr, 1963 or Dobzhansky, 1970). Other concepts of populations use measures of genetic identity (Felsenstein, 1976). The last concept seems the most appropriate to populations whose members reproduce asexually, but the inability of the present study to resolve phenotypes into their allelic components prevents its use here. Instead, heterogeneity chi-square comparisons of phenotypic distributions for each locus, similarity of populations calculated from the phenotypic frequencies of individuals and clones and estimates of shared clones were used to examine differentiation of reef populations.

Comparisons for LGG, MPI, MDH and PGI show Station No 4 to be distinct for all four enzymes, Station No 2 distinct for three (with a further one at $p < 0.1$), Station No 6 distinct for two and Station No 8 for one. Stations No 2 and No 6 usually show similar distinct patterns. While this would represent a substantial differentiation of a sexually reproducing population, it can be directly related in this case to the distribution of a single clone. Stations Nos 2 and 6 have the highest proportion of clone P1 (53% and 63%, respectively) and Station No 4 the lowest (5%). The distinctness of Station No 4 in the dendrogram resulting from individual phenotype frequencies (Fig. 3a) also stems from this distribution, but if only clonal frequencies are recognised this distinction disappears (Fig.3b). The distinctness of Station No 2 in this latter dendrogram is difficult to assign to any single factor. Overall, the degree of population differentiation appears to be small, with respect to that reported for P. damicornis populations from southwestern Australia (Stoddart, 1983a). Within Kaneohe Bay the three most abundant clones occur on all eight stations and pooling samples from different stations does not result in an increase in the ratio of sample size to number of clones (in fact there is a decrease from an average of 0.32 clones per individual for individual stations to 0.13 for the pooled sample. Neither is genotypic diversity raised by pooling, as it is in southwestern Australia. The average genotypic diversity for the eight stations is within one standard deviation of the genotypic diversity of the pooled sample. Thus, the eight stations may be effectively grouped into a single population which probably comprises most reefs in Kaneohe Bay. Within this population there is some subdivision in response to physical separation of reefs, as indicated by the clustering of reefs on a shared clone basis.

While selection may mask the effects of gene flow in some cases (Gartner-Kepkay et al., 1983), in its absence differentiation should occur on a scale commensurate with the dispersal ability of larvae. In these cases, if the geographic separation of the sample populations is small compared to dispersal ability, differentiation may appear to be chaotic (Johnson and Black, 1982). The concordance of the dendrogram derived from the shared clone estimates with geographic distance suggests that the dispersal of asexual planulae may begin to be limited within a few kilometres. Unless there is an alternate mechanism for gene flow, widely separated populations are likely to be substantially genetically isolated. Indeed, populations of P. damicornis from Hawaii (Clausen and Roth, 1975; Richmond and Jokiel, 1984), Enewetak (Richmond and Jokiel, 1984), Panama (Birkeland, 1977; Glynn and Macintyre, 1977) and southwestern Australia (Stoddart and Black, in prep.) have distinct growth rates, reproductive characteristics and vertical distributions. Until the reproductive biology of this

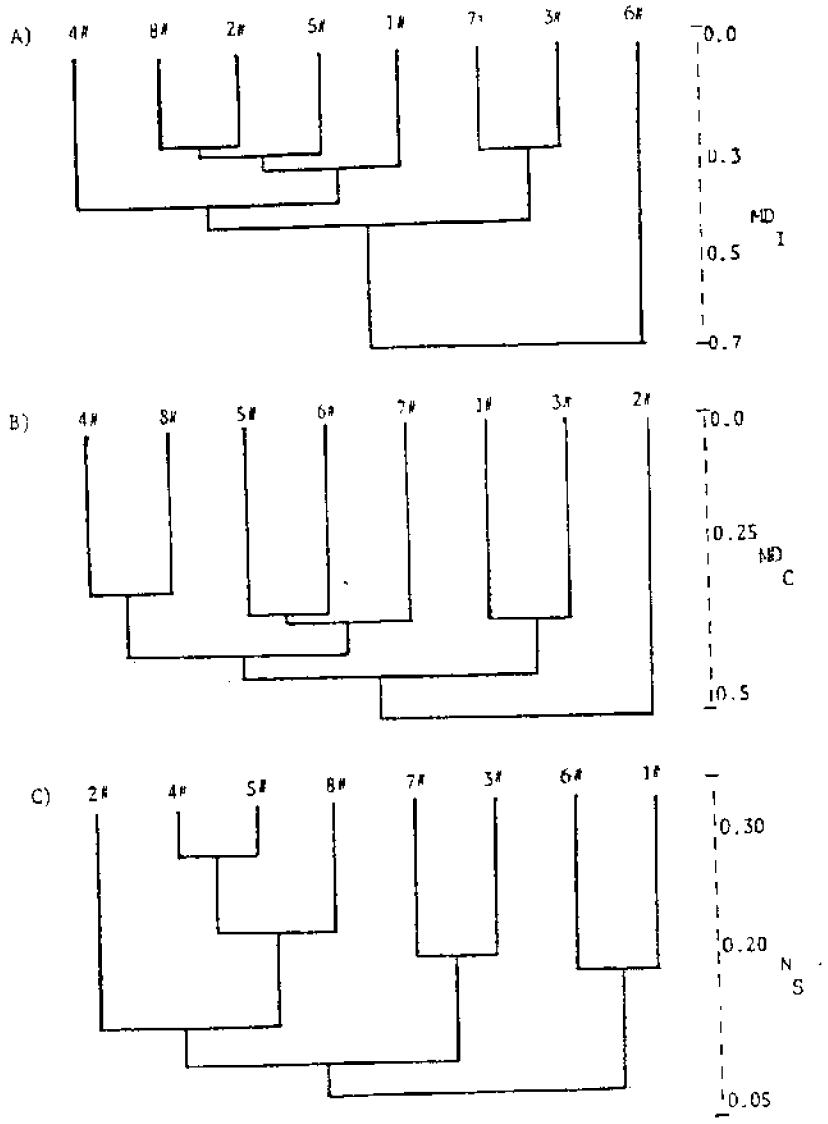

Fig. 3. Dendograms constructed for the eight reefs by clustering using the UPGMA algorithm. Similarity measures were based on
A) Manhattan distance of phenotypic frequencies based on individual,
B) Manhattan distance of phenotypic frequencies based on clones, C) the proportion of shared clones.
Actual values appear in Table 4.

species is better understood, the taxonomic implications of this, apparently genetic differentiation will remain speculative.

The results of the discrimination trials between the "Y" and "not-Y" forms equivocate about the biochemical distinctness of such forms. While there does appear to be an association of morphology and biochemistry, there are no major differences between the two forms at the single locus level. In spite of this, the "Y" and "B" forms, which planulate asynchronously and have several other behavioral and morphological differences may represent distinct taxa. Restriction of gene flow through separation of reproductive timing is theoretically able to produce reproductive isolation and speciation (Stam, 1982).

Studies of population genetics have much to contribute to the knowledge of reproductive biology, recruitment processes and the general ecology of corals. This study has provided some data on these subjects, but perhaps more importantly, has defined specific research areas where significant progress may be made towards our understanding of them.

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Tissue compatibility between colonies and between primary polyps of Pocillopora damicornis: A preliminary study

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Abstract

Grafting experiments with adult colonies of the coral Pocillopora damicornis showed that fusion of the tissues was observed only in isografts. Colonies belonging to different color morphs did not fuse with each other.

Planulae spawned by the same colony were observed to fuse with each other to form an aggregated colony. When two primary polyps spawned by different colonies were kept in contact, they also fused. Even polyps derived from colonies belonging to different color morphs fused with each other.

Colonies of P. damicornis did not discharge nematocysts against conspecific colonies. They discharged nematocysts against Fungia, Montipora, and Porites, but not against P. meandrina.

Introduction

Many workers have reported that, in scleractinian corals, two pieces from the same colony (isografts) fuse when kept in contact, while intercolony allografts are invariably incompatible (Hildemann et al., 1975, 1977; Potts, 1976, 1978; Rinkevich and Loya, 1983). If two colonies are compatible, they are assumed to have the same genetic composition and hence to be asexually produced from the same colony. Thus, intercolonial grafting within the same species provides a tool for assessing genetic diversity of corals and relative importance of asexual and sexual reproduction in reef-coral population (Bak and Criens, 1982; Jokiel et al., 1983; Neigel and Avise, 1983).

However, early workers reported that when planulae settled close to one another, grew and came into contact, they fused to form an aggregated colony (Stephenson, 1931; Atoda, 1947a, b, 1951a, b). Planulae of corals are generally believed to be produced sexually so they must be genetically different from each other. It is interesting that these planulae do not reject each other by an allogeneic histoincompatibility response. One possibility is that primary polyps have no histoincompatibility system and that they obtain it as development proceeds. Another possibility is that allogeneic rejection is not elicited by individuals genetically very similar to self such as kin planulae. Recently, Rinkevich and Loya (1983) reported that, even when allografts appear to fuse with each other, a narrow gap exists between the two tissues when observed with a SEM. Thus it is also possible that no true fusion occurs in an aggregated colony. It seems necessary to investigate tissue compatibility between primary polyps of the same species in more detail.

To examine the above possibilities, tissue compatibility between settled planulae from the same colony or from different colonies of Pocillopora damicornis was examined as well as tissue compatibility between adult colonies. It will be shown that primary polyps from the same colony or even from different colonies fused with each other to form an aggregated colony. In adult colonies fusion was observed only in isografts. These observations strongly suggest that corals lack a histoincompatibility system in the early stage of development.

Materials and Methods

Collection of Animals

Colonies of P. damicornis were collected from the reef in Kaneohe Bay and were transported into holding tanks with care not to expose animals to the air.

There are two color morphs, "Y" and "B" types, of P. damicornis in the reef of Kaneohe Bay (Richmond and Jokiel, 1984). These two morphs differ not only in color and growth form but also in the timing of planulation (Richmond and Jokiel, 1984). As colonies belonging to these two morphs may occur side by

side, their differences are unlikely to be a result of environment and are probably genetic. So, two colonies belonging to different color morphs were mainly paired in the allogeneic graftings.

Grafting Experiments with Adult Colonies

Branches of about 5 cm length were removed from a colony with forceps. Two branches from the same colony or from different colonies were tied to a plastic petri dish with thread so that their tips would touch each other. Four replicated pairs were made in each combination. Paired branches were reared in holding tanks supplied with running sea water for 32 or 50 d. They were observed under a dissecting microscope at intervals of 1-2 weeks.

In P. damicornis, it is difficult to make good contact points since colonies of P. damicornis are highly branched and have rough surfaces. It is possible that tissue fusion does not occur only because the tissue contact is not sufficient. So in this experiment, the paired branches were detached at the end of the contact experiment and the surface of the branches at the contact point was examined. The data were obtained only with the pairs which showed exposed skeleton at the contact point indicating continuous contact between the coenosarc tissues of both branches.

When tissues appeared to be fused, a gentle mechanical stimulus was applied to a polyp close to the interface to examine whether or not the excitation propagates through the interface to cause retraction of the polyps of the other branch.

Grafting Experiments with Primary Polyps

Planulae of P. damicornis were collected by the method used by Richmond and Jokiel (1984). Colonies of P. damicornis were placed in containers (2.5 l) supplied with running sea water. Overflowing water was held in collectors made from Polyvinyl chloride (PVC) pipe, the base of which was covered with 180 micron plankton netting. The lateral inner surface of the collector was covered with plastic sheet. The surface of the sheet was made rough by rubbing with sand paper. Usually most of the planulae settled on the plastic sheet in a few days after being spawned.

When settled planulae became flattened and began to secrete skeleton, a piece of plastic sheet with a settled planula on it was cut off from the lateral wall of the collector. Two pieces of plastic sheet, each with one primary polyp on it, were held on a slide glass so that the primary polyps were placed side by side (Fig. 3A). Primary polyps derived from different colony, usually belonging to different color morphs, were paired. The paired polyps were maintained in a chamber made of PVC pipe, the base of which was covered with 300 micron plankton netting. The chambers were immersed in a holding tank and were aerated. The paired primary polyps were observed at intervals of 2-4 d under a dissecting microscope. Some specimens were examined under a light microscope and photomicrographs were taken at 32 or 63X. There was also an attempt to examine whether or not the retraction of the polyp propagates through the interface to the adjacent polyp by applying a gentle mechanical stimulus on one of the paired polyps.

Planulae spawned by a colony have a tendency to settle in aggregates just below the surface of sea water as reported previously (Stephenson, 1931). Plastic sheets each with one to several aggregates of primary polyps on it were cut off and were maintained as described above.

Nematocyst-discharge Response

Tissues (tentacles or coenosarc) of other colonies of P. damicornis were brought in contact with a tentacle of the subject colony for about one second. This was repeated at least three times and tentacles of more than three polyps were used in each combination of colonies. The nematocyst discharge was monitored by examining whether the tentacle adhered to the target tissue or not. There was an attempt to determine whether the tentacles of P. damicornis discharge their nematocysts against other species of corals.

Results

Tissue Compatibility between Adult Colonies

Fusion or nonfusion of tissues could be definitely recognized under a dissecting microscope in most pairs of P. damicornis colonies in 32 or 50 d after the initiation of the contact experiment. When fusion occurred, the tissue appeared continuous with no sign of junction and zooxanthellae were uniformly distributed in the region of contact as seen in normal tissue (Fig. 1A). When a gentle mechanical stimulus was applied to a polyp close to the interface between two branches, retraction of polyps propagated through the interface. When tissues were not fused, they were separated by a white line which may represent two layers of ectoderm lacking zooxanthellae (Fig. 1B). Sometimes the skeleton in the narrow region close to the contact point was exposed in one branch of the pair (Fig. 1C). The retraction of polyps did not propagate through the interface. When the branches of the nonfused pair were detached, tissue bridges connecting two branches were frequently observed at the site of contact. This may indicate that the tissue of one branch was attached to the exposed skeleton of the other branch. Sometimes a cylindrical tissue bridge was observed when the paired branches were slowly detached. Mesenterial filaments were observed in such a cylindrical tissue bridge.

There were, however, some cases in which tissues of allogeneic colonies were apparently fused. In these cases, however, the distribution of zooxanthellae was not uniform. The region at the interface was white with less zooxanthellae than on other parts of the branch. No propagation of polyp retraction was observed in apparently fused pairs. When the branches were detached, there was a tissue bridge as described in nonfused pairs. A small thin skeletal ridge was frequently observed at the contact surface indicating the presence of interfacial cementation. Both nonfusion and apparent fusion were frequently observed at different contact points in the same pair of branches. So it seems that nonfusion and apparent fusion may be identical responses. It is likely that, in apparent fusion, tissue of one branch grows over the exposed skeleton of the other branch but two tissues are separated by a fine groove.

The results of the contact experiment with adult colonies of P. damicornis are summarized in Table 1. Fusion was observed only in the pairs of branches which were derived from the same colony (isografts). Nonfusion or apparent fusion were observed in the pairs of colonies belonging to different color morphs (allografts). In this experiment, only two pairs of colonies belonging to the same color morph were examined. Tissue fusion was not observed in these pairs (Table 1; B21-B22, Y24-Y25).

Tissue Compatibility between Primary Polyps

Planulae spawned from the same parent colony often settle in aggregates. At first these planulae were independent and attached one another with their aboral surfaces facing each other. They fused to form an aggregated colony in a few days (Fig. 2A, B). The tissues at a growing margin of the polyps fused first and then the groove separating the polyps disappeared. Calices did not fuse in these cases but were separated by intervening skeleton. When a gentle mechanical stimulus was applied to one polyp, retraction of the neighboring polyp also occurred. The propagation of polyp retraction was observed in 29 out of 49 aggregated colonies in 3-8 d after settlement. Polyps of other aggregated colonies were contracted or not sensitive to mechanical stimuli, so it was not determined whether propagation of polyp retraction occurred or not.

When two planulae spawned by the same parent colony settled close to each other, they also fused when they came into contact (Fig. 2C, D). In this case, the skeleton between two calices was smooth without interfacial cementation as in normal colonies.

When primary polyps derived from different parent colonies were paired, they came into contact as they grew and then fused (Fig. 3). Even primary polyps derived from colonies belonging to different color morphs fused (Table 2). Zooxanthellae distributed uniformly in the interface zone as in other regions of the polyp (Fig. 3D). Although propagation of polyp retraction through the interface could not always be observed, in some cases, one polyp of the pair retracted when the neighboring polyp was stimulated mechanically (Table 2). In some other cases, when one polyp retracted in response to a mechanical stimulus, the other polyp extended. This may also indicate that the coelenteron of both

Fig. 1. Typical outcomes of grafting experiments between colonies of P. damicornis (X5). A) Isograft showing compatible fusion at interface (arrow). B) Allograft showing a white border line (arrow) at interface which indicates incompatibility. This pair consists of branches of Y11 (left) and B13 (right) colonies and was maintained for 48 d. C) Allograft showing cytotoxic incompatibility. This pair consists of branches of B21 (left) and Y24 (right) colonies and was maintained for 32 d. Note blanching and tissue death of the right branch at contact zone.

Table 1. Tissue compatibility between adult colonies of P. damicornis. Numbers of fused, not fused, and apparently fused pairs are shown. Number of contact points in each category is also shown in parentheses, since some pairs had more than one contact point.

Colony pairs[1]	Fusion	Nonfusion	Apparent fusion
syngeneic pairs			
B22-B22	3 (5)	0	0
Y24-Y24	4 (5)	0	0
Y11-Y11	2 (3)	0	0
Y12-Y12	2 (2)	0	0
B13-B13	4 (5)	0	0
allogeneic pairs			
B21-Y24	0	2 (3)	0
B22-Y25	0	2 (3)	1 (1)
B23-Y26	0	3 (4)	2 (2)
B13-Y11	0	1 (3)	0
B13-Y12	0	1 (1)	0
B21-B22	0	0	1 (1)
Y24-Y25	0	2 (5)	0

[1]The letter indicates the color morph. The numbers following the letter each designate a different colony.

Table 2. Tissue compatibility between primary polyps derived from different colonies of P. damicornis. Numbers of fused pairs and of pairs which showed propagation of polyp retraction are shown. Number of pairs which died or made no contact with each other during the observation period is also shown.

Source colonies of paired polyps[1]	Fusion	Propagation of polyp retraction	Died	No contact
B1-Y1	11	6	4	12
B3-Y1	2	0	9	4
B2-Y1	3	2	2	1
B1-Y2	3	0	2	4
B1-B3	3	1	0	0
Y1-Y2	0	0	1	2

[1]The letter indicates the color morph. The numbers following the letter each designate a different colony.

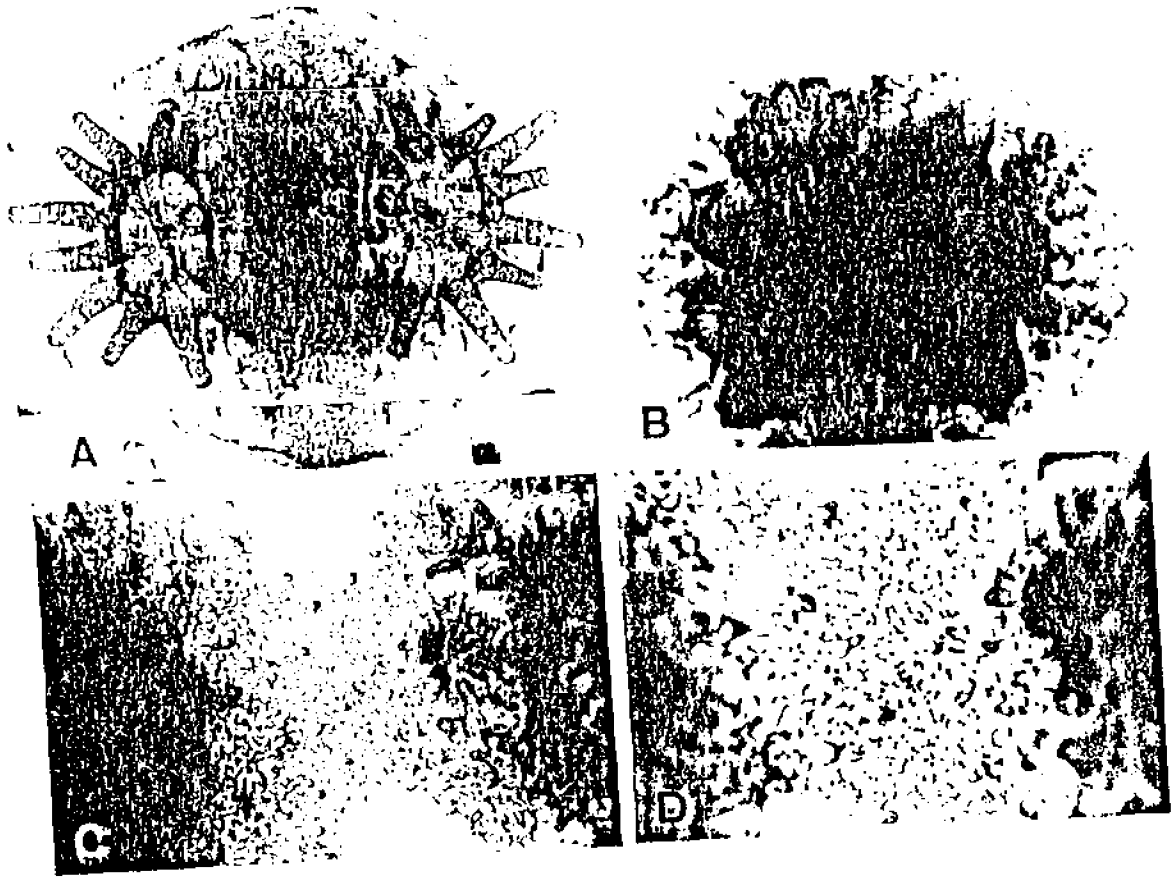

Fig. 2. Fusion of primary polyps derived from the same parent colony of P. dasicornis. A) Two planulae fused with their aboral surface facing each other. B) Four planulae fused with their aboral surface facing one another. C) Two planulae settled close to each other fused when they came into contact. Tissues and skeletons fused smoothly with no sign of junction. D) Interface zone of C observed at a higher magnification. Note uniform distribution of zooxanthellae. Magnification, approximately X48 in A, B, and C, X94 in D.

Fig. 3. Fusion of primary polyps derived from different colonies of P. damicornis. A) Fused primary polyps showing technique of grafting of primary polyps. Plastic sheets mounting primary polyps were held on a slide glass so that paired polyps could be placed side by side (X3). B) Fusion of primary polyps derived from Y1 (left) and B1 (right) colonies. This pair was maintained 10 d after the setting. C) Fusion of primary polyps derived from Y1 (left) and B2 (right) colonies. This pair was maintained 13 d after the setting. D) Interface zone of C observed at a higher magnification. Note uniform distribution of zooxanthellae. Magnification X48 in B and C, X94 in D.

polyps is continuous and that these two polyps are functionally united. In this experiment, the observation was made up to 11-15 d after the setting of the polyp pairs. No sign of allogeneic rejection was observed during this period.

A preliminary electrophoretic study was performed to test whether primary polyps, or parent colonies, used in this experiment were different genotypically from one another as well as their parent colonies. Three isozymes (leucyl glycylglycine peptidase, phosphoglucomutase, and phosphoglucose isomerase) were examined according to the method described in Stoddart (1983, 1984). Five colonies used for sources of planulae in this experiment could be divided into four groups according to the present electrophoretic study: Y1, Y2, B1=B2, B3. Fused primary polyps were separated with a razor blade and each polyp was separately treated for electrophoretic study. In this preliminary experiment, only three pairs were examined. These pairs consisted of primary polyps derived from Y1 and B1 colonies or from Y1 and B2 colonies. In all the cases, paired polyps displayed different isozyme patterns from each other. Each polyp displayed the same electrophoretic pattern of isozymes as its parent colony as described previously by Stoddart (1983). This indicates that primary polyps which are genotypically different from each other can fuse.

Nematocyst-discharge Response

In all the colony pairs used in the above grafting experiment, tentacles of one colony did not adhere to the target tissue of the other colony of the pair. This means that polyps of P. damicornis did not discharge their nematocysts against conspecific colonies.

Tissue of some other corals was also applied to the tentacles of P. damicornis. Tentacles of P. damicornis discharged their nematocysts against Fungia, Porites, and Montipora, but did not discharge against Pocillopora meandrina.

Discussion

The present grafting experiment with adult colonies of P. damicornis shows that isografts are invariably compatible, while allografts are incompatible. This is consistent with previous studies on tissue compatibility of other corals (Hildemann et al., 1975, 1977; Potts, 1976, 1978; Bak and Criens, 1982; Jokiel et al., 1983; Rinkevich and Loya, 1983; Neigel and Avise, 1983). Though apparent fusion was observed in allogeneic pairs of P. damicornis, this can be distinguished from true fusion by the following points. The retraction of polyps did not propagate through the interface between two branches in apparently fused pairs. Zooxanthellae were distributed irregularly at the interface of apparently fused branches contrary to the uniform distribution in syngeneic pairs. Furthermore apparent fusion and nonfusion were frequently observed in different sites in the same pair of colonies. Apparently fused tissues may well be separated by a fine groove which is not discernible under a stereomicroscope. Rinkevich and Loya (1983) reported that apparently fused tissue of allografts of Stylophora pistillata was separated by a fine groove when observed with a SEM. Bak and Criens (1982) stated that decalcification always proved the tissue to be discontinuous even when no suture could be seen between the adjoined tissues of the two allogeneic colonies of Acropora palmata. Allogeneic rejection in P. damicornis also appeared to be relatively mild, though in some cases cytotoxicity was observed.

Planulae produced by the same parent colony fused with each other to form an aggregated colony when they settle in clusters. Planulae of corals are generally believed to be produced sexually, and hence are genotypically different from each other. In P. damicornis, however, the planulae derived from one colony seem to be genotypically identical to each other and to their parent colony according to an electrophoretic study (Stoddart, 1983). The manner of planula production in P. damicornis is still in debate. So the fact that planulae spawned by the same parent colony fuse with each other does not necessarily mean that genotypically different planulae can fuse with each other.

The present results also show that primary polyps produced by genotypically different colonies could fuse with each other. Since adult colonies of B and Y types were incompatible, this implies that young polyps lack the histoincompatibility system as shown by adult colonies.

Early workers reported that planulae settling close to each other fuse to form an aggregated colony (Pocillopora bulbosa and Porites haddoni, Stephenson 1931: Pocillopora damicornis, Atoda 1947a: Stylophora pistillata, Atoda, 1947b; Galaxea aspera, Atoda, 1951a: Seriatopora hystrix, Atoda 1951b). However, in these early studies, it was not clearly described whether the planulae were from the same parent colony or from different colonies. Even if the planulae were from different colonies, it is not known whether primary polyps forming an aggregated colony were derived from a single colony or rather, they were a mixed population of planulae produced by different colonies. This is the first study that proves that primary polyps derived from genotypically different colonies can fuse with each other.

The idea that young animals lack an immunological system is not uncommon. Such a masking of immunological reaction in fetus of mammals is well known. Inhibition or masking of a histoincompatibility system in young animals might be necessary for brooding species. If a histoincompatibility system appears in early stages of development, brooded planulae will suffer allogeneic rejection by brooding polyps.

It could not be known in this short term study whether the fused colony would show intermediate characters between two parent colonies from which the planulae were derived or if it would separate into two different parts as it grew. Further study is needed to determine at what stage of development the polyp attains a histoincompatibility system.

In sponges, allograft reactions typically proceed through an initial stage of tissue fusion or "tissue bridging" (Hildemann et al., 1980). There is a lag period before allografts display cytotoxicity in corals as well (Johnston et al., 1981). However, the initial stage of tissue fusion was not described in allografts of corals nor observed in the present grafting experiment with adult colonies of P. damicornis. Thus, it is unlikely that the fusion of primary polyps observed in this short term experiment was due to a lag period before cytotoxicity appears. A further study might be necessary to exclude the above possibility.

Polyps of P. damicornis did not discharge their nematocysts against polyps of conspecific colonies. They did not discharge nematocysts even against colonies belonging to a different color morph. It seems that sensory epithelium controlling nematocyst discharge did not recognize conspecific colonies as non-self. So nematocyst discharge response was not so sensitive as tissue compatibility in discriminating self and non-self. It is also interesting that P. damicornis did not discharge nematocysts against P. meandrina, while it did discharge against Fungia, Porites, and Montipora.

The present study shows that primary polyps derived from phenotypically and genotypically different colonies fused with each other, while allografts were invariably incompatible in adult colonies.

Acknowledgements

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Diurnal periodicity in planula release by the reef coral Pocillopora damicornis

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Abstract

The hourly planula production rates of the common hermatypic coral Pocillopora damicornis in Kaneohe Bay, Hawaii were measured for three 48 h periods in order to detect any ordered periodicity that might exist in the daily cycle. A single peak in daily production was found. This peak occurred during periods of low tide and appeared to be independent of photoperiod.

Introduction

With the increasing amount of attention which is being focused on the subject of planula production in corals, the occurrence of periodicity in planulation (in some species) is becoming more thoroughly documented. Lunar periodicity in the reef coral Pocillopora damicornis (Linnaeus, 1758), for example, has been described particularly well (Marshall and Stephenson, 1933; Abe, 1937; Atoda, 1947; Harrigan, 1972; Richmond and Jokiel, 1984). Only a limited amount of research, however, has been done on the subject of diurnal variation in planula production. Harrigan (1972) found no evidence of diurnal variation in Pocillopora damicornis, but these studies were done using an artificially induced photoperiod under laboratory conditions. Richmond (personal communication), however, observed evidence of a peak in planula release immediately following sunset by P. damicornis at Enewetak. The current study was designed to investigate the possibility of the existence of periods of peak planula production in the diurnal cycle.

Materials and Methods

In order to monitor the lunar cycle of planulation, daily observations of planula production by P. damicornis colonies from Kaneohe Bay, Hawaii (21° 60' N; 157° 47' W) were made. These colonies were maintained in containers of 3 l volume with a continuous flow of non toxic sea water, which overflowed into collecting cups constructed of 180 micron plankton netting.

Two different morphological variations of P. damicornis were collected and monitored. These two types vary in appearence, in that type "Y" exhibits yellow animal pigment and type "B" exhibits only the brown color of the symbiotic zooxanthellae and has a stouter growth form. The lunar cycles of planula release of these two types also show dimorphism in that they are unsynchronous (Richmond and Jokiel, 1984). Two approximately equal sized colonies of each type were collected. These colonies were replaced with fresh colonies on alternate days so that they might represent the planular activity in the field more accurately. This method has been shown to be effective (Richmond and Jokiel, 1984).

The numbers of planula produced daily were monitored until an approaching peak in the lunar cycle of planula production was indicated. At this time, hourly observations were made for several days during peak production. In the first experiment (Exp. 1), these observations were carried out at an approximate peak in production by the "Y" type corals. This peak in production normally occurs after the time of full moon (Richmond and Jokiel, 1984). Due to an extended period of cloudy weather, however, peak numbers of planula were unusually low. Lack of planulae of the normal time of production prompted us to attempt an experiment. We decided to try to stimulate production with artificial night illumination. Five of the 10 coral heads were subjected to an artificial light

of approximately full lunar intensity on the first night of the 48 h period of observation. The light was then placed over the other set of coral heads on the second night. Exp. 2 was also performed using "I" type corals and Exp. 3 was performed using "B" type corals (see Fig. 1). No artificial illumination was needed in either case due to lack of cloud cover. Natural moonlight was quite high.

The results were plotted using several different methods. Daily production of planulae varied by three orders of magnitude. Therefore, in the case of the lunar variation in production (Fig. 1), the results were plotted as log (mean + 1) as a function of the time of month. For the diurnal data, the mean number of planulae produced in a given hour was plotted as a function of the time of day (Figs. 2 and 3). A plot of the tide levels was superimposed in order to facilitate comparison in Fig. 2.

Results

The data obtained in Exp. 1 (Fig. 2) indicated a definite peak in planula production near midday. The 5 colonies that were subjected to the light treatment on the first night and the colonies which were left under natural conditions both showed mid-day peaks. However, peaks exhibited by the light treated colonies were much more dramatic. When the other half of the set were treated with light on the second night, they also showed a dramatic increase in production on the following day. The colonies subjected to night light treatment on the first night but not on the second night still exhibited a pronounced peak on the second day.

In Exp. 2 (Fig. 2), the peak was indicated around 0400 h which again was coincidental with low tide. Exp. 3 (Fig. 2) involved the "B" type corals, but still produced results indicating a peak near low tide. In this case, the peak occurred around 0300 h.

Discussion

Results of this investigation indicate a definite daily periodicity in larva production. All three experiments produced data showing extremely well defined daily peaks in production (Fig. 2). Because the peaks occurred at different times of the day, the possibility of the periodicity being controlled by the diurnal photoperiod is doubtful. The only obvious corellation between the periodicity and an environmental factor is that which occurs with the tide. In each case, peak production occurred within 3 h of low tide. A possible mechanism might be one in which changing tidal pressure is responsible for regulation of the period. Korringa (1947) describes a similar mechanism for the regulation of bimonthly periodicity in P. damicornis in Australia. The fact that the colonies still followed this rhythm after they were isolated from the tidal stimulus suggests that the cycle has become entrained but is still regulated by the tide. This lack of tidal stimulus in the collecting bowls may explain the slight observed deviations from low tide.

The data for Exp. 1 shows that the use of artificial light to induce planulation did not alter the periodicity, but rather the amplitude as compared to the control (Fig. 3). The fact that the colonies did respond to the light treatment can be attributed to the fact that night illumination is the main controlling factor in lunar periodicity for this species (Jokiel, in prep.).

There are at least two possible selective advantages for peak release of planulae at low tide. It may serve to retain those planulae which settle almost immediately (Richmond, personal communication) on the same reef by way of the current patterns produced when the tide rises. This could increase survival rate by insuring these planulae with a compatible environment. The idea that planulae are held on the reef by incoming tides is supported by the findings of Hodgson (this volume). Hodgson found that the number of planulae in the water column over the reef increased until high tide. This would indicate that the planulae released throughout the period of rising tide accumulated near the reef until the tide started dropping, at which time the number of planulae in the water column above the reef drops rapidly as they are swept away. The second possibility is that mass spawning satiates predators and insures that more larvae survive. In this case time of release or state of tide is unimportant. The tidal signal serves only as a cue to synchronize spawning. In any event, these observations raise interesting questions as to mechanisms and adaptive value of diurnal periodicity of larvae release.

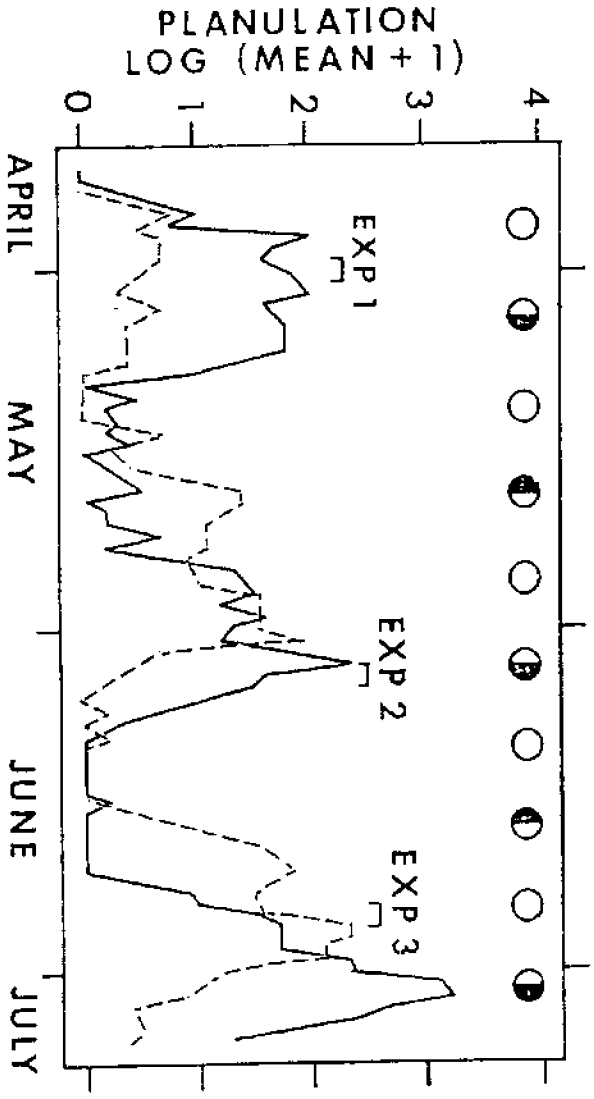

Fig. 1. Lunar variation of planulation during period of study showing the point in the cycle at which each experiment was carried out.

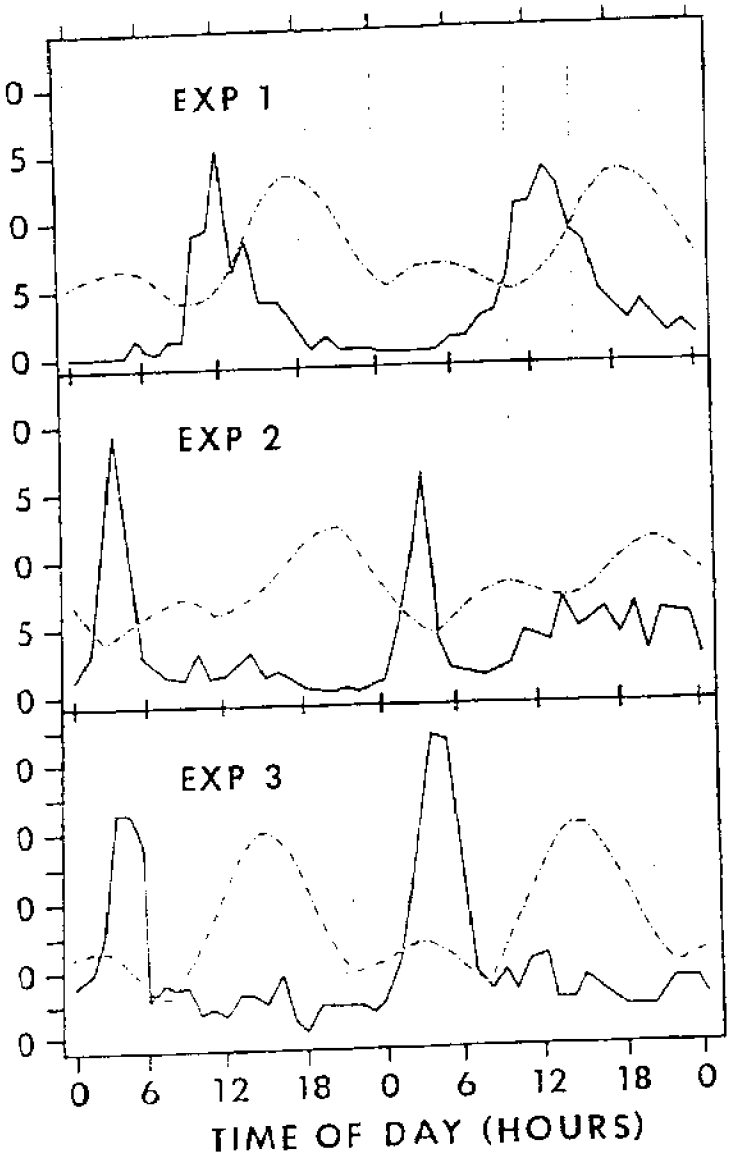

Fig. 2. Diurnal periodicity during the three different experiments (solid line) and the corresponding tide levels (dashed line).

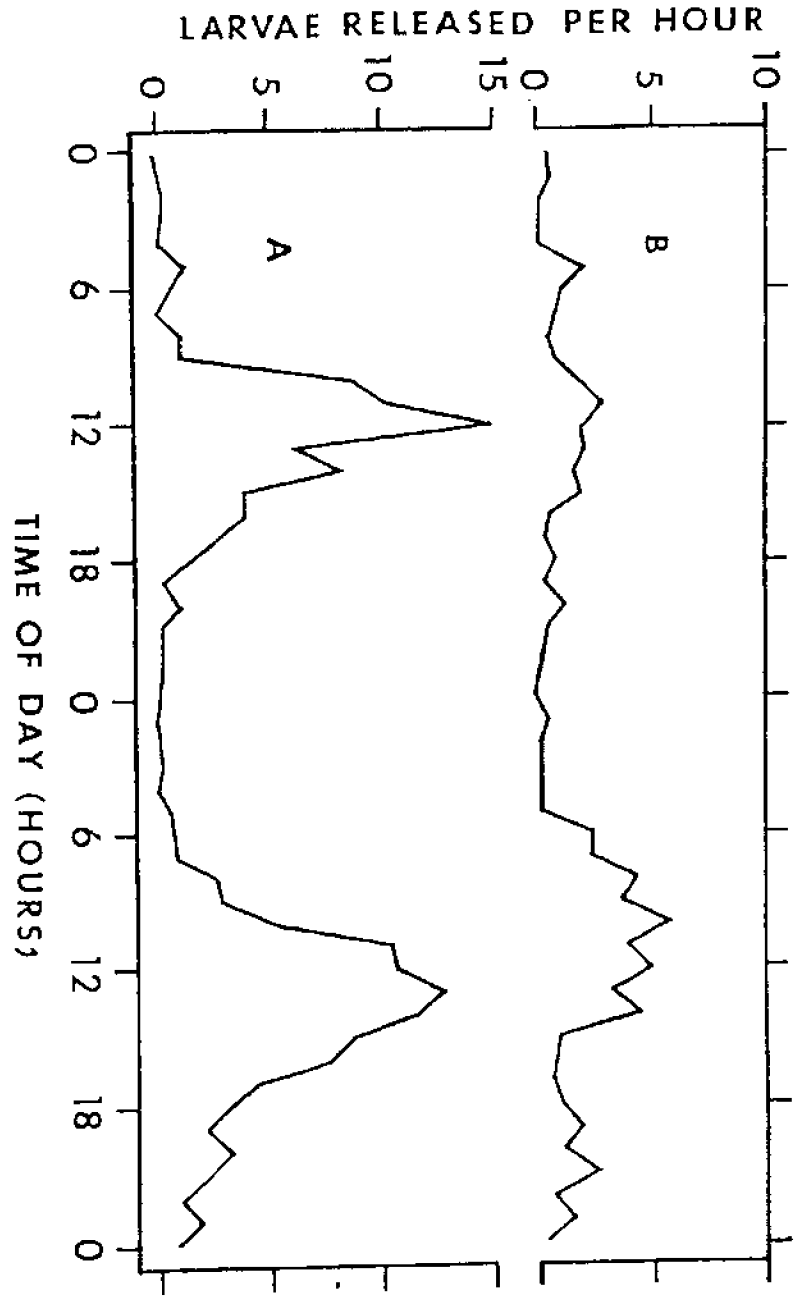

Fig 3. (A) Diurnal planula production by the set of corals exposed to artificial illumination on the first night of Exp. 1 and (B) on the second night of Exp. 1.

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The relationship between colony size and larva production in the reef coral Pocillopora damicornis

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Abstract

The planulation rates of Pocillopora damicornis colonies from throughout the size range in which they commonly occur in Kaneohe Bay, Hawaii were experimentally determined. It was found that the planulation rate increased with colony size until a size of 8 cm in radius was reached. The planulation rate in colonies greater than 8 cm decreased with increasing colony size.

Introduction

In the field of coral research, relatively little work has been done on the relationship of fecundity to coral colony age (as implied from size). Several reports are available which relate various species to a minimum reproductive size or age. Abe (1937) noted that Fungia actiniformis extruded planulae only after growing to a size of 7 cm in diameter. Harrigan (1972) found that Pocillopora damicornis colonies were reproductively mature in as little as 1 to 2 years. A few other reports also relate various species to a minimum reproductive size or age (Loya, 1972; Polacheck, 1978; Stimson, 1978). There is no available literature, however, which relates reproduction rates to colonies over the whole size range in which they are found. This investigation was designed to define this relationship through measurement of planulation rates of Pocillopora damicornis colonies throughout the size range in which they occur in Kaneohe Bay, Hawaii.

Materials and Methods

In Hawaii, Pocillopora damicornis colonies are commonly found in sizes which range from single polyped, newly settled planulae to colonies with a radius of 10 cm. A few larger colonies can be found, but these are comparatively rare. At least two different morphological variations of P. damicornis occur in Hawaii (see Richmond and Jokiel, 1984, for descriptions). The "Y" type coral was chosen for this study because it is more sturdy and easier to work with than the "B" type coral. Colonies ranging in size from 2 cm to 10 cm in radius were collected from the Coconut Island reef. These colonies were then placed in appropriately sized containers (from 1 to 5 liters) through which a continuous flow of seawater was maintained. The overflow from these containers flowed into collecting cups constructed of 180 micron plankton netting. The planulae which were collected were removed and counted daily and the numbers recorded.

The experiments were always carried out within a period of three days from a peak in the lunar cycle of planula production (Holloran and Ritteman, this volume). Data was taken on ten different days. In each case, 5 colonies from the stated size range were used.

Results

Daily planula production rates are reported in Table 1. The results suggest that there is an optimum colony size in terms of numbers of planulae produced. All of the colonies which were sampled produced planulae, although the numbers produced by the smallest colonies (2 cm radius) were rather low. Maximum production occurred in colonies which were approximately 8 cm in radius. Colonies which were greater than 8 cm in radius exhibited a decline in production.

Table 1. Pocillopora damicornis daily larva production as a function of colony size.

Date	Coral Radius (cm) 2	4	6	8	10
5/1	2	0	4	333	25
5/2	0	0	0	646	7
6/2	3	320	998	3103	233
6/3	18	62	919	1767	219
6/4	4	61	285	2413	120
6/5	13	57	384	1896	77
6/25	1	6	11	1533	-
6/26	86	88	412	918	-
6/27	55	37	217	604	41
6/28	13	25	209	701	12

Discussion

The initial rise in the numbers of planulae which are produced is relationship to increasing colony size (up to 8 cm in radius) can be expected. The mere existence of larger numbers of polyps on the larger colonies could account for this initial linear increase. This same linear increase has also been found in P. damicornis colonies of similar sizes at Enewetak (Richmond, personal communication).

The downward trend in larva production which was observed in the larger colonies supports recent studies of canopy-understory effects in this species (Jokiel and Morrisey, in prep.). This suggests that the canopy which is formed by the larger colonies of this highly branched species severely shades the understory (inner regions of the colony). This, in turn, limits the light which is available to these inner regions and therefore could limit the energy which is available for reproduction. For this reason, these colonies would have a smaller number of reproductive polyps even though the colonies themselves are larger.

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Sexual reproduction in five species of the coral Montipora

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Abstract

The timing and mode of sexual reproduction were investigated in five Hawaiian corals of the genus Montipora. All species were simultaneous hermaphrodites. M. verrucosa and M. dilitata were observed to shed gametes following the new and full moon, respectively, in July. Spawning was also inferred for M. studeryi and M. verrilli following the July full moon. Oocytes contained zooxanthellae when released. Fertilization and development were external.

Introduction

Descriptive studies on reproduction in corals appear to be undergoing a renaissance. The importance of asexual reproduction in population dynamics has been demonstrated for several species (Jokiel et al., 1983; Neigel and Avise, 1983; Heyward and Collins, in press; Stoddart, this volume). Furthermore the most recent research (Harrison et al., 1984) into sexual reproduction suggests that the majority of coral species release gametes for external fertilization. Abandonment of the planulation paradigm (e.g. Hyman, 1940) has also focused attention on previously investigated species where planulation was not observed.

Stimson (1978) noted developing gonads in many species of Hawaiian corals, particularly in spring and summer, yet did not detect planulation in the majority. He hypothesised that many of these species may not brood planulae. Certainly if such corals culminated their gametogenic cycles with the brief summer spawning of many broadcasting species (Fadlallah, 1983; Harrison et al., 1984) the 'planulation' event would easily escape notice.

The majority of the Acroporidae are broadcast spawners (Bothwell, 1981; Oliver, 1979; pers. obs.) and this is true of many species of Montipora in Australia (Robertson, 1981; Heyward and Collins, in prep.). In the present study five species of Montipora were studied in Hawaii during the summer months to determine the mode and timing of their reproduction.

Materials and Methods

Site and Sampling

M. flabellata and M. studeri were found in zones of high wave energy along the barrier reef crest, while M. verrucosa, M. dilitata and M. verrilli were sampled from the more sheltered patch reefs within the bay. All species exhibited considerable morphological plasticity but were typically encrusting or plate-like, M. verrucosa and M. dilitata often had branch like projections arising from the plates while M. studeri typically took a low thick branching form. All colonies were collected at approximately weekly intervals, commencing on 25 May, 1983. M. studeri was first sampled on the 31 June. Pieces of each colony were broken off with hammer and chisel, transported to the laboratory in seawater and immediately fixed in 10% formalin seawater for 24 h.

The arrangement and size of gonads were studied using a stereo-dissector microscope with ocular micrometer, by dissecting soft tissues following decalcification in 5% formalin - 10% formic acid solution. The identification of oocytes and spermatogonia was confirmed from histological sections. In treatment for histology, fixed tissue was decalcified in 5% formalin - 2% formic acid solution, processed to paraffin, sectioned on a rotary microtome at 5 um and stained with Haematoxylin and Eosin as per Winsor (1981).

Synchrony and sampling:

A field survey on 26 May revealed that every adult (i.e. $\geq$ 20 cm diameter) colony had gonads at an early stage of development. In order to determine sampling procedure, 5 colonies of each species were collected and investigated for

synchronous gamete maturity. Ten polyps were dissected from the edge, middle and center of each colony. Mean oocyte diameters and numbers per polyp showed considerable but non-significant ($p<0.05$) differences within and between colonies of each species. However, a sterile zone of varying width was present at the plate edges and branch tips. Consequently, 5 colonies (>50 cm diameter) of M. verrucosa and M. dilitata and 2 colonies of the less abundant M. verrilli were tagged and sampled sequentially each week. M. studeri and M. flabellata occurred in a wave swept environment where relocation of individuals was difficult. Subsequently, 5 untagged colonies of each were sampled at random each week.

Fixed and decalcified specimens were only used for histology. Number of eggs per mesentery and egg size were recorded from live material which was fractured using wire cutters and supported in seawater under the stereo-dissector. This avoided fixation artifacts when measuring oocytes and gave a better feeling for macroscopic changes in the gonads. Thirty eggs per species were measured on two diameters each week.

Spawning and embryogenesis

When fresh squashes of spermatogonia from the weekly samples revealed motile spermatids, some colonies were placed in flow through aquaria for close observation. Individual colonies were isolated in buckets or aquaria when spawning appeared imminent. Immediately following spawning the buoyant egg sperm bundles of each species were collected. In four dishes gametes of individual colonies were isolated to test for self fertilization while four other dishes contained a mixture of gametes from several colonies.

Results

Gonad structure and development

The five species of Montipora were simultaneous hermaphrodites with male and female reproductive structures on separate mesenteries in the same polyp. Gonads were arranged on eight mesenteries, two male alternating with two female (Fig. 1). The appearance of the gonads was very similar for all species although M. verrucosa was always more advanced in development.

On 25 May ovaries were prominent with 3-5 oocytes along the oral-aboral axis of each mesentery. Testes also developed within the mesenteries but at this stage were translucent, strap-like bodies and were of smaller volume than the ovaries. Oocytes increased steadily in size until spawning (Fig. 2). Tests increased markedly in volume in the month prior to spawning when testes and ovaries were similar in volume and both structures were cream to white. At this stage, density of zooxanthellae in the mesenteries surrounding the gonads increased, particularly around the ovaries. A week prior to spawning the oocytes were surrounded by a dense accumulation of zooxanthellae, making them appear brown. Zooxanthellae had invaded some oocytes up to 12 d prior to spawning (Fig. 3). Testes were usually quite locular 3 weeks prior to spawning, with spermatids developing tails as the lumens of the locules developed. Some spermatids were motile at this stage but the sperm heads appeared spherical and translucent. A week prior to spawning, squashes revealed very active spermatids and many had a condensed, well-defined acrosomal body. The white testes were the most prominent, macroscopic reproductive structure immediately prior to spawning.

Spawning

M. verrucosa broadcast gametes on the 10th, 11th and 12th of July following the new moon on the 10th. M. dilitata, M. verrilli and M. studeri spawned throughout the week following the full moon on July 25th. Spawning of M. verrucosa and M. dilitata occurred simultaneously in the aquaria and in the field, where polyps began spawning behavior approximately 30 min after sunset. Each polyp elongated, gathered the gonads under the oral disc, then contracted the body wall. The gametes were formed into a sphere which distended the oral disc. This posture was maintained for 30 minutes before the gametes were ejected. Egg and sperm release were simultaneous, each polyp releasing a single cluster of eggs, packaged around the sperm (Fig. 4). It appeared that each gamete cluster represented the entire reproductive complement of the polyp, containing 12-20 ova. At release, all the ova contained zooxanthellae. The inheritance of parential zooxanthellae was also noted for Porites compressa which

Fig. 1. Transverse section of Montipora dilitata polyp.

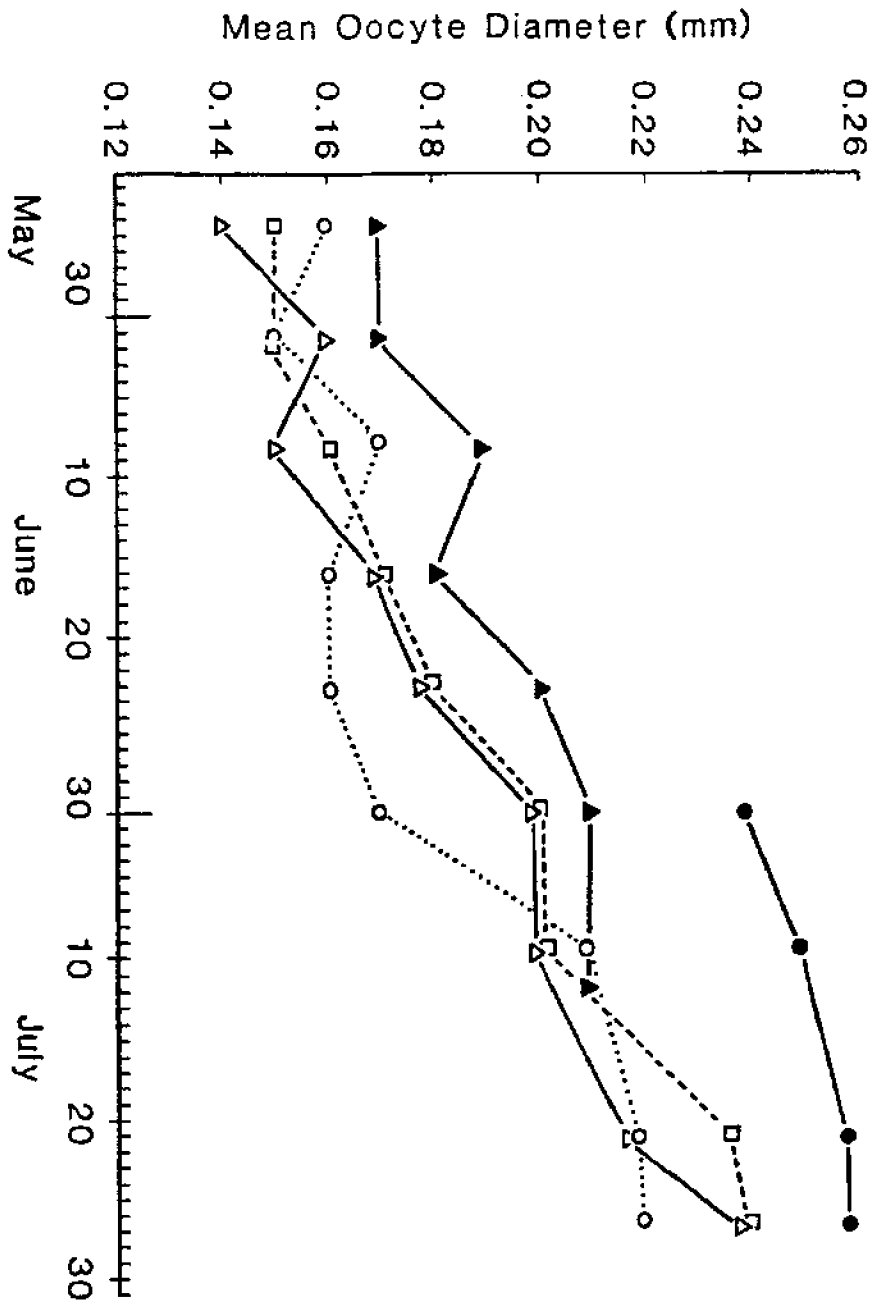

Fig. 2. Mean oocyte diameter for five species of Montipora throughout the summer.

Fig. 3. Zooxanthellae in oocyte (12 d prior to spawning).

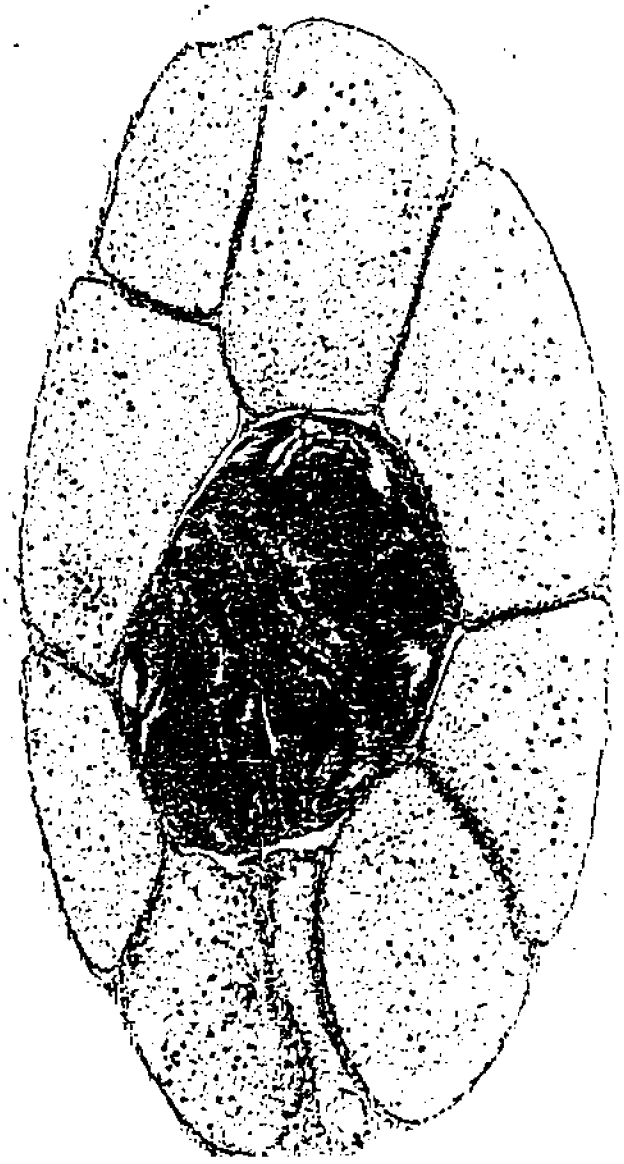

Fig. 4. Transverse section of Montipora dilitata gamete cluster.

spawned on the new and full moons throughout the summer. Presence of zooxanthellae was checked with fluorescence microscopy.

During spawning the gamete cluster was usually propelled clear of the colony and floated quickly to the surface where it broke up within 30 min. In M. verrucosa and M. dilitata release of gametes commenced between 2045 h and 2100 h. Individual colonies continued to release gametes until 2145 h. A particular colony would release most of its gametes during one evening. The major population spawning occurred on 11 July for M. verrucosa and on 27 July and 28 July for M. dilitata. However small areas of a colony might retain some gravid polyps which spawned over subsequent nights. Spawnings on successive nights always occurred at about 2100 h, suggesting some photoperiod cue as the final trigger.

Following spawning, up to 50 colonies of each species were collected from the field. No gravid colonies were found after the colonies kept in aquaria had spawned, indicating a synchronous population spawning. M. verrilli and M. studeri were not observed to spawn. Spawning time was inferred by the absence of gonads in the weekly samples following the spawning of M. dilitata. M. flabellata still contained gonads in August and early September, although not all colonies were gravid. This species may have a multiple spawning during the late summer and fall. It was noted that small pieces of M. flabellata which had become separated from their original colony by an area of dead skeleton were sterile, while the larger parts of the original were fertile. This suggests the importance of not only age but size in reproductive status.

Embryogenesis

Gametes collected from isolated colonies were mixed together at 2230 h. The first cell divisions were noted at 2345 h, however by 0045 h less than 1 % of the population were at 2 or 4 cell stage. Some embryos at 2 cell stage were isolated for observation. Cell divisions occurred every 45-60 min in irregular radial development (Giese and Pearse, 1974, pg. 176). Cell divisions were complete and equal, although not always synchronous beyond the 8 cell stage. Seven h after spawning, morulae were common and gastrulae were apparent within 12 h. At 14 h many embryos were ciliated, but the cultures were deteriorating rapidly. Many embryos developing at the surface formed irregular shapes, probably due to surface tension effects, and ceased to divide. Agitation is a key factor in maintaining the embryos through to viable planulae (Heyward and Babcock, in prep.).

Cells in the selfing experiments lysed by 0800 h and only one egg showed signs of dividing. Although inconclusive, this suggests that selfing, if at all possible in these populations, has a lower probability of occurring than cross fertilization.

Discussion

These species of Montipora in Hawaii broadcast spawn after the new or full moon during summer and fall. This is a common reproductive pattern for scleractinian corals (Harriott, 1983; Gushiken, 1981; Krupp, 1983; Fadlallah, 1983; Szmant-Froelich et al., 1983; and others). The sequence of gametogenesis and the timing of spawning is very similar to Montipora famosa on the Great Barrier Reef in Australia (Heyward and Collins, in prep.).

Although the energetics of reproduction in corals are poorly understood, the annual cycles of water temperature and insolation are likely to affect reproductive effort (Jokiel and Gunther, 1978; Szmant-Froelich et. al., 1980) and have been suggested as a major trigger for gonad maturation and spawning (Harriott, 1983). Like Fungia scutaria in Hawaii (Krupp, 1983), the Montipora spp. spawn at the time of maximum water temperature and solar irradiance.

There was no evidence of a second reproductive cycle commencing following spawning. However, the study was terminated at the start of fall. Stimson (1978) noted eggs present in one colony as late as October, and Robertson (1981) found some suggestion of a bimodal spawning during summer and fall for Montipora spp. in Australia. If light and temperature permit, (Szmant-Froelich et al., 1980), a second cycle may well appear and this possibility should be investigated more comprehensively. Similarly, the sequential spawnings of the dioecious Porites compressa on the new and full moons throughout the summer lend themselves to a detailed quantitative study.

The incorporation of parental zooxanthellae into the oocytes at least 12 d prior to spawning is notable. It would appear to be characteristic of the genus but many other Acroporidae do not acquire zooxanthellae until after settlement (Heyward and Babcock, in prep; Harrison, personal communication). One day old Montipora planulae collected from the plankton have an extensive symbiont flora (See Hodgson, this volume). If these zooxanthellae can translocate to their planktonic hosts (Richmond, 1981) dispersal potentials may be quite high. Porites and Montipora both inherit parental zooxanthellae and are widespread in the Hawaiian archipelago, in contrast to the restricted occurrence of Acropora (Grigg, 1983).

At the time of spawning, no germinal vesicle was apparent in the ova, suggesting that these eggs were mature and ready for fertilization. Considering the proximity of eggs and sperm in the gamete bundles (Fig. 6), selfing had every chance of occurring. Outcrossing mixtures were far more successful than selfing trials at producing cleavages and embryos. Recent observations on the Great Barrier Reef (Heyward and Babcock, in prep.) where larvae of broadcast spawners were successfully raised to settlement for several species, suggest that some mechanisms must exist which reduce the probability of selfing. Investigations into coral self fertilization need to be continued on a rigorous basis to clarify the issue.

This study, while only of short duration, confirms Stimson's (1978) proposal that many corals broadcast gametes. It is likely that many do this in summer and fall. Recent work in the Caribbean (Szmant-Froelich et al., 1983) reveal similar patterns for the timing of coral reproduction but also indicate the diversity of coral reproductive modes. Many species of Hawaiian coral await longterm investigation of their reproductive patterns.

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Aspects of reproduction and planula development in the reef coral Cyphastrea ocellina

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Abstract

Gametogenesis and planulae development and production were followed in small and large colonies of the hermatypic coral, Cyphastrea ocellina. This species is a viviparous, simultaneous hermaphrodite and planulae are produced continuously and asynchronously in the Coconut Island population. Ovaries and testes are intermingled within the same mesenteries by hollow vessels. The potential for self-fertilization and the possible nutritive function of the vessels are discussed.

Introduction

Traditional views of reproduction in hermatypic corals (Ryman, 1940; Vaughn and Wells, 1943; Wells, 1956) have been revised in the light of recent research, and it is now recognized that scleractinians may display a variety of sexual characteristics and timing in reproduction (Padlallah, 1983). Despite the current interest in coral reproductive studies, the origin of planulae is an issue which remains largely unresolved. The question of whether planulae are produced sexually or asexually has rarely been addressed. Pioneer electrophoretic studies (Stoddart, 1983; Stoddart, this volume) have shown that the planulae of Pocillopora damicornis may be generated asexually, thereby revealing a further uncharted dimension to the propagative capabilities of corals. Patterns of coral gametogenesis are poorly known, and crucial developmental studies of planulae remain undocumented, although they are of profound importance to the understanding of coral reef ecology and demography.

This paper focuses on the gametogenesis and development of planulae in Cyphastrea ocellina (a shallow water species of Hawaiian coral) known to produce larvae throughout the year (Edmondson, 1946; Stimson, 1978), together with observations on the timing of planula release, in an attempt to provide an insight into the reproductive system underlying the propagation and brooding of planulae.

Materials and Methods

The study site was located on the southern portion of the fringing reef surrounding Coconut Island, in Kaneohe Bay, Oahu, Hawaii. The reef flat zone is about 25 m wide and is covered by 1-2 m of water but may become emergent at low tide. Cyphastrea ocellina is a massive species of coral restricted to shallow water habitats. Typically, C. ocellina colonizes dead coral substrata, predominantly Porites compressa (the dominant structural reef coral) forming irregular "knob shaped" colonies or encrustations which reach 10-15 cm in diameter. Commonly, C. ocellina is a sandy brown coloration at the top of the colony, becoming darker at the base.

Several approaches were adopted to study the reproduction of this species. Firstly, the polyps of the coral were examined histologically for evidence of gametogenesis. Secondly, since C. ocellina is viviparous, an attempt was made to follow the frequency and timing of reproduction by monitoring the release of planulae from individual colonies.

Histological preparations

Each week, over a period of two months, three large colonies (8-10 cm diameter) and three small colonies (2-4 cm diameter) were collected in order to study the development of genital cells. The colonies were fixed in seawater containing 4% formalin for a period of 48 h. Large fixed colonies were sectioned on a diamond wheel, and cm^2 samples were extracted from the top and lower regions of each colony. Samples were decalcified in either Decal Brand decalcifying solution or a solution of 5% formalin with 1% formic acid. Decalcified specimens

revealed a mat of algal material directly beneath the coral tissues, apparently ramifying the skeletal framework. The identity of this algal tissue and its possible significance to the coral is unknown. The remaining coral tissue was separated from the underlying algal mat, and rinsed in distilled water.

Dehydration, clearance and paraffin infiltration of tissue samples was automatically by a Techicon Tissue Processor. Six micron serial sections were prepared and stained with Mayers, Haematoxylin and Eosin.

Planulation

Fifteen colonies (of approximately equal size) were collected from different locations on the reef site. Each colony was placed in individual "planula collection bowls" supplied with running seawater and maintained in ambient sunlight. Planulae were collected each day from overflow water, in 180 micron mesh cups. The captured planulae were counted and settlement activity was observed periodically under a dissection microscope. Those planulae which had settled within the mesh cups were counted before removal. The production of planulae from these colonies was monitored over a period of six weeks, during which the colonies showed no signs of deterioration. Some planulae were fixed in a % formalin/seawater solution for histological preparations.

Preparations for scanning electron microscopy

Free-swimming and newly settled planulae were fixed in 2% gluteraldehyde in millipore-filtered seawater. Whole polyps were dissected from decalcified formalin fixed material to reveal their internal anatomy. Fixed tissues were dehydrated to 70% alcohol, in which they were stored. Final dehydration was performed using a series of alcohols before subsequent critical point drying. The samples were plated with gold and viewed under a scanning electron microscope.

Results

Reproduction

From the histological study, it is apparent that C. ocellina is hermaphroditic. Ova and testes are found intermingled on the same mesenteries throughout reproductively mature polyps (Fig 1a). Mature eggs reach a size of 140-160 micron mean diameter. The mean polyp diameter of this species is 1.8 micron, and each of the twelve gonads per polyp may contain two or three eggs. There is a marked asynchrony in the development of genital cells between colonies. Planulae develop to an advanced state within the adult polyp, suspended from the mesenteries.

Female gonads

Ovaria are found with testes within the same gonad on each mesentery of sexually mature polyps. Early stages of egg development are first seen as small yolky ovoid structures developing within the mesenterial tissue (Fig. 1b). Two or three eggs may grow in the plane of the mesentery, intermingled between testes within each gonad. Zooxanthellae may be found in the endodermal tissue surrounding the eggs but the eggs themselves do not contain these algal cells. The eggs are ovoid in shape, and contain globules of yolky material which has a high affinity for eosin, staining pink (Fig. 1c). Mature eggs grow to 160 microns diameter, with an oval nucleus (60 micron diameter) and a dark red stained nucleolus (6 micron diameter).

Male gonads

Testes develop in the same gonad as the ova, throughout the polyp from the base to the pharynx, but were not observed within the tentacles. The testes consist of variously shaped sacs of different sizes. The gonad, incorporating both ova and testes, is enveloped by a layer of endoderm extending from the mesenteries. Each testes may have several lobes in which different stages of development may be observed. The male gonads may reach a diameter of 100 microns. The development of male gonads is initiated with a primary spermary within the endoderm of the mesenteries (Fig. 1d). The spermary increases in size by successive division, and gradually fills up with spermatogonia (Fig. 1e). The cavity typically seen in immature spermaries is progressively lost with the growth of the spermatids and spermatocysts. The spermatogonia (6 micron diameter) appear ovoid or circular in shape showing dark staining activity. Spermatids and

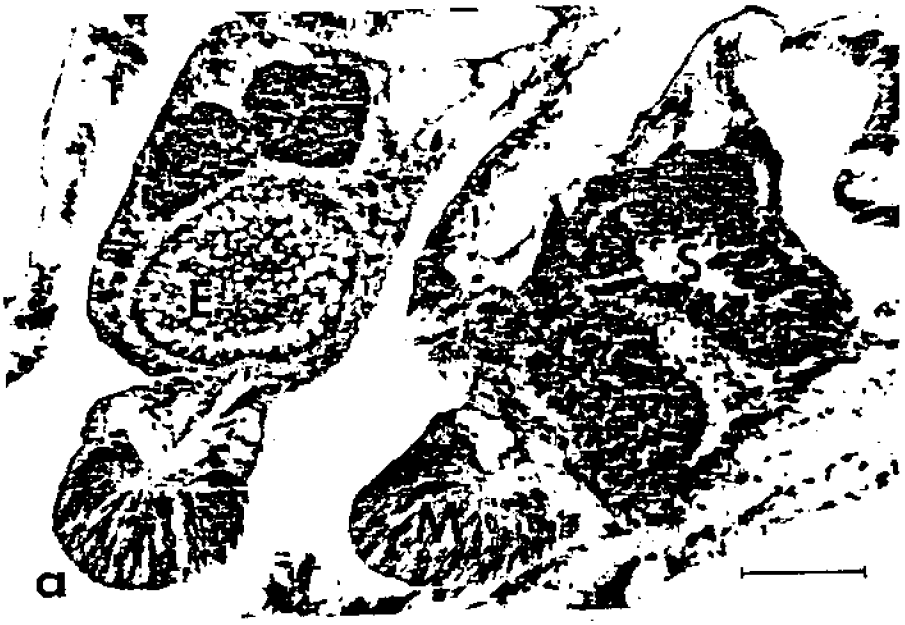

Fig. 1. Cyphastrea ocellina. Scale Bar = 50 microns. Abbreviations: BQ = Sperm "Bouquet"; E = Egg; En = Endoderm; N = Nucleus; S = Spermaries; M = Mesentery.

A) Transverse section through intermingled testes and ova on the same mesentary.

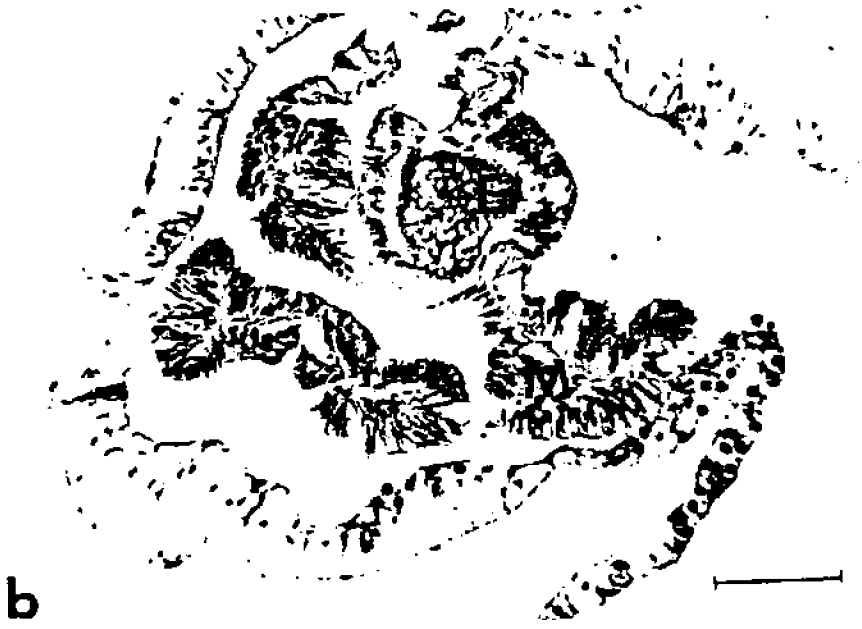

Fig. 1b. Transverse section of early female Cyphastrea ocellina gonad.

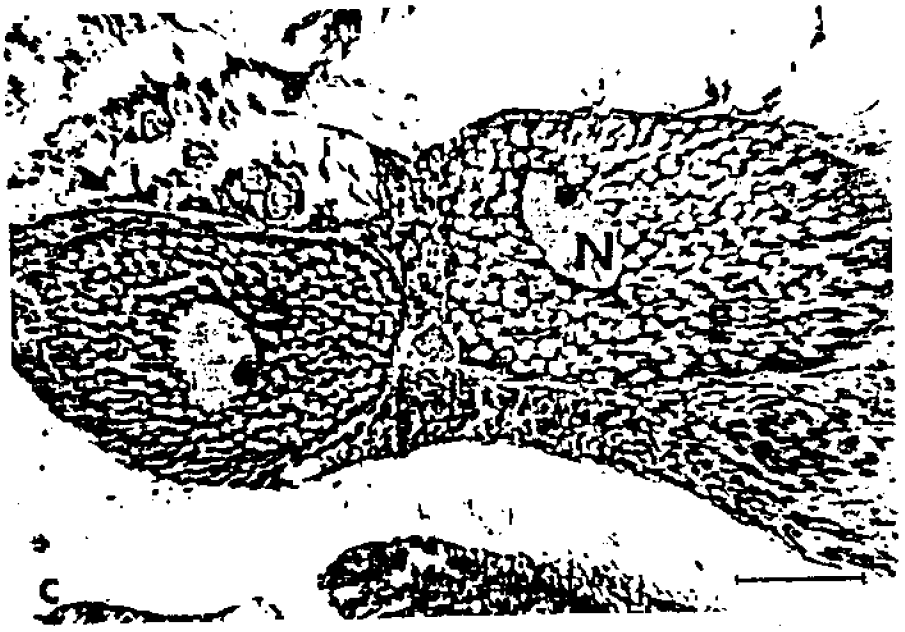

Fig. 1c. Transverse section of Cyphastrea ocellina egg.

Fig. 1d. Transverse section of early male Cyphastrea ocellina gonad.

Fig. 1e. Transverse section of immature Cyphastrea ocellina testes with characteristic lumen.

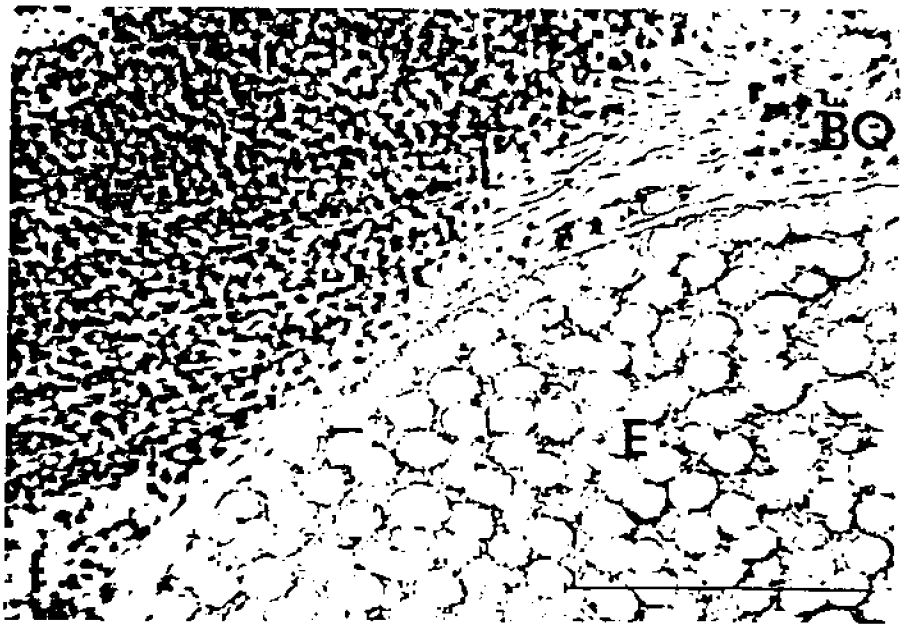

Fig. 1f. Longitudinal section through mature Cyphastrea ocellina goand illustrating the sperm "bouquet" arrangements adjacentto mature eggs.

spermatocysts also show such staining. As development progresses the spermary becomes densely packed with sperm. The sperm heads are darkly stained from which extend long tails, which stain pink in eosin, forming "bouquet" type arrangements (Fig. 1f).

Planula development

Cyphastrea ocellina is viviparous and broods its planulae to an advanced state of development before release. The primordial planula is first observed within breeding colonies containing mature eggs and sperm (Fig. 2a) beyond which no gonads were present in polyps containing planulae. The early planula which develops on the mesenteries consists of an ovoid structure, composed of two layers of cells: the endoderm and an outer layer of columnar ectoderm. Few zooxanthellae are present within the tissues of the early planula. As development progresses, attachment structures extend from several mesenteries ajoining the planula laterally as well as at the base (Fig. 2b, 2c). Typically the planula grows suspended at one side of the polyp, where there is an intimate association of adult polyp and planula tissues. Several layers of tissue enclose the planula. In transverse section attachment vessels extending from the mesenteries are evident within the tissues of the planula. These attachments appear as hollow vessels surrounded by columnar cells and may either extend through the endoderm of the planula or may be continuous with the ectodermal layer (Fig. 2d). In longitudinal section these attachments (Fig. 2e) extend from the base of the polyp or from the lateral edges of the mesenteries. No such structures have been previously described, and their function is unclear, although they may be involved in the transfer of nutrients. As the planula grows, zooxanthellae become more numerous, the mesenteries enlarge and differentiate. Nematocysts become clearly visible in the ectoderm. In the final stages of development, the planula occupies most of the space in the gastrovascular cavity of the polyp, and the attachments are finally lost (Fig. 2f).

Planula behavior

If newly settled planulae were removed and transferred to fresh seawater, the planulae would reattach with no apparent detrimental effects. This phenomenon was first observed by Richmond (1983) in larvae of Pocillopora damicornis.

Frequency of planulation

Preliminary observations on the release of planulae showed a marked asynchrony within and between colonies (Table 1). Some colonies produced pulses of planulae, while others appeared to generate larvae almost continuously. Certain colonies did not produce any planulae throughout the sampling period. There was no relationship between the number of planulae produced and colony size. No lunar phase could be detected in the timing of planula release, which is in contrast to previous observations by Stimson (1978) who found a peak in planulation at new moon. The maximum number of planulae released from an individual colony of C. ocellina (10 cm diameter) was 330. Ideally, planulae should be collected from individual colonies in the field, since maintenance of colonies in aquaria is likely to disturb gametogenic and planulation rhythms by removing possible cues for planula release. However, this was not feasible for this cursory study.

Discussion

Cyphastrea ocellina is a hermaphroditic species of massive coral. Its gonad structure resembles that of other species in which ovaries and testes develop intermingled on the same mesenteries, such as Favia pallida (Marshall and Stephenson, 1933), Goniastrea favulus (Babcock, 1980) and Favites abdita and Leptoria phrygia, (Kojis and Quinn, , 1981). C. ocellina exhibits simultaneous hermaphroditism, which allows the opportunity for self fertilization. It has been suggested (Tomlinson, 1966) that self fertilization is a mechanism to reduce reproductive wastage, and may be of prime importance in areas of recolonization in which population densities are low. However, this mode of reproduction is also found in common species such as Acropora formosa and Favia faves on the Great Barrier Reef (Pichon, unpublished).

In C. ocellina, gonads are present throughout breeding colonies, irrespective of their position, as observed in other massive species of coral (Kojis and Quinn, 1981), whereas in branching species gonads are absent from the actively growing tips. This has been observed in Pocillopora damicornis (Harrigan, 1972)

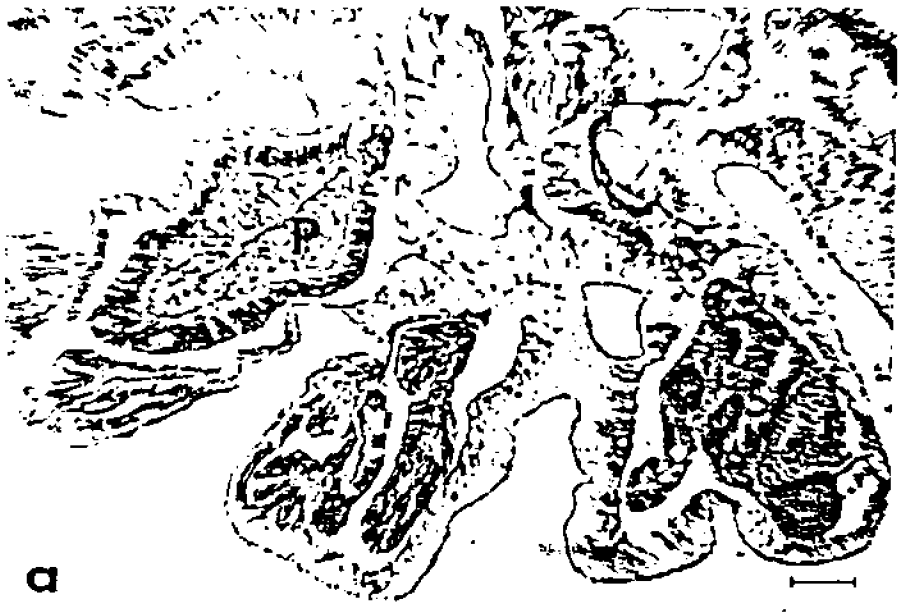

Fig. 2. Cyphastrea ocellina: planula development. Scale Bars = 50 microns. Abbreviations: AV = Attachment Vessels; Ec = Ectoderm; S = Spermaries; P = Planula; u = Planula Mesenteries. Cyphastrea ocellina: Transverse section of planula and mature gonads in adjacent mesenteries.

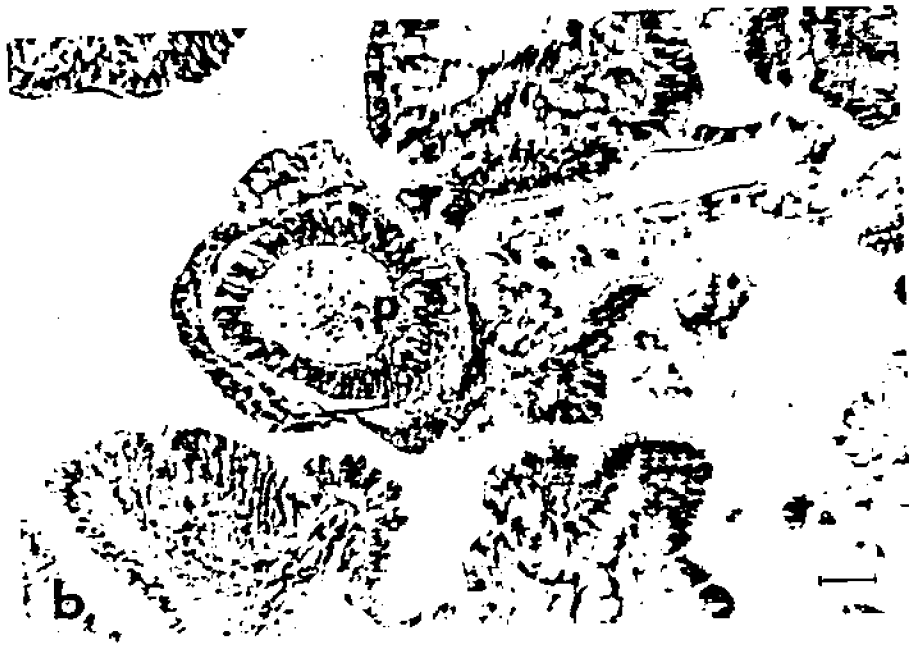

Fig. 2b. Longitudinal section of developing Cyphastrea ocellina planula.

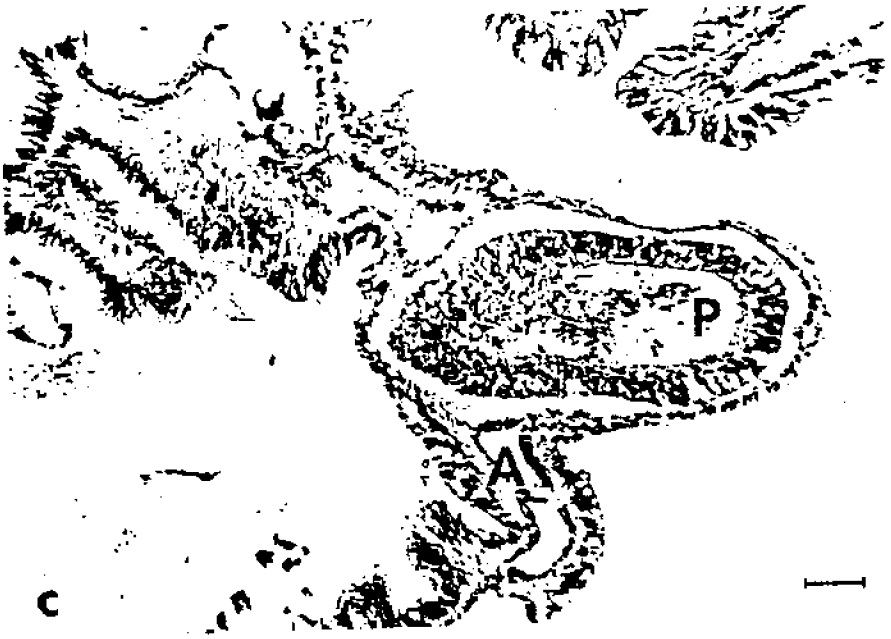

Fig. 2c. Oblique section of developing Cyphastrea ocellina planula with lateral attainment structures.

Fig. 2d. Transverse section of Cyphastrea ocellina planula with adult polyp showing attachment vessels.

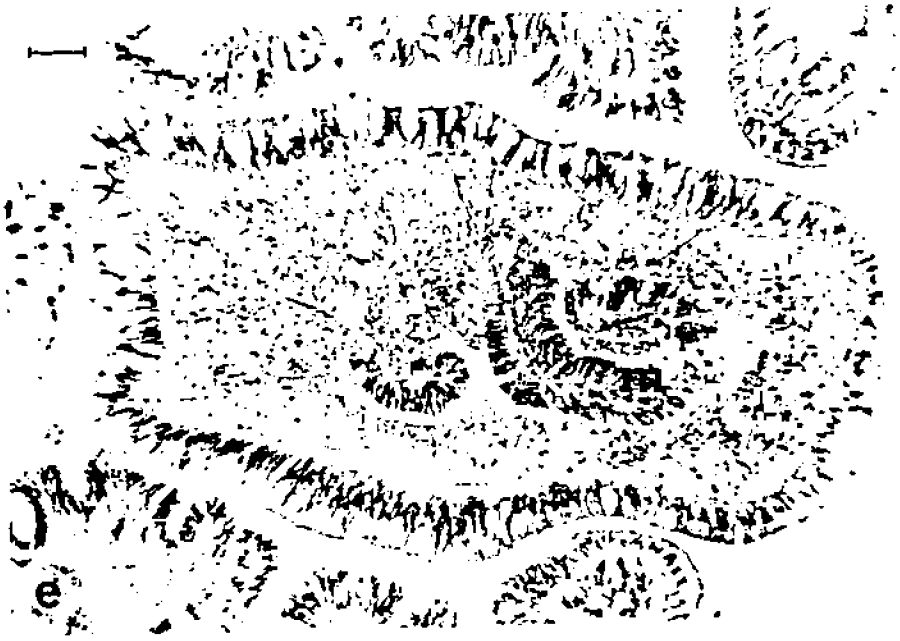

Fig. 2e. Longitudinal section of mature planula.

Fig. 2f. Scanning Electron Micrograph of a settled Cyphastrea ocellina planula.

Table 1. Daily production of planula larvae in 15 individual colonies of *Cyphastrea ocellina* between 6 June 1983 and 10 July 1983.

Day	Number of Planula Released Per Day														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	-	0	-	0	0	0	0	0	2	0	0	0	0	0	7
2	30	0	10	0	0	0	2	1	0	0	0	0	0	0	7
3	10	0	0	0	0	10	0	0	5	35	0	15	0	10	6
4	5	0	10	0	0	0	0	1	0	0	0	0	0	0	0
5	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	4	0	1	0	0	0	0	0	0	10	0	0	0	0	0
7	3	0	1	0	0	0	0	0	0	20	0	1	2	2	0
8	0	0	0	0	0	0	0	0	0	30	0	0	0	0	0
9	30	0	0	0	0	0	0	0	1	40	0	0	2	5	2
10	10	0	10	0	0	0	0	0	0	5	0	0	0	2	0
11	20	0	0	0	0	0	0	0	0	15	18	0	0	4	0
12	0	0	5	0	0	0	0	0	0	11	0	15	0	4	0
13	0	0	0	0	0	0	0	0	0	0	0	10	0	5	0
14	3	0	0	0	0	0	0	0	0	3	0	0	0	0	0
15	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	5	0	0	0	0	0	0	0	0	8	0	1	0	0	0
17	-	0	0	0	0	0	0	0	0	2	0	8	0	0	0
18	5	0	0	0	0	0	0	0	0	0	0	10	0	1	0
19	10	0	0	0	0	0	0	0	25	0	0	20	0	2	0
20	1	0	0	0	0	0	0	0	0	0	2	10	0	3	0
21	0	0	0	0	0	0	0	0	0	0	0	5	0	3	0
22	0	0	5	0	0	0	0	1	0	10	0	0	0	2	4
23	2	0	0	0	0	0	0	0	0	50	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0	0	4	10	0	3	0
25	5	0	0	0	10	5	10	3	0	5	10	0	4	0	5
26	2	0	0	0	4	0	0	0	0	0	10	0	0	10	32
27	0	0	0	0	3	0	0	0	0	5	5	0	0	0	6
28	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
29	5	0	0	0	0	0	0	0	0	0	0	2	5	0	1
30	8	0	0	0	0	0	0	0	0	1	0	0	0	0	105
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9
32	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5
33	3	0	0	0	0	0	0	0	0	0	0	0	1	0	4
34	0	0	0	0	1	0	0	0	0	0	0	0	3	0	5
35	4	0	0	0	2	0	0	0	0	0	0	0	0	0	10
36	5	0	0	0	0	0	0	0	0	0	0	0	0	0	12
37	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
38	3	0	0	0	0	0	0	0	0	0	0	0	0	0	115
39	0	0	5	0	0	0	0	0	0	0	0	0	0	0	3
40	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0

and Stylophora pistillata (Rinkevich and Loya, 1979a,b). In Montipora verrucosa, the outer rim of this plating species is sterile (Heyward, this volume). The differences in the distribution of gonads may reflect the contrasting growth characteristics of massive and branching species of coral (Buddemeier and Kinzie, 1976). If skeleton formation is considered as an energy requiring process, then potential resources for reproduction may be rendered unavailable in rapidly growing branch tips. However, in massive corals, growth is radial and not concentrated in one specific region which may allow simultaneous skeletal and reproductive growth. Analysis of X-radiographs revealed a number of concentric growth bands in sectioned colonies of C. ocellina, which indicate radial growth. Furthermore, banding patterns indicate that colonies of 2 cm diameter found to contain planulae, are less than 2 years old.

It has been proposed by Rinkevich and Loya (1979a,b) that morphological constraints of polyp size predispose coral species to certain forms of reproduction. They suggested that branching, small polyp species in which gonads develop in the body cavity, exhibit brooding, while large polyp or massive species (in which gonads develop on the mesenteries) broadcast gametes. The present study conflicts with this hypothesis, together with observations by other workers. C. ocellina is a massive species in which the gonads develop on the mesenteries, but in contrast to the theory, it broods its planulae. Szmant-Froelich et al. (1980) concluded that there was "no universal rule" to the relationship between polyp size, eggs size and developmental mode. Bothwell (1981) found Acropora species with small polyps that broadcast eggs. This is opposite to the suggestion that brooding generally occurs in small polyp species. Fadlallah and Pearse (1982) have shown that large polyp solitary corals may exhibit brooding or broadcast spawning.

Nevertheless, it is obvious that there will be a limit to the number of planulae or eggs developed simultaneously, imposed by the space within individual polyps available for brooding embryos to an advanced stage of development. The brooding of planulae must exact some energetic cost to the adult polyp. The presence of a planula filling the gastrovascular cavity is likely to impair its feeding capabilities. The importance of energy transfer between polyps of a colony is not known. Perhaps only a small percentage of polyps are reproductively active at any one time, due to energetic constraints.

It is likely that there is a physiological minimum amount of energy required for metamorphosis, which sets a lower limit to the size of planula depending upon how the energy is packaged. Energy rich lipids are often found in larvae and serve as a concentrated energy source, thereby minimizing the size of planulae. However, planulae contain zooxanthellae, and it is not known what contribution they make to the energy requirements of planulae.

Released planulae vary considerably in shape from a contracted sphere to an extended pear-shape. Characteristically, small "pearly vesicles" are scattered throughout the planula tissues of C. ocellina, (first described by Edmondson, 1946). Free swimming larvae move by ciliary action and undergo frequent changes in shape. When viewed under ultra-violet light, the planulae exhibit a general green fluorescence, with the zooxanthellae appearing as bright spheres. It has been suggested that this green fluorescent pigment, originally observed in the planulae of Stylophora pistillata (Rinkevich and Loya, 1979a) is capable of converting short wave radiation into light which may be utilized by the zooxanthellae in photosynthesis (Kawaguti, 1973).

The planulae of C. ocellina move slowly throughout the water column, and show no obvious phototactic responses. Most of the forms of movement described by Harrigan (1972) and Rinkevich and Loya (1979a,b) were also observed in the larvae of C. ocellina. Close observation of the oral pore revealed the movement of particulate material into and out of the planula. However, it is not clear whether material incorporated into the larva in this fashion can be utilized at this stage.

Laboratory observations of settlement activity in planulae showed that the period between release and settlement is highly variable, which may reflect the range of developmental stages released from colonies. Planulae from some colonies settled in the collecting cups whereas others showed a more protracted settlement period. The temporal aspects of settlement may be modified by not only differential stage at release, but also environmental regime, substrate availability or a combination thereof. It is not known if the time period to settle-

ment is programmed to time of release, or whether a particular stage of development must be attained before settlement is possible.

A few planulae were observed to settle on glass slides and deposit skeletal material. Under stress (for example, if colonies were left in stagnant water) such planulae would withdraw their living tissue from the attached skeleton or detach completely.

Egg number per gonad may be indicative of reproductive mode (Connell, 1973; Rinkevich and Loya, 1979a,b) although its predictive value requires further substantiation. Although male gonad structures have been recorded (Duerden, 1902; Gardiner, 1902; Marshall and Stephenson, 1931; Rinkevich and Loya, 1979a,b; Fadlallah and Pearse, 1982) spermatogenesis in corals has rarely been described (Rinkevich and Loya 1979a). Perhaps this is because it is not readily quantifiable, since measurements of spermary dimensions do not reflect developmental stage. In C. ocellina mature sperm can be observed directly adjacent to mature eggs. Different stages of development may be seen within lobes of the same testes. The interaction of sperm and egg remains poorly documented.

A number of studies have described the existence of planula brooding and considerable differences have been observed in the stages at which planulae are released (Hyman, 1940; Edmondson, 1946; Atoda, 1953; Harrigan, 1972; Fadlallah, 1983). However, the development of planulae from the mesenteries in which attachment vessels suspend the planula within the polyp, as seen in C. ocellina has not been previously described. The unusual hollow vessels which pass through the inner tissues of the planula may have some nutrient transfer function. The brooding of planulae in this unique fashion might facilitate the development of the planulae to reach an advanced stage before release. This could be an adaptation for rapid settlement and establishment of new colonies.

Considerable interest has been focused on the seasonality and timing of planulation (Marshall and Stephenson, 1931; Atoda, 1947; Harrigan, 1972; Rinkevich and Loya, 1979a,b). Observations by Edmondson (1946) and later, Stimson (1978) revealed that C. ocellina was capable of releasing planulae throughout the year. Stimson (1978) also suggested that the release of planulae in C. ocellina was related to the lunar phase. The present study failed to detect any such periodicity, but a marked asynchrony was observed between colonies, which is consistent with the observations of other workers (Jokiel, unpublished). The time period between planula release and settlement also showed considerable variability. The underlying cues for larval release, and the adaptive significance of synchronous or asynchronous release of planulae is unknown. A consequence of the asynchronous gametogenesis and planulation in C. ocellina is the perpetual availability of propagules for the colonization of new substrata.

The numbers of planulae released from individual colonies of C. ocellina, a massive, slow growing coral, are low in comparison with Pocillopora damicornis (Harrigan, 1972) which is a rapid growing branching species. This difference could be attributed to either the number of polyps per unit surface area available for development of planulae or perhaps due to differential energy accumulation and reproductive energy budgets. Alternatively, the differences in planulation may result from the differential time schedules involved in the asexual production of planulae in P. damicornis and the sexual reproduction which gives rise to planulae in C. ocellina.

Attempts to decipher possible trends in coral reproductive patterns have failed to adequately encompass the observed complexity. The hypothetical r-K continuum, developed by Pianka (1970) has been invoked to rationalize coral reproduction. Loya (1976) discusses the reproductive characteristics of Stylophora pistillata in terms of r-K selection theory. However, the criteria often used to categorize species have not been consistent, and a number of deviations from this theoretical framework are known (Menge, 1975; Grassle and Grassle, 1974). Fadlallah and Pearse (1982) suggested that solitary corals may be selected to reproduce at opposite extremes of various modes of sexual reproduction. Stimson (1978) endeavoured to explain coral reproductive patterns in terms of habitat. He suggested that shallow water species (including C. ocellina) produce planulae, whereas deeper water species adopt modes of broadcast spawning. Furthermore, it was proposed that shallow water species reproduce in a fashion which favors the retention of reproductive propagules within the parental habitat. However, with the influx of new data, the validity of such generalizations is now questionable.

It is apparent from the foregoing discussion, that no profound trends or generalizations can be made to explain the observed patterns of reproduction in corals. Numerous combinations of sexual characteristics including gonochoric and hermaphroditic species, brooding and broadcast spawning have been described in both solitary and colonial corals. Superimposed upon these reproductive mechanisms are a range of gametogenic and planulation schedules which compound the problems in rationalizing such phenomena. Reproduction is a vital process to which the life history of each species is geared. A particular environment presents a set of environmental contingencies which must be met in order for a species to survive. It is evident that coral species have solved their ecological problems by their mere existence, but each may have employed a different combination of life history characteristics. Perhaps certain combinations of life history traits may lead to particular forms of propagation. It may therefore be essential to view reproductive patterns together with growth characteristics in the context of further ecological dimensions in order to decipher any meaningful trends in coral reproduction and life histories.

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Gametogenesis and origin of planulae in the hermatypic coral Pocillopora damicornis

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Abstract

In order to describe the gametogenesis of Pocillopora damicornis and relate this process to the origin of planulae in this monthly planulating species, three colonies were tagged on the reef flat of a fringing reef in Kaneohe Bay, Oahu, Hawaii. Samples were taken every 2 to 3 d during the summer of 1983, and prepared for histological study. Gametogenesis in P. damicornis is similar to that reported for other scleractinians, but differs in the final stages in that no consummation of spermatogenesis takes place. Ovogenesis takes approximately 5 weeks. Larvae develop within 2 weeks. The planulae appear to originate from oocytes by parthenogenesis with eventual production of asexual planulae. The ability of single colonies and single polyps to produce larvae over a period of two consecutive monthly cycles is described.

Introduction

Planulation in corals is well documented (Marshall and Stephenson, 1933; Connell, 1973; Stimson, 1978; Kojis and Quinn, 1981; van Moorsel, 1981; Fadlallah and Pearse, 1982; Fadlallah, 1983) and has been assumed to be the mechanism of sexual reproduction in scleractinians (Hyman, 1940). Very little is known about the transition from gametes to planulae in the corals that brood larvae (Rinkevich and Loya, 1979; Szmant-Froelich et al., 1980; Fadlallah, 1983). Recently, it has been proposed by Stoddart (1983) that the planulae are asexually produced in the widely distributed hermatypic coral Pocillopora damicornis. This hypothesis is supported by electrophoretic evidence of genetic identity between the planulae and the parent colony, raising the question about the possibility of non-sexual origin of the coral larvae. P. damicornis is a very common inhabitant of the reef flats of Kaneohe Bay, Hawaii (Maragos, 1972), with a fairly constant lunar periodicity in planulation throughout the year (Harrigan, 1972; Stimson, 1978; Richmond and Jokiel, 1984). Despite the fact that many people have studied the reproductive and larval biology of this species (Edmondson, 1946; Atoda, 1947; Harrigan, 1972; Stimson, 1978; Jokiel and Guinther, 1978; Richmond, 1981; Stoddart, 1983; Richmond and Jokiel, 1984), the temporal development of gonads remains undocumented. The present study describes the gametogenic cycle of P. damicornis in Hawaiian waters and discusses the relationship between this process and the uncertain origin of the planulae.

Materials and Methods

In order to follow the development of the gonads within the same colony throughout a planulation cycle, three large (>20 cm diameter) and healthy colonies of Pocillopora damicornis type "Y" (Richmond and Jokiel, 1984) were tagged on the reef flat of the Coconut Island fringing reef in Kaneohe Bay, Hawaii. The field collection of samples for histological examination was done every 2 to 3 d during the months of June and July, 1983, following the same procedure used by Rinkevich and Loya (1979), and assuming synchronization in breeding between different branches within the same colony (Harrigan, 1972). The branch tips were immediately fixed in 10% formalin in seawater for 24 h; rinsed in tap water and partially decalcified in a 2% formic acid - 5% formalin solution for 3 to 5 d. Once decalcified, small pieces of tissue were peeled from the middle portion of the branches. This area has the highest proportion of polyps with brooding planulae (Harrigan, 1972; Rinkevich and Loya, 1979). These were prepared for histological sectioning. An Autotechnicon tissue processor was used to dehydrate, clarify and imbed samples in paraplast. Longitudinal and horizontal cross sections of polyps were obtained, sectioned 6 to 8 microns thick and stained with either Mayer's hematoxylin and eosin or Mallory-Heindenhain (Winsor, 1984). Better results were obtained with the former stain.

Since P. damicornis is an hermaphroditic coral (Harrigan, 1972: Grigg and Boucher, unpublished manuscript: Stoddart, personal communication), the gametogenic cycle of male and female gametes was followed in the same 3 tagged colonies. For the qualification of spermary state, an arbitrary system of 5 stages was used, based on a visual assessment of their maturity (Table 1). Female gonads were difficult to separate on an arbitrary basis. Therefore, size was used as a relative index of maturity of oocytes (Giese and Pearse, 1974), and was estimated as the mean value of the maximum diameter of oocytes and the perpendicular diameter of this maximum length. Several polyps per branch for each colony were examined until 10 spermaries and 5 oocytes were measured with a calibrated ocular micrometer. Photomicrographs were taken with a light phase Zeiss microscope.

Table 1. Arbitrary developmental stages of spermaries in Pocillopora damicornis as seen in histological sections of the mesenteries.

Stage No.	Spermary Condition
I	Bulging of spermaries from mesenteries
II	Oval shaped, filled with spermatocytes
III	Beginning of lumen formation
IV	Conspicuous lumen, and bouquet-like arrangements of spermatocytes
V	Presumably in reabsorption

The frequency of oocytes and planulae per polyp was estimated by observing and counting a large number of polyps (>30) from each of several different colonies.

Results

The three colonies showed a similar temporal pattern of development of gonads and planulae (Figs. 1-4). As expected, all 3 showed a simultaneous hermaphroditism; a single polyp has male and female gonads but never on the same mesentery. In general, a mesentery bearing spermaries faced mesenteries bearing ovaries.

The gonads develop from the mesenteries as in other anthozoans (Fadlallah, 1983) and while growing, fill the gastric cavity of the polyp. These polyps often contain twelve fertile mesenteries upon which the gonads are attached by stalks derived from the endoderm. Both male and female gonads are enveloped by two layers of endodermal tissue and mesoglea.

An individual colony planulates at least for two consecutive months (Figs. 1-3) and even though very few polyps of the colony produce planulae at the same time (Harrigan, 1972), most of the mid-branch polyps are fertile (Table 2).

Table 2. Relative distribution of polyps with mature oocytes and/or planulae. Values shown in table are numbers of polyps examined followed by percent frequency in parentheses.

	Number of Planulae per Polyp			
	0	1	2	3
Oocytes	5(9%)	40(70%)	12(21%)	0(0%)
Planulae	5(10%)	29(61%)	12(25%)	2(4%)

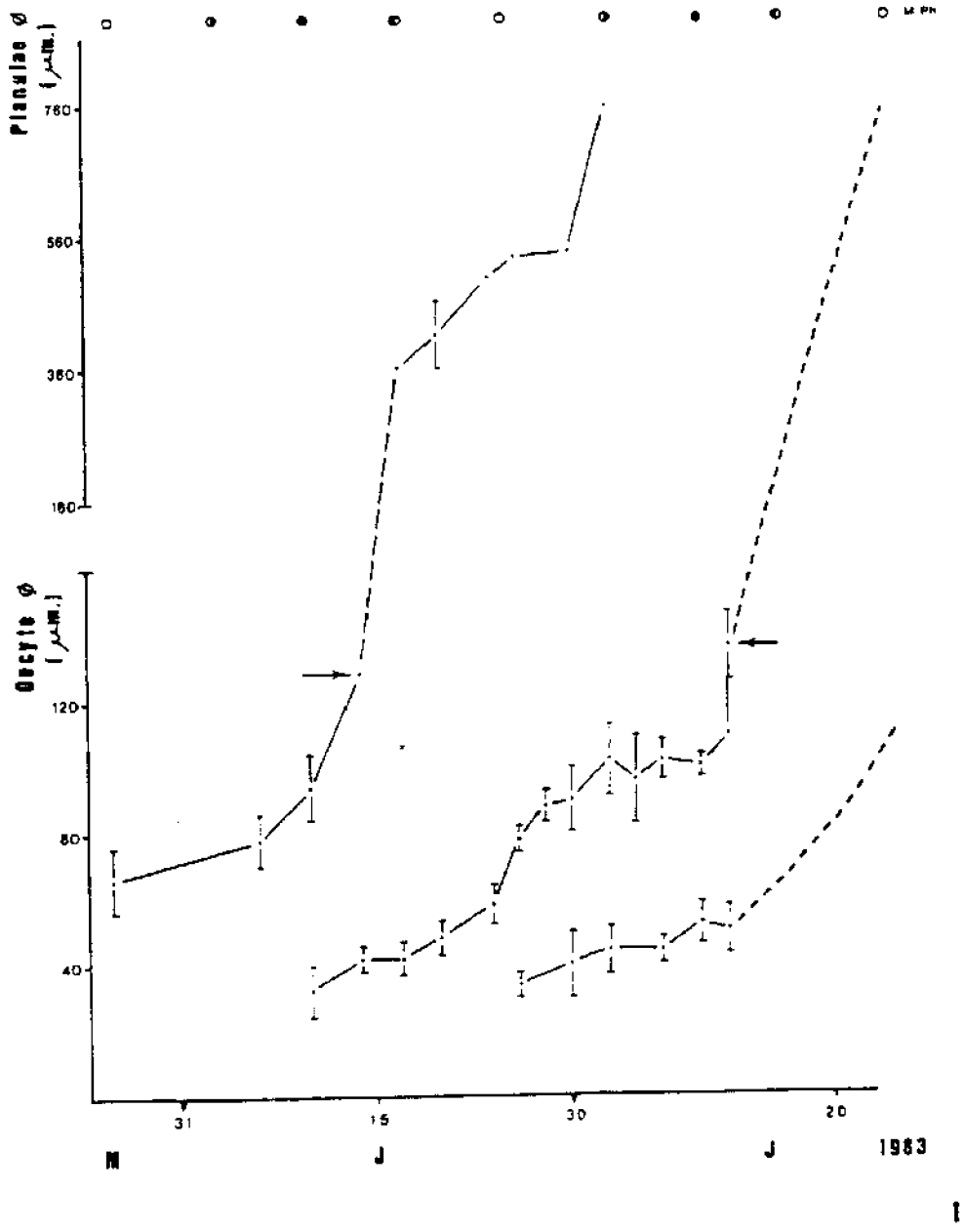

Fig. 1. Oocyte and planula growth in Pocillopora damicornis colony No. 1. Arrows indicate where embryo-like structures began to appear. Bars represent one standard deviation.

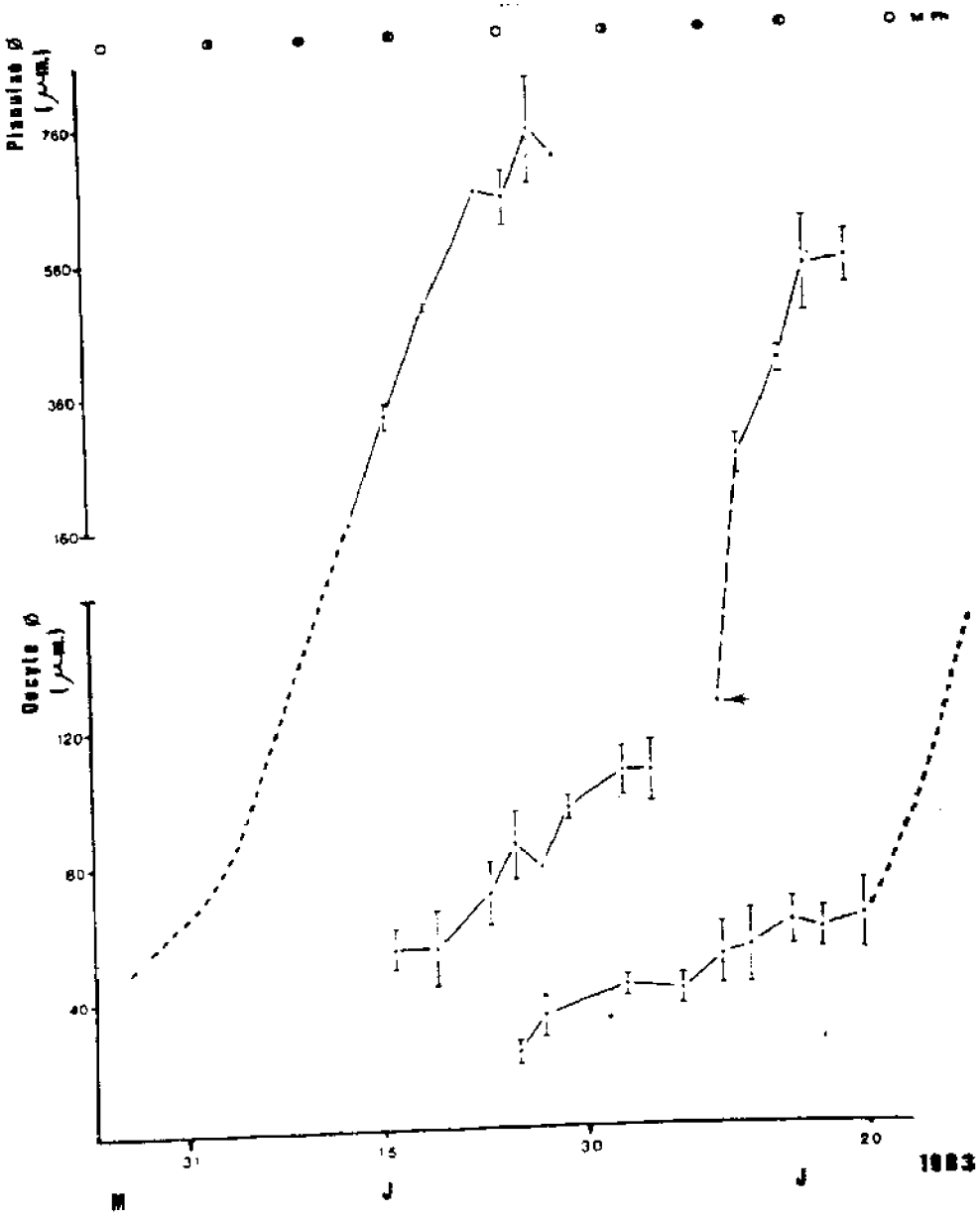

Fig. 2. Oocyte and planula growth in Pocillopora dasicornis colony No. 2. Arrows indicate where embryo-like structures began to appear. Bars represent one standard deviation.

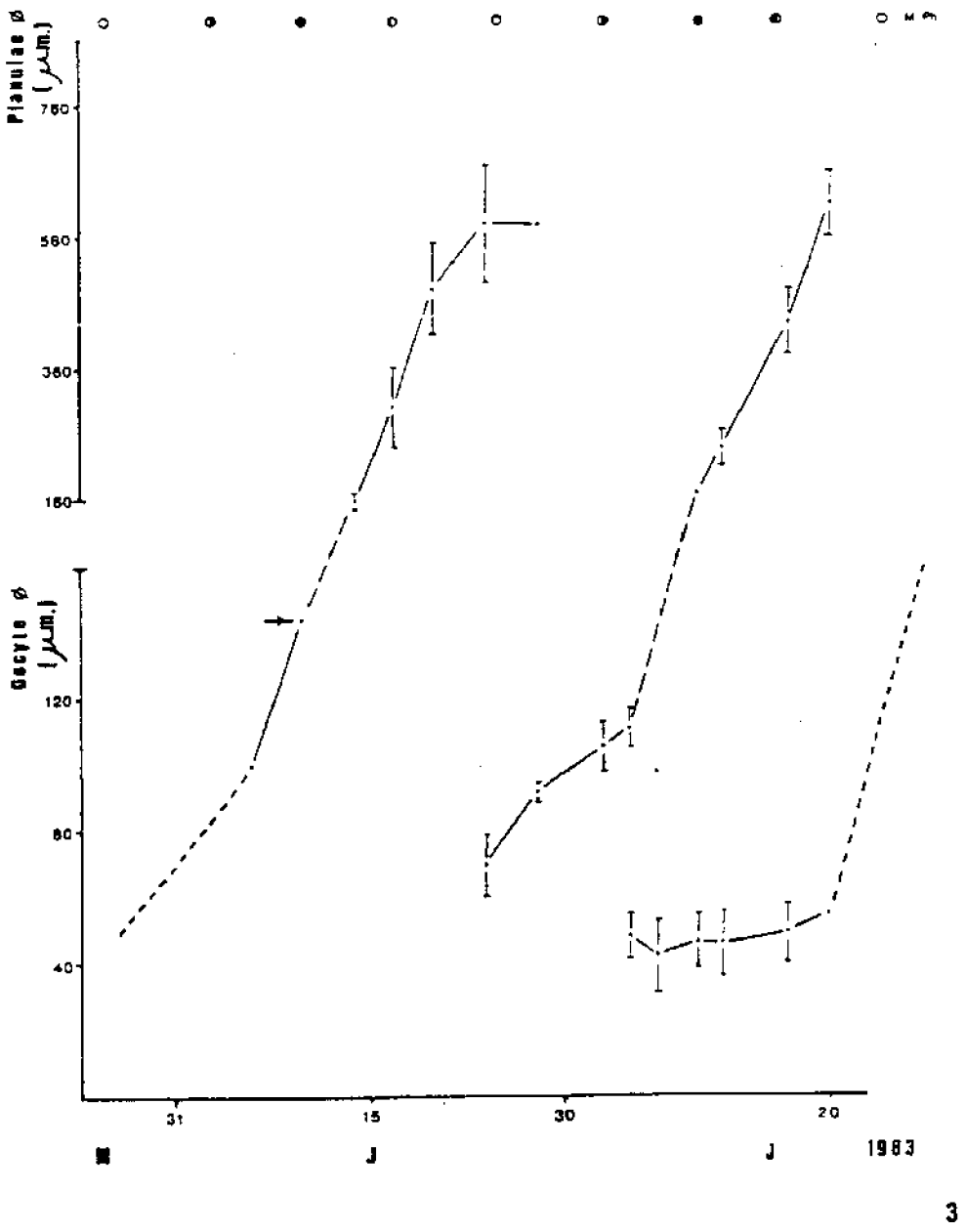

Fig. 3. Oocyte and planula growth in Pocillopora damicornis colony No. 3. Arrows indicate where embryo-like structures began to appear. Bars represent one standard deviation.

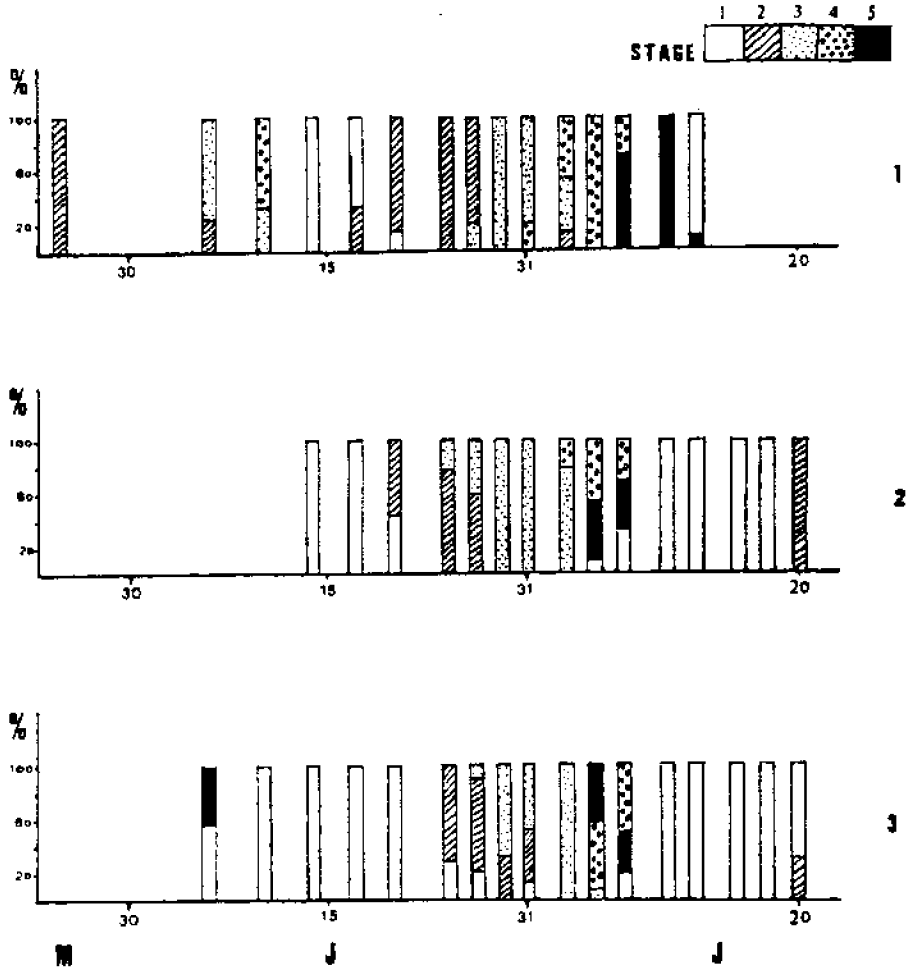

Fig. 4. Percentage of male gonads at arbitrary stages of development (see text) for colonies No. 1, No. 2 and No. 3.

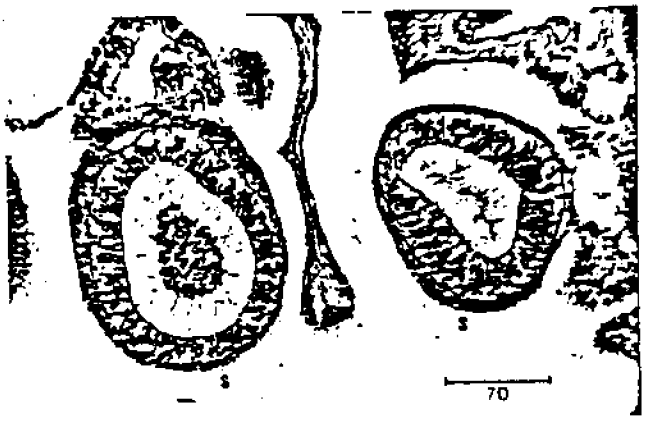

Fig. 5. Resorbtive stage of spermaries. Scale bar in microns.

Fig. 6. Longitudinal section of a polyp with male gonads located in the lower part of the mesenteries. Spermaries at early stages of development. Scale bar in microns.

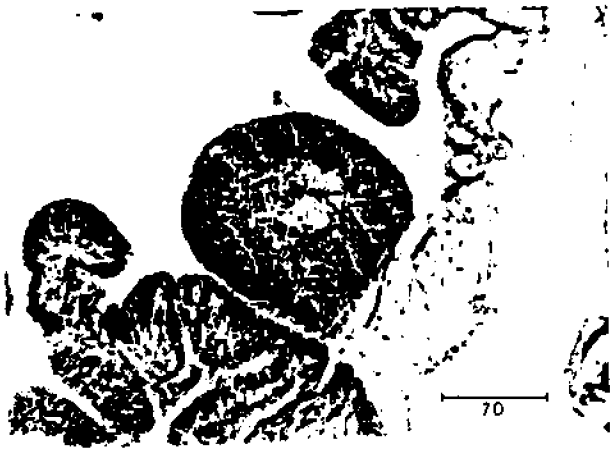

Fig. 7. Spermary starting to develop a lumen. Scale bar in microns.

Fig. 8. Early stages of development of female gonads (o), nucleus (n) and nucleolus (nl). Scale bar in microns.

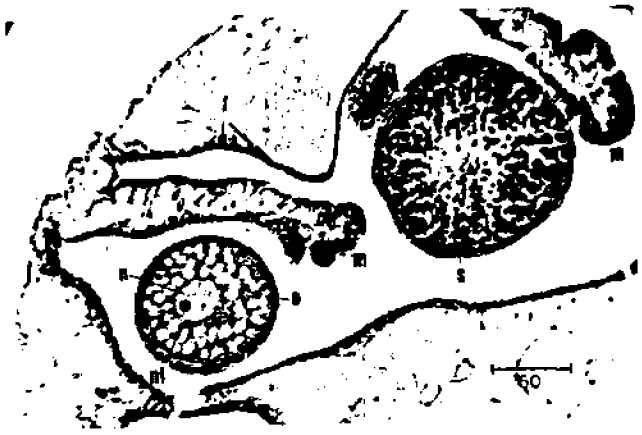

Fig. 9. Two mesenteries (m) of the same polyp, one bearing a spermary (s) and the other an oocyte (o) with prominent nucleus (n) and nucleolus (nl). Scale bar in microns.

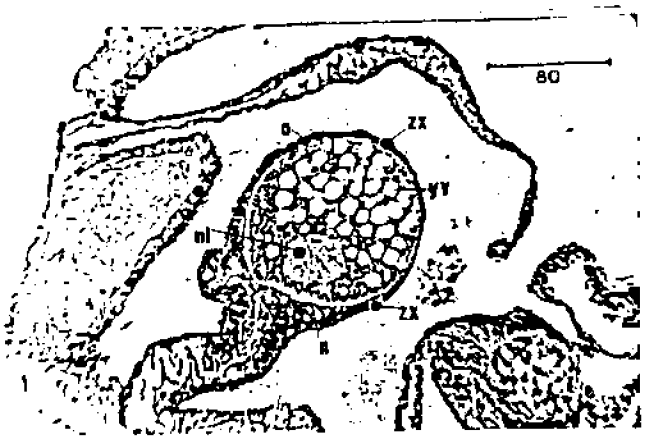

Fig. 10. Mature oocyte with zooxanthella (zx) in the surrounding endoderm. Note the prominent yolk vesicules, nucleus (n) and nucleolus (nl). Scale bar in microns.

Fig. 11. Early stage in the formation of a planulae (p) still attached to the mesentery by a stalk (st). Scale bar in microns.

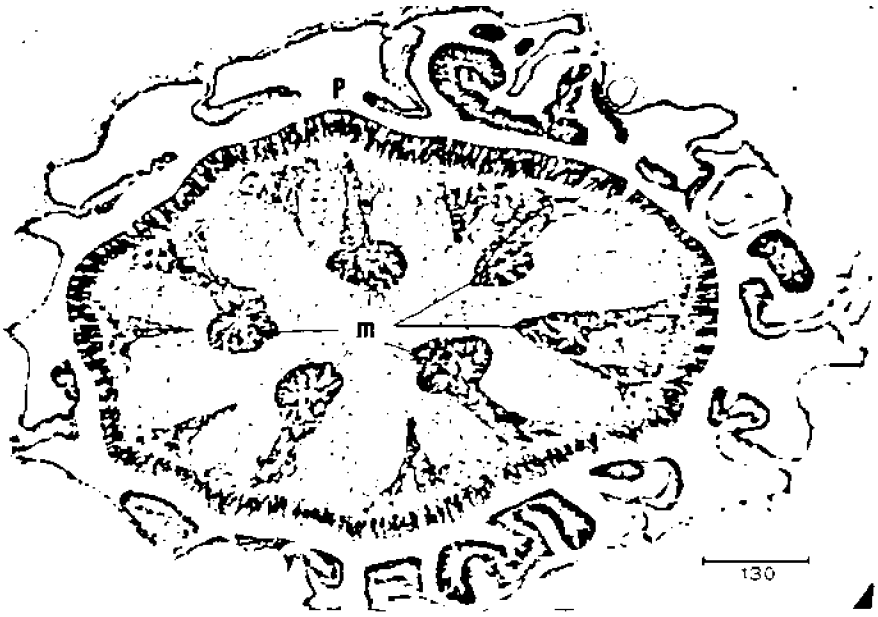

Fig. 12. Transverse section of a polyp completely filled with a mature planula (p) with fully developed mesenteries (m). Scale bar in microns.

The planulae (and ovaries and testes) present in a given colony at any particular time were all at about the same stage of development. This was also observed by Harrigan (1972).

Discussion

The gametogenic cycle of P. damicornis is similar to those reported for other species of anthozoans (Fadlallah, 1983), but differs in the final stages because spermatogenesis is rarely completed and oocytes not commonly fertilized.

If fertilization of female gametes is not the rule, the origin of planulae must be explained by other means for this species. Stoddart (1983) postulated the asexual origin of planulae and gave two possible explanations: formation of larvae occurs independently of gametes, by budding for example, or in relation with female gametes, by parthenogenesis. Results from this study negate the first possibility and support the second. No evidence of budding planulae or similar modes of reproduction were observed in more than one hundred histological sections prepared. On the contrary, several facts support the gametic origin of larvae in P. damicornis. Figs. 1 to 3 clearly show the relation between oocytes and the first appearance of small planulae, without participation of spermatozoa. This could mean that oocytes developed parthenogenetically in planulae. Results from Table 2 also show a clear relationship between oocytes and planulae; the distribution of both in the polyps is similar.

This inferred asexual process has not been previously described. The possible adaptive advantages of this reproductive pattern in a colonizer species of highly perturbed environments are discussed by Stoddart (1983). He also mentions that genetic variability between adjacent populations is not expected in obligately asexual organisms. The eventual observation of mature sperm enables possible self or cross fertilization, assuring genetic recombination during the infrequent production of sexual planulae.

Even though it is well known that the population of P. damicornis of Kaneohe Bay planulates in a lunar cycle throughout the year (Harrigan, 1972; Stimson, 1978; Richmond and Jokiel, 1984), it is not clear if a single colony could planulate every month. From this study it is apparent that the same colony could produce planulae at least for two consecutive months, and also suggests that a single polyp has this capability because of the coexistence of planulae and female gametes in the same polyp.

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Preliminary observations on the abundance and distribution of planktonic coral larvae in Kaneohe Bay, Oahu, Hawaii.

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Abstract

Little quantitative information is available concerning the abundance and distribution of coral planulae following their release from parent colonies. A plankton sampling technique was designed for the capture of coral planulae. It was based on surface tows using a small, fine-mesh net. More than 250 tows were made along five transects established near the southeast fringing reef of Coconut Island. Time between collection and sorting was minimized and low temperature storage was employed in lieu of chemical fixatives to prevent decomposition of the planulae prior to identification.

More than 100,000 cnidarian larvae, most of which were scleractinian planulae, were collected and sorted. Twelve different types of cnidarian larvae were differentiated. Two appear to be the zoanthina larvae of the zoanthids Palythoa vestitus and Zoanthus pacificus. Six were identified as the planulae of the corals Pocillopora damicornis, Porites compressa, Montipora verrucosa, M. dilitata, Cyphastrea ocellina and Fungia scutaria. Peak recovery of planulae generally occurred 3 - 7 days after the onset of spawning or planulation. Limited data on the vertical distribution of 3 species of coral planulae indicate that they may undertake a diurnal migration similar to that of other demersal plankton. The potential for the export of large numbers of coral planulae from Kaneohe Bay is considered high, but whether this export is significant to recruitment on reefs outside the bay remains to be seen.

Introduction

An increasing amount of work has focused on the subject of coral reproduction and recruitment. These studies have documented the timing and mode of reproduction, the recruitment of juveniles on artificial and natural substrates and the behavior of coral planulae in the laboratory (see citations in chapter introduction). Recent attention has shifted to the question of planula dispersal. The calorimetric work of Richmond (1981) has demonstrated that the century old assumption that coral planulae are capable of dispersing over long distances is at least energetically justified in certain species. Despite these advances, and the enticing biogeographic possibilities they suggest, little effort has been made to measure the abundance and distribution of coral planulae in the field.

Plankton sampling with nets first came into vogue in the early 1800's (Fraser, 1979). Since then dozens of reports have been published concerning tropical plankton in the open ocean and near shore (Table 1). However, not many have recorded larval cnidarians (Rickstead, 1965). Although several of these studies were devoted to a description of the zooplankton found living near coral reefs, surprisingly few have reported coral planulae.

Vaughan (1910) claimed that "Madreporarian planulae" were frequently obtained in the plankton tows off the Dry Tortugas, but provided no supporting data. In contrast, nearly every researcher since then who has tried to obtain coral planulae using nets has remarked on their scarcity.

The most recent concerted effort to net coral planulae appears to be that of Yamaguchi (1972) who searched through 60 plankton hauls made in Palau and recovered only a single specimen. He wrote, "The paucity of coral planulae in the plankton samples has been recorded by previous workers who tried to find them. The present survey agrees well with those results." Perhaps more surprising is the complete lack of planulae caught by the specialized demersal plankton traps of Porter and Porter (1977), Porter et al., (1977), Alldredge and King (1977), Birkeland and Smalley (1981) and Walter et al., (1981). These traps were placed directly over the reef substrate. In contrast, Kitalong (this volume) reports that hundreds of coral planulae were routinely caught in her demersal traps.

Table 1. Selected tropical plankton studies. This list includes tropical plankton studies in which cnidarian larvae might have been recovered given the sampling methods employed. Note that cnidarian larvae have rarely been reported, and coral planulae only 7 times. CP = coral planulae, CL = cnidarian larvae.

Study	Location	Larvae reported
Balachandran (1973)	Indian Ocean	CL
Birkeland et al. (1976	Palau Islands	
Bogorov (1967)	Pacific	
Chacko (1950	India	
Clayshulte et al. (1978)	Truk Islands	
Clutter (1973)	Hawaii (Kaneohe Bay)	CP
Edmondson (1929)	Hawaii	
Emery (1968)	Florida	
George (1953)	India	
Gilmartin (1958)	Enewetak	CL
Glynn (1973)	Caribbean	CL
Harrigan (1972)	Hawaii (Kaneohe Bay)	CP
Hirota and Szyper (1976)	Hawaii (Kaneohe Bay)	
Hobson and Chess (1978)	Enewetak	
Johnson (1954)	Marshall Islands	
Kawaguti (1940)	Palau Islands	CP
King and Demond (1953)	Central Pacific	
Lassuy (1978)	Yap Islands	
Le Borgne (1977)	Atlantic	
Moore (1949)	Bermuda	
Moryakova and Rampos (1966)	Cuba	
Odum and Odum (1955)	Enewetak	
Peterson (1975)	Hawaii (Kaneohe Bay)	
Pikyakarnchana (1975)	Hawaii (Kaneohe Bay)	
Qing-chao (1980)	Hong Kong	CL
Riley (1938)	Caribbean	
Russell and Colman (1934)	Gr. Barrier Reef	CP
Sale et al. (1976)	Gr. Barrier Reef	
Santhakumari and Saraswathy (1981)	India	
Smith et al. (1950)	Florida	
Stephenson (1931)	Gr. Barrier Reef	CP
Suarez-Caabro et al. (1965)	Mexico	
Tranter and George (1969)	Laccadive Islands	
Vaughan (1910)	Dry Tortugas	CP
Wickstead (1958)	Singapore	
Wickstead (1961)	Kenya	
Win (1977)	Burma	CL
Woodmansee (1958)	Florida	
Yamaguchi (1972)	Palau Islands	CP
Yamazi (1952)	Kyushu, Japan	
Ziemann (1970)	Hawaii (Kaneohe Bay)	

Information gathered during the present study points to numerous technical and biological factors which may account for the low catches of coral planulae previously reported. This reconciles the low reported catch rate with the high fecundity of corals measured in the laboratory (Stimson, 1978).

The purpose of the present paper is to identify and quantify species of coral planulae found near coral reefs in Hawaii. Information on the residence time of planulae in the plankton after release, and their horizontal distribution near the surface is also presented. To the writer's knowledge, no previous quantitative work has been attempted in this area.

Materials and Methods

Plankton Tows

In many cases the number of planulae per m^3 was very low. In order to avoid the use of small fractions of planulae, all values in this study will be normalized to 100 m^3 of seawater filtered.

The primary study area was located at the southeast fringing reef of Coconut Island, Kaneohe Bay, Oahu, Hawaii (Fig. 1). This portion of reef was chosen because of the abundance of Pocillopora damicornis colonies. This species is known to produce abundant planulae following a lunar cycle (Richmond and Jokiel, 1984).

Three plankton tow transects were initially established parallel to the reef front. The reef flat transect (No. 1) was located between the zone of active coral growth on the outer reef flat and the sandy inner reef flat. This clear ecological demarkation line is generally 10 m from the seaward reef edge. Transect No. 2 was located directly along the seaward reef edge. Transect No. 3 was established 10 m seaward of the reef front and parallel to it. Transect No. 4 was not established until halfway into the study period. It ran parallel to transects 1, 2 and 3, 20 m seaward of the reef front. Transect No. 5 was located in an outflow channel of the Kaneohe Bay southeast basin, several hundred meters northwest of the main study area. The beginning and end points of the transects were marked relative to pilings along the reef edge. Due to the curvature of the reef, the outer two transects (No. 3 and No. 4) were slightly longer than the 220 m long seaward reef edge transect (No. 2). Plankton samples were occasionally taken in various other locales within and outside the bay.

All plankton tows were made using a 30 cm diameter, 104 micron mesh nylon net fitted with a TSK flow meter. To enable sampling over the reef flat, the net's mouth-ring was suspended beneath a flat (35 x 30 x 5 cm), styrofoam float. The net was fastened below the float so that the top of the mouth was at the level of the water surface. A smaller float was tied to the cod end to prevent the net from dragging across the bottom. Plankton tows could be taken over the reef flat whenever the water depth exceeded about 35 cm. To maintain continuity of the sampling regime, all plankton tows were carried out with the floats in place. In this way, only the top 30 cm of water was filtered by the net.

The net was towed behind a skiff at an average speed of 2 to 3 knots for all tows except those taken when there was insufficient water over the reef flat. At these times the net was towed by hand while walking over the reef flat along the transect. Separate calibrations were made for the TSK meter at the boat tow and the walking speeds. A sample run consisted of one pass along a given transect. This would usually take 3 to 4 minutes and filtered an average of 17.5 m^3 of water. At the end of a sample run the net was washed down and the plankton collected in a 6 ounce (177 ml) cod end bottle. Clogging was occasionally apparent during test runs therefore the net was handwashed in seawater after each tow.

Generally, sampling was carried out every other day between 22 June through 1 August. An exception was the seaward 20 m transect which was not established and sampled until mid-July. During June, sampling was carried out primarily just after low tides, because preliminary results of a related study (Holloran, this volume) indicated that the diurnal rhythm of Pocillopora damicornis planulation showed a peak abundance during low tide. After June, samples were taken at a variety of times and tidal stages.

One 24 h and one 12 h contiguous sample series were also carried out. For the 24 h series (29 - 30 June), 4 sample runs were taken every 4 h along the

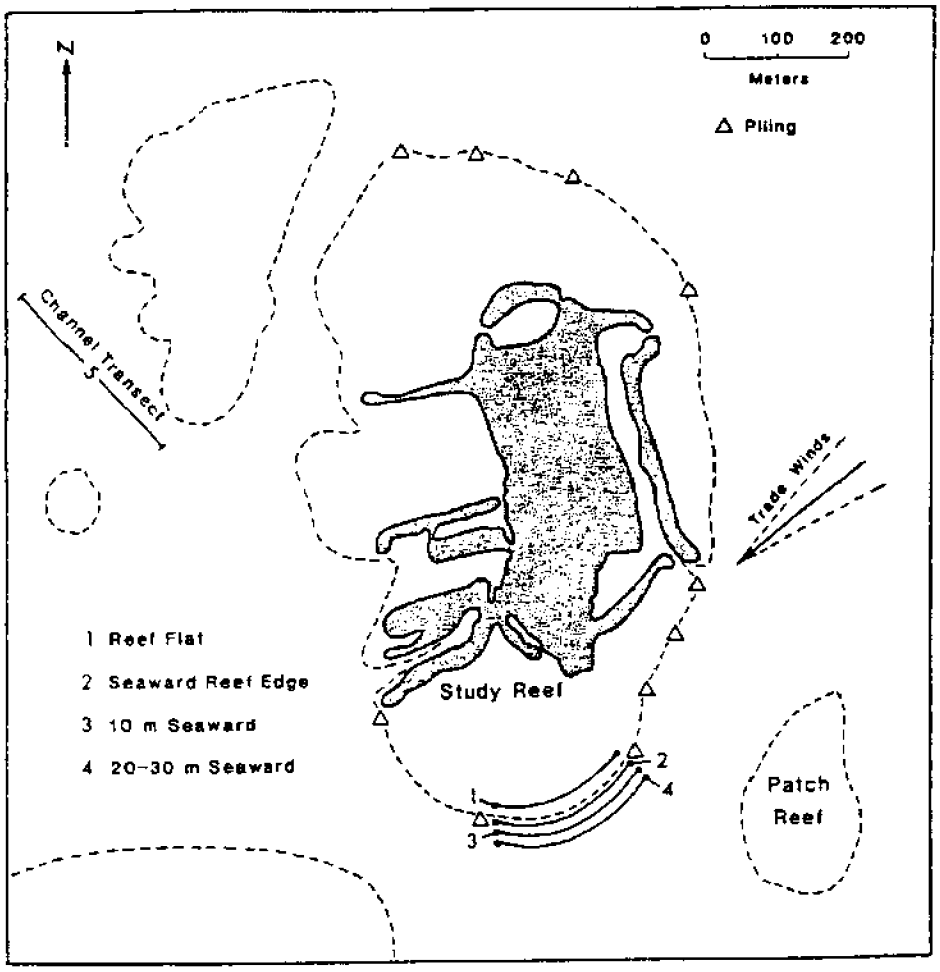

Fig. 1. Map of study reef off Coconut Island with the 5 plankton sampling transects.

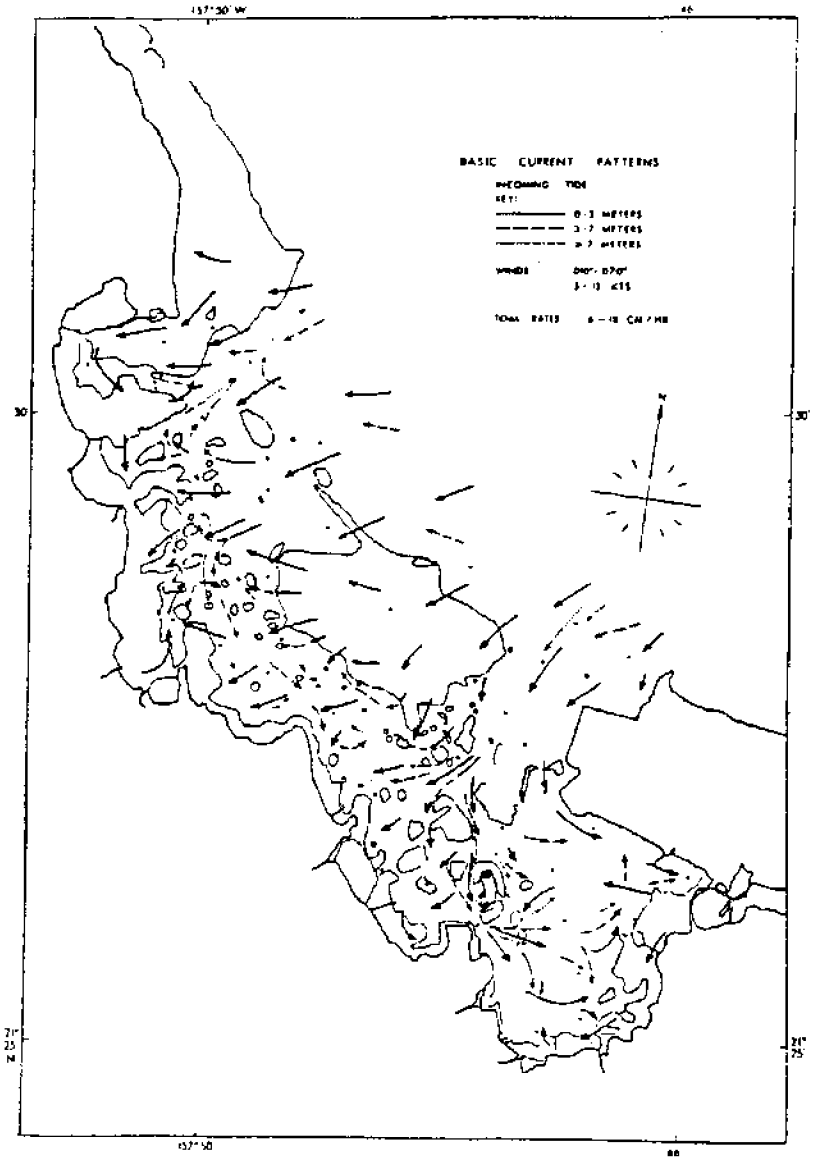

Fig. 2. Basic current patterns in Kaneohe Bay, incoming tide (from Bathen, 1968).

seaward reef edge transect. The sampling regime of the 12 h series entailed 3 double sample runs (up and back) along the seaward reef edge every 2 h from noon to midnight (29 July). The 24 h study was designed to clarify the diurnal pattern of abundance of P. damicornis planulae, whereas the purpose of the 12 h study was mainly to estimate sampling error, making use of the great abundance of Porites compressa planulae present at that time.

Two short experiments were conducted in order to describe the vertical distribution of planulae in the water column. For the first test a hand-operated, 3 l min^{-1} bilge pump (Edson Corporation, Diaphragm pump model 117a) was used to sample the plankton abundance at two depths: 10 cm and 200 cm below the surface. Both samples were taken at one location 3 to 4 m seaward of the central, study reef edge, between 1200 h and 1300 h on 30 July. Each sample was obtained by pumping 1.74 m^3 from the specified depth via a hose into the plankton net used for the plankton tows.

The second test of the vertical distribution of planulae was performed using the previously described plankton net with the floats removed. Four hauls were taken along the transect 10 m seaward, at 3 depths; surface, 1 m, and 5 to 6 m. The water depth at this location is approximately 13 m. This test was performed between 1500 h and 1600 h on 4 Aug. The water transparency on the day of the test was such that the net disappeared from view below a measured 5 m depth. To accomplish the 5 to 6 m depth tow, the net was maintained at the level where it was just visible by adjusting the tow speed and towline length.

On three occasions, the sea was calm enough to allow plankton tows to be made outside the "barrier" reef of Kaneohe Bay using a skiff. These surface tows were made within 100 m of the seaward reef front and parallel to it.

Processing Samples

In the field, all plankton samples were decanted from the cod end bottle into 279 ml glass bottles and stored in a 20 l insulated plastic container. The samples were cooled with seawater and ice chips. All samples were counted with the aid of a dissecting microscope within 3 h of collection. No formalin or other fixatives were added. All planulae were counted individually in a sorting dish and removed for settling experiments unless their abundance was greater than 200. In this case, subsampling was carried out for the abundant species, with the less abundant species counted individually from the total sample.

Results

Weather and Water Circulation

During the study period the water temperature off the reef edge was 26.4 °C (±0.5 °C). The normal northeast tradewinds for this period blew at an average velocity of 9.7±5.9 mph. The average direction was from 50° east of north with a range of 10° (National Weather Service). The strength of the wind has a profound effect upon the water circulation in the bay as noted by Bathen (1968). This effect is especially marked in shallow areas such as the reef flats. There the wind can create strong currents which may run in opposite directions to the tidal currents.

Although the general water circulation patterns in Kaneohe Bay have been characterized by Bathen (1968), additional drogue and fluoroscene dye release experiments were performed to provide a more detailed picture of the water circulation around Coconut Island, and especially the study reef. Figs. 2 and 3 show the general circulation patterns in the bay as determined by Bathen (1968). Figs. 4 and 5 provide the more detailed results of the present study. A 10 mph wind generated a current over the study reef along the reef flat transect (No 1) ranging between 7 and 10 cm sec^{-1} when the water depth was 70 cm. It is important to note the presence of a gyre near the south end of the study reef which exists during an incoming tide (Fig. 4). Another significant feature of the local circulation is that during an outgoing tide, dye and drogues released at the surface near the north end of the patch-reef located just over 100 m east of the study reef, were swept directly onto the study reef within 1 to 2 h (Fig. 5). They crossed the study reef within 2.5 h and were then swept into the outflow channel south of the island. Kaneohe Bay has a modified semi-diurnal tidal cycle which had a range of 1 m during the study period.

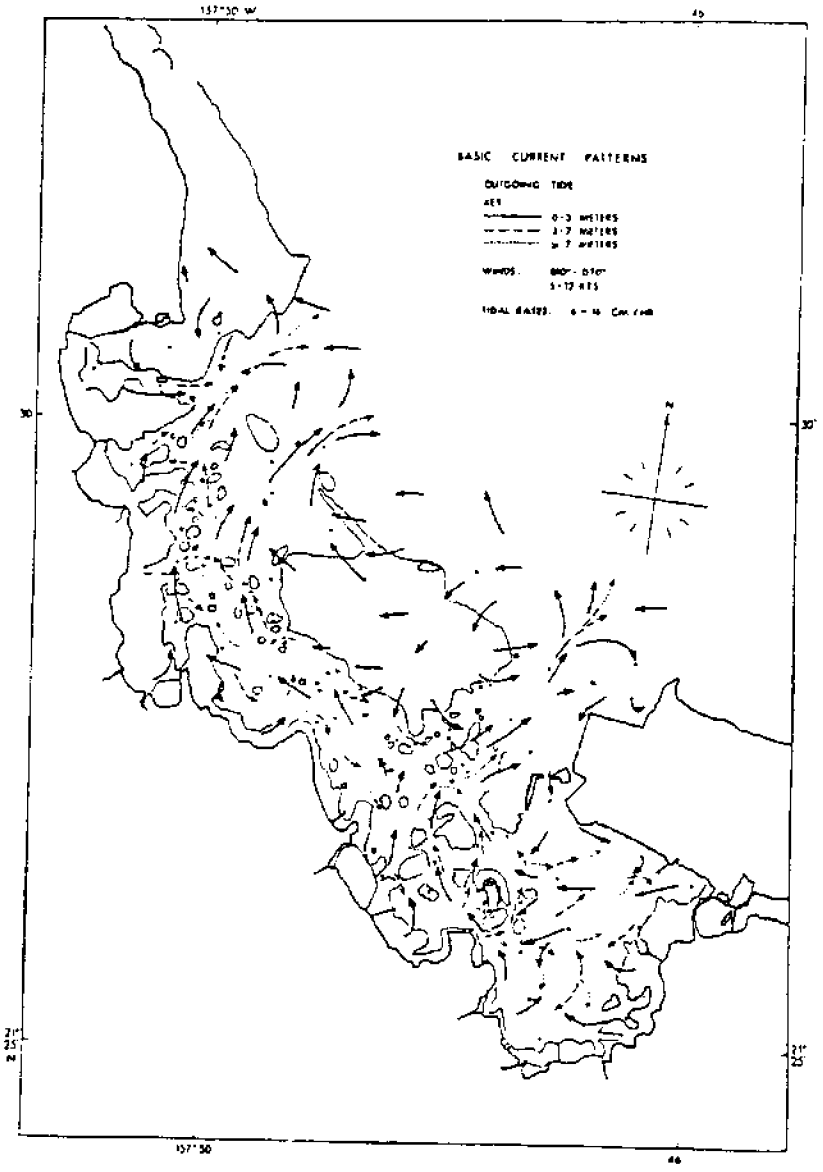

Fig. 3. Basic current patterns in Kaneohe Bay, outgoing tide (from Bathen, 1968).

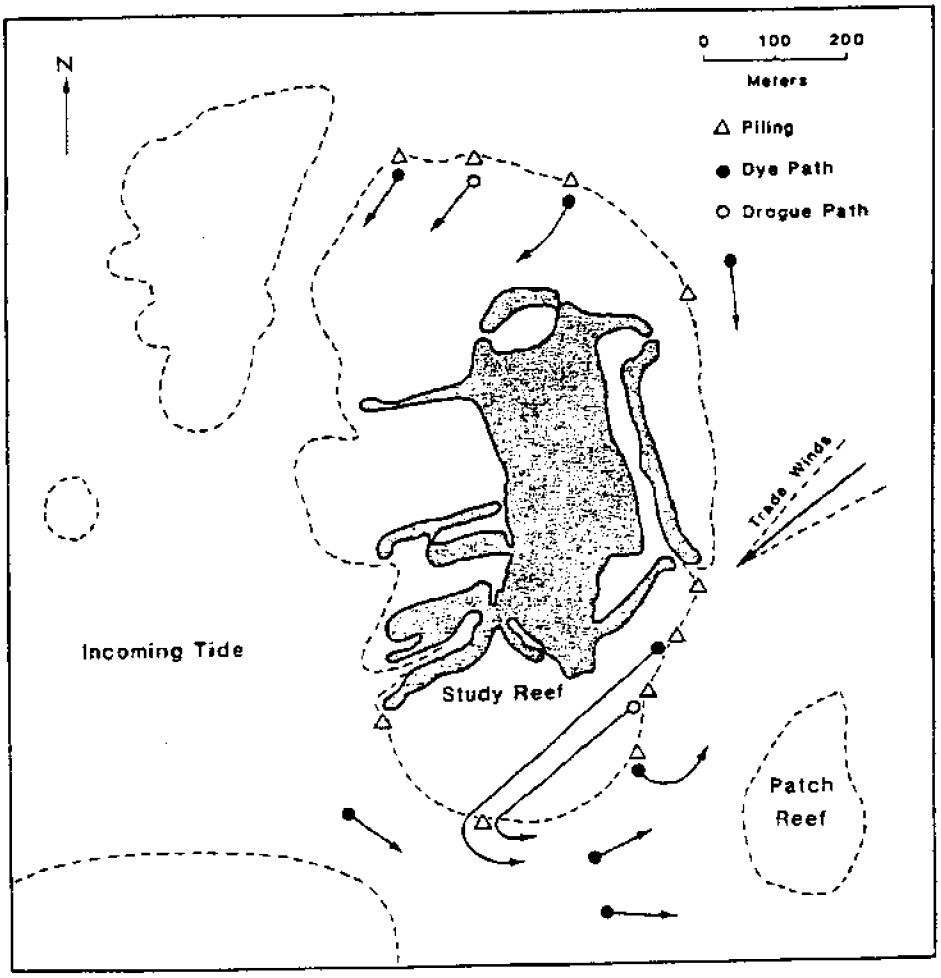

Fig. 4. Current patterns near study reef, incoming tide

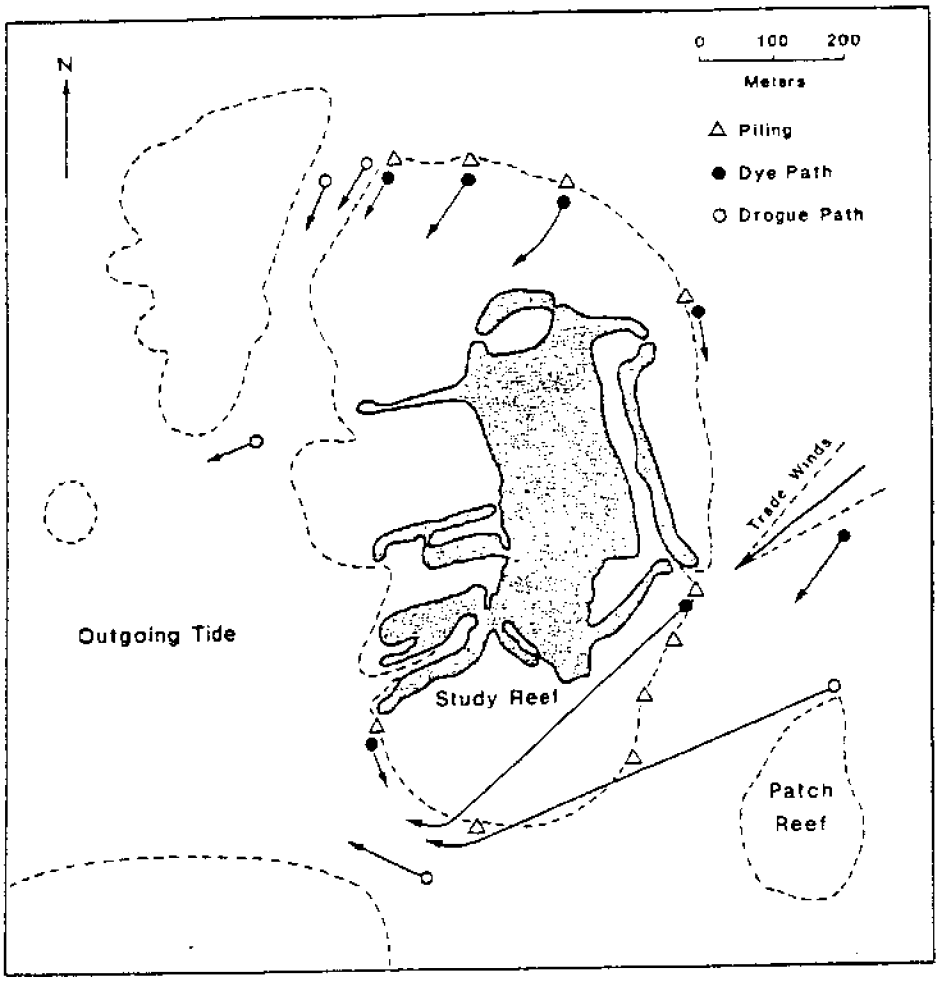

Fig. 5. Current patterns near study reef, outgoing tide

Types and Abundance of Planulae

Well over 100,000 cnidarian planulae were collected and counted over the course of the study; the majority of these were scleractinian planulae. Twelve types of larvae were differentiated, of which two were tentatively identified as Zoanthids and six were positively identified to the species level as coral planulae. The six were: Pocillopora damicornis, Porites compressa, Montipora verrucosa, Cyphastrea ocellina, and Fungia scutaria. These identifications were confirmed via laboratory settling experiments. The remaining types of planulae remain unidentified.

The planula larvae of P. damicornis have been described in detail by Barrigan (1972) and Vandermeulen (1974). The average daily number of P. damicornis planulae collected per 3 tows along each transect is plotted in Fig. 6. Although the planulae of P. damicornis, Type B (Richmond and Jokiel, 1984) may be smaller on the average than those of Type Y, there is no way to positively assign a given individual planula taken in a plankton tow to its proper type because of the large overlap in their size ranges. Therefore all P. damicornis planulae are lumped into one group for the present analysis. The major peak in the catch occurred between 27 June and 29 June, reaching over 100 planulae per 100 m^3. There were 3 smaller peaks around 23 June, 6 July and 18 July, with the last peak subsiding slowly through 4 August when the study ended.

Porites compressa colonies were observed spawning eggs in the field and in the laboratory at approximately two week intervals (at new and full moon) beginning on 26 June. The water surface of the channel at the south end of Coconut Island (Fig. 1) was covered with beige Porites compressa eggs and planulae during each one to two day spawning period. A sample of 10 P. compressa planulae (age 2 days) had the average dimensions 278 ± 25 microns x 227 ± 27 microns (Fig. 7).

The average daily catch of P. compressa planulae per 3 tows along each transect is plotted in Fig. 8 using the natural logarithm of the quantity n+1; where n=average catch. There are 3 main peaks of abundance at about 2 week intervals. At peak abundance, the number of P. compressa planulae recovered reached 1000 per 100 m^3.

Montipora verrucosa colonies spawned the majority of their egg - sperm packets in the laboratory and in the field between July 10 and 12 (full moon) at approximately 2100 h (Fig. 9a). Small numbers of remaining egg - sperm packets were released on the following 3 nights. A complete description of the spawning of this species is given by Heyward (this volume). Egg - sperm packets, eggs and later planulae, were collected in the plankton tows between 10 July and 22 July, with a peak on 16 July which reached 16,000 planulae per 100 m^3. The natural logarithm of the quantity n+1; where n=average catch, is plotted in Fig. 10.

Montipora dilitata colonies were observed to begin spawning in the laboratory and in the field on 26 July. Eggs and planulae were subsequently recovered in numbers reaching 100 planulae per 100 m^3 on the final two days of the study, 1 Aug and 4 Aug (Fig. 10).

The distinct planulae of Cyphastrea ocellina, originally described by Edmondson (1929), were caught sporadically from all transects throughout the study period (Table 2). A maximum of 6 planulae per 100 m^3 was recovered: too few to detect any peaks in abundance during the study.

The planulae of Fungia scutaria are small (90 - 120 microns), but can usually be distinguished by their unique, rapid swimming pattern described by Krupp (1983). Fungia larvae were sporadically taken from all transects just after their June spawning and prior to their next spawning in July, as assessed by observations of colonies held in the laboratory. Because of their small size, it is reasonable to assume that most Fungia scutaria larvae slipped through the 104 micron mesh net.

A number of specialized, fast moving planulae which appear to belong to the sea anemone Cerianthus sp. were caught sporadically from all transects except the channel (Table 2). These distinct larvae have been described by Carlgren (1906). The present types ranged in color from tan to brilliant orange, usually with a darker band around their white, oral end (Fig. 11). Their entire surface

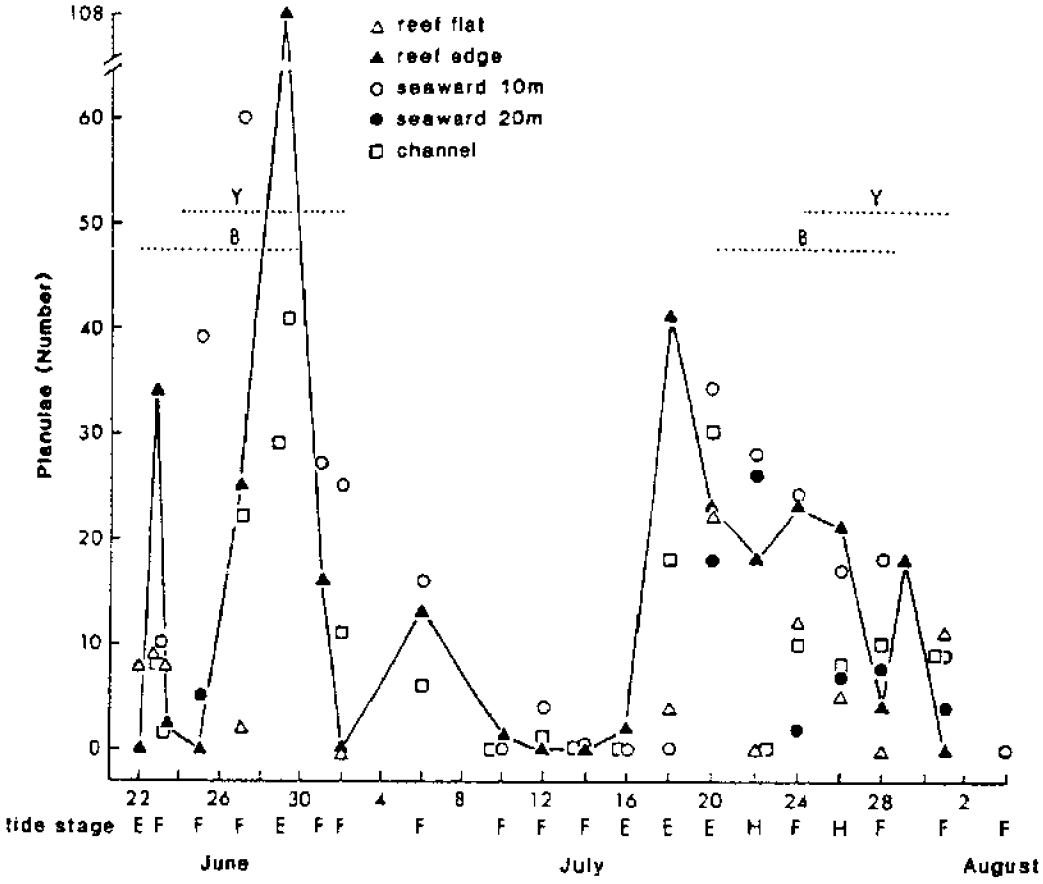

Fig. 6. Average number of P. damicornis planulae collected per 100 m³

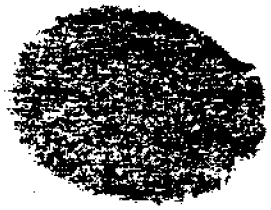

Fig. 7. Three to 4 day old P. compressa planula (fixed)

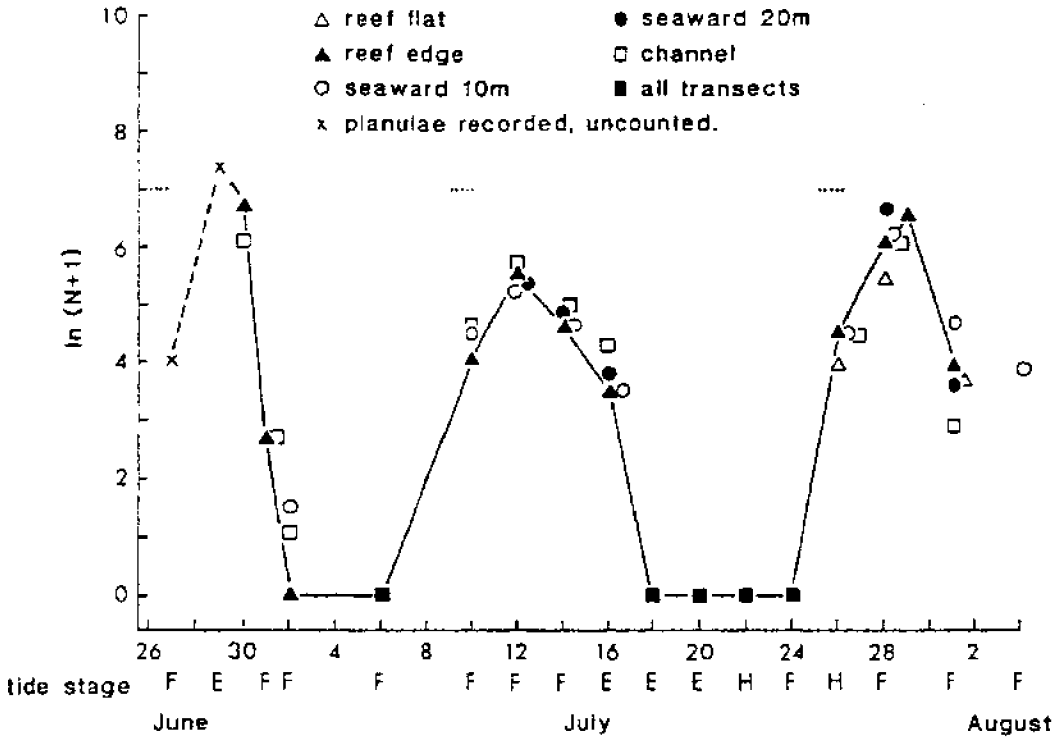

Fig. 8. Average number of P. compressa planulae collected per 100 m³

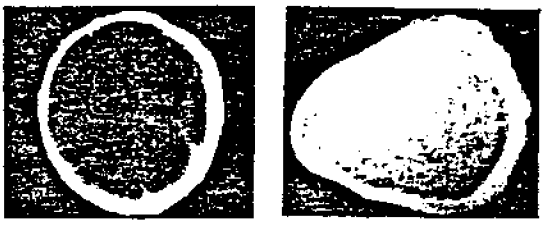

Fig. 9. Montipora verrucosa: A) freshly spawned egg-sperm packet (backlit). Sperm is contained in the center of the ball. Maternally derived zooxanthellae appear as dark specks within each egg. Packets break up into individual eggs within 0.5 h after they are spawned. Diameter = 1300 microns. B) Planula (3 d old, fixed). In life, shape is more elongate. Size = 330 X 260 microns.

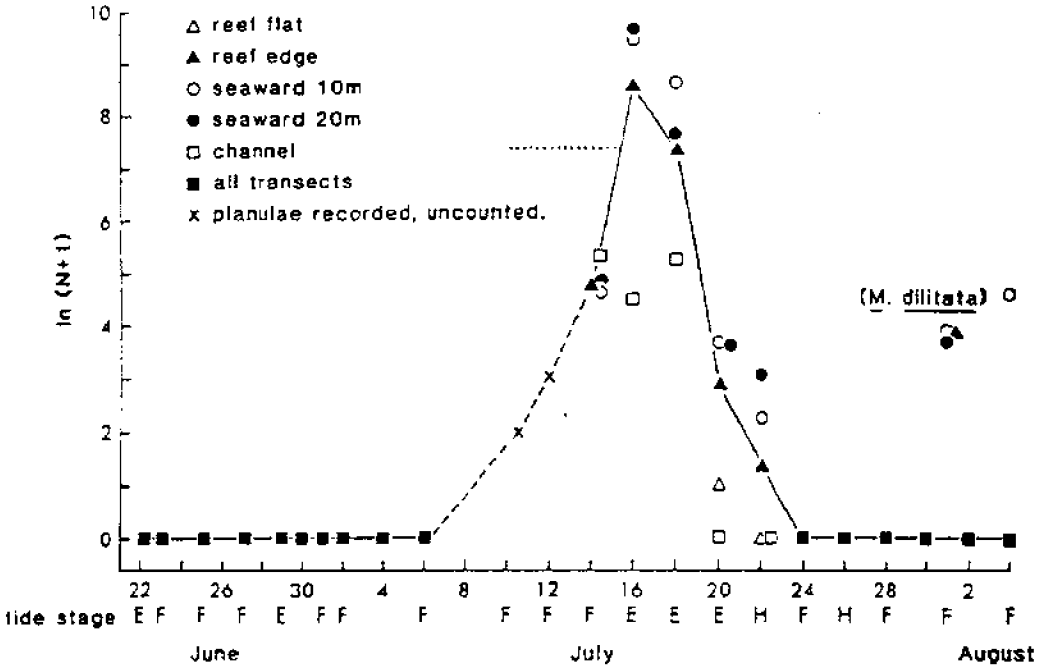

Fig. 10. Average number of M. verrucosa planulae collected per 100 m^3.

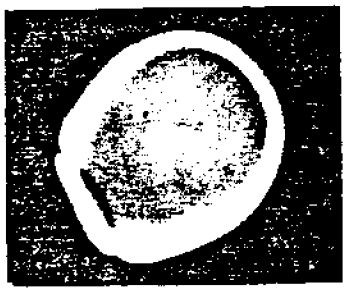

Fig. 11. Swimming Cerianthus sp. larva (lateral view)

except the flattened oral end is covered with slightly longer cilia which propel them through the water at 5 to 8 mm sec^{-1}, faster than most of the other planulae observed. Since settling experiments with these larvae failed, their identity has not been confirmed. In fact, it is pertinent to note that Kawaguti's (1941) description and figure of the planulae of Euphyllia glabrescens, an Indo-Pacific coral not found in Hawaii, resembles the present Cerianthus-like planulae in all respects except size. With a diameter of 0.7 mm, the Euphyllia planulae are about double the size of those recovered from Kaneohe Bay.

Table 2. Abundance of C. ocellina, F. scutaria and Cerianthus sp. larvae. Each number is the combined total from 3 tows along the specified transect. A blank indicates no larvae recovered. Reef, 10 m, 20 m, Channel indicate areas sampled moving seaward (deeper) from reef edge to channel. Ce = Cerianthus sp., Cy = Cyphastrea ocellina, Fu = Fungia scutaria

Date	Reef Flat	Reef Edge	Seaward 10 m	Seaward 20 m	Channel
6-22					
6-25	10Ce				
6-29		5Fu			
7-06		2Ce			
7-10	1Ce			1Cy	
7-14			6Ce	2Ce	
7-18	2Cy			2Cy	
7-20	2Fu			2Fu	2Fu
7-22		3Fu	4Cy		
7-24	2Cy	2Cy,Ce	3Fu		
7-26		2Ce			
7-28	2Cy,4Ce	2Ce			
7-29		1Cy			

Two types of what appear to be the larvae of zoanthids were obtained from tows along all transects in large numbers. These unique larvae correspond to the "zoanthina" type discovered by Semper (1867) and described in detail by Van Beneden (1890, 1898), Conklin (1908) and Cary (1911). They are essentially piriform, but have a latitudinal constriction located between their equator and oral end (Fig. 12). Emanating from this circular groove is a ring of long (100 micron) cilia which beat with a jerky motion in an anterior - posterior direction. The remainder of the larval surface is covered with the normal, short (20 micron) cilia found on most planulae. Type 1 Semper's larvae are colored greenish - brown by the numerous zooxanthellae they contain. As they grow larger, they become more darkly colored. Semper's larvae Type 2 are longer, thinner and a lighter shade of brown without the greenish tint.

Type 1 Semper's larvae were caught consistantly throughout the study period but showed abundance peaks around 6 July (400 planulae per 100 m^3) (Figure 13). Unfortunately none of the larvae of either Type 1 or 2 were induced to settle in the laboratory. But because of their abundance, these larvae are assumed to be derived from Palythoa vestitus and Zoanthus pacificus, the two most common zoanthids in the bay. Spawning of these species has not yet been observed directly (Cooke, 1983).

An unidentified cnidarian planula was quite abundant in July with a peak just prior to the full moon, of about 200 planulae per 100 m^3. These planulae are small (220 x 340 micron), rod-shaped and transparent except for a bright red - orange center at the oral end (Fig. 14). Unfortunately none of these larvae were induced to metamorphose in the laboratory, although several settled temporarily. Because of their abundance, it is suspected that they may be the larvae of one of the common sea anemones, e.g. Anthopleura nigrescens (Dunn, 1974).

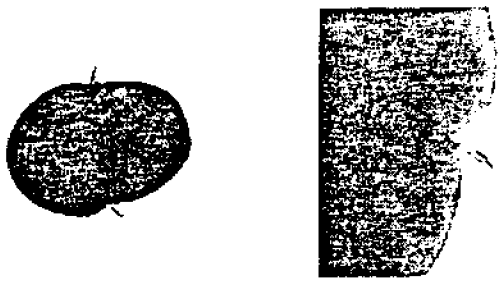

Fig. 12. Type 1 Semper's larva (fixed)
a. Lateral view, oral end to right
b. Silhouette of same
c. Circular groove and long cilia
d. High magnification of long cilia

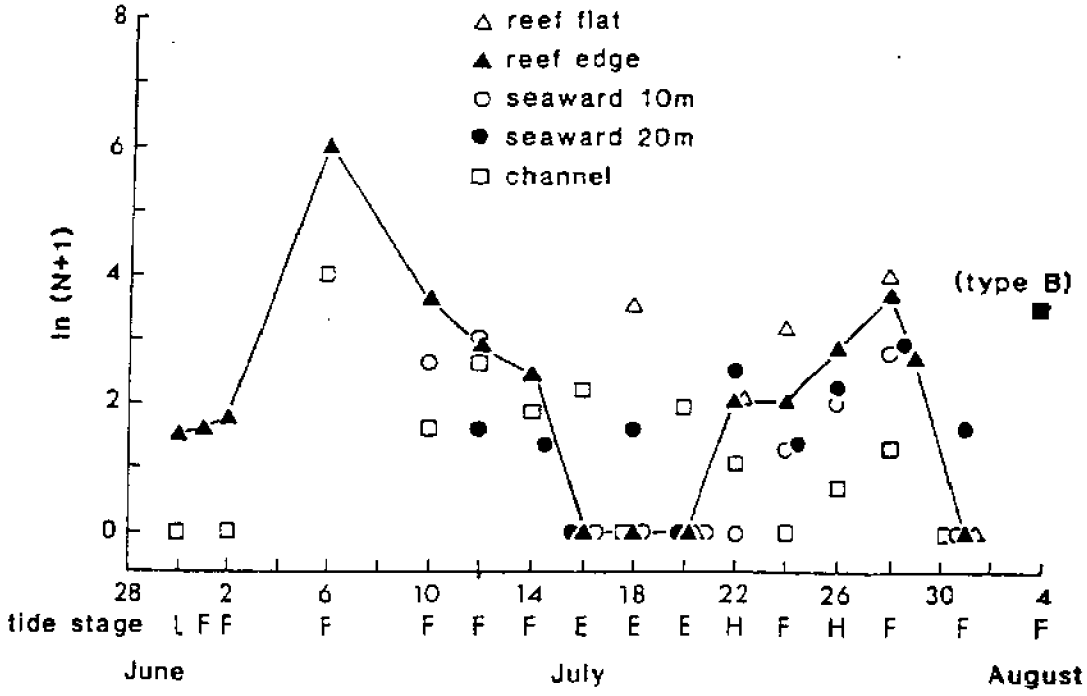

Fig. 13. Average abundance of Semper's larvae collected per 100 m³

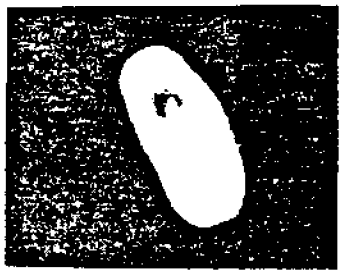

Fig. 14. Planula of Apthoplegra nigrescens (?)

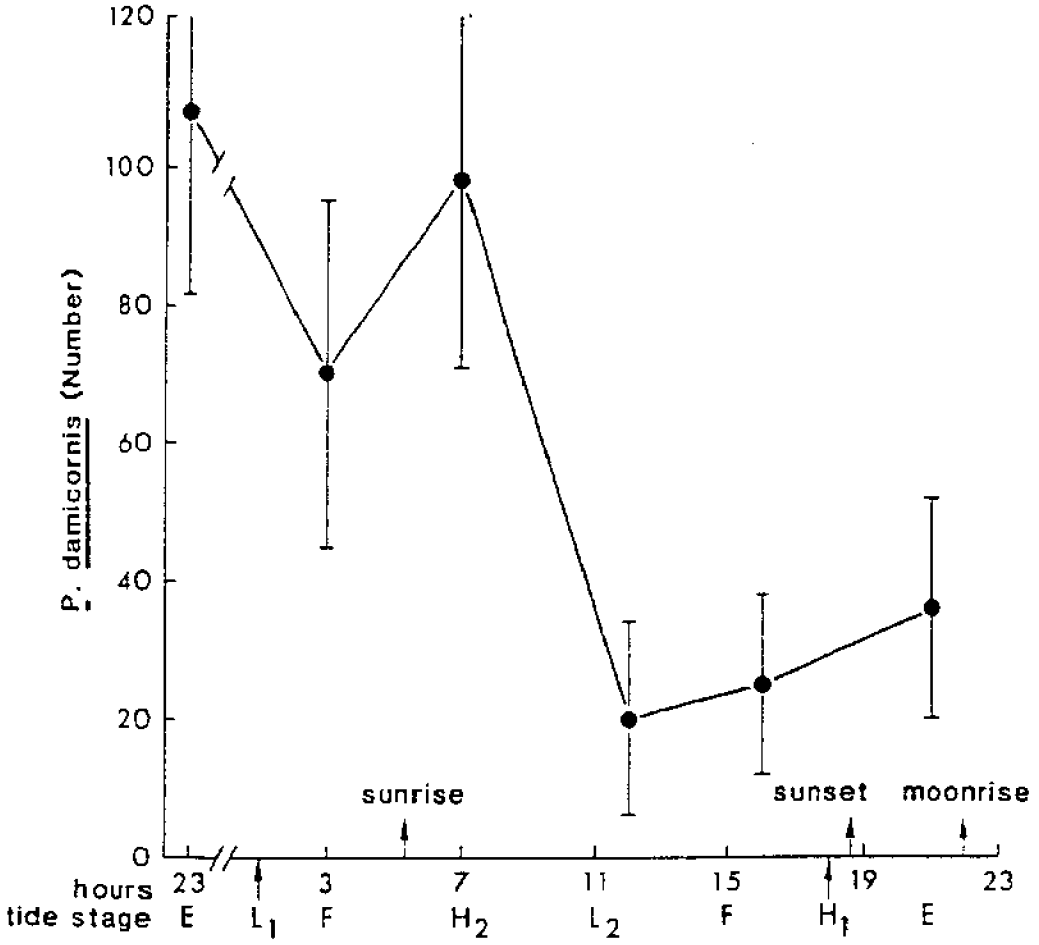

Fig. 15. Average abundance of P. damicornis

Diurnal Cycles

The changes in abundance of Pocillopora damicornis planulae over a 24 h period (29 - 30 June) and of both P. damicornis and Porites compressa planulae over a 12 h sampling period (29 July), along the seaward reef edge transect are shown in Figs. 15 and 16. There were significantly more P. damicornis planulae recovered from the night tows than from the day tows over the 24 h period ($p < .001$) and the 12 h period ($P < 0.025$). Although the total abundance of P. compressa planulae captured during the night is nearly 1.5 times higher than the number caught during the day (12 h study), this difference is not significant.

Horizontal Distribution

More P. damicornis planulae were usually recovered along the transect 10 m seaward than from each of the other transects (Fig. 6). Although fairly consistent, this difference is not statistically significant using a Sidak's t - test to compare all main effects means (SAS Inst., 1982). The distribution of the catch of the other types of planulae among the 5 transects shows only a few consistent trends. One trend is that the planulae of M. verrucosa were caught in greater numbers from the transect 20 m seaward than from the other transects. In contrast, the Semper's larvae tended to be more common along the reef flat and seaward reef edge transects than from the tows made 10 and 20 m away from the reef.

The results of the tows made outside the "barrier" reef are presented in Table 3. Only Zoanthina, M. verrucosa larvae and an unidentified cnidarian larva were collected.

Table 3. Abundance of planulae from tows taken outside the "barrier" reef of Kaneohe Bay. Tows were made within 100 m of the reef front and parallel to it.

Date	Time	Larvae recovered	Water filtered (m^3)
6-29	1030 h	unknown 1, Semper's 1	203
7-12	1255 h	P. compressa 221, Semper's 8	54
7-18	1530 h	none	89

Vertical Distribution

The results of the pumping experiment (1200 to 1300 h on 30 July) were 7,000 planulae per 100 m^3 recovered just below the surface versus 56,854 per 100 m^3 at 2 m depth. The series of tows at 3 depths on 4 August are presented in Table 4. Together these results suggest that during these two daytime sampling periods, more M. dilitata and P. compressa planulae were found below one meter than at the surface. They further suggest that there may be an increase in abundance with increasing depth from below 1 m to 6 m. These differences are not statistically significant (Sidak's t-test).

Discussion

Problems With Traditional Procedures

This study suggests several reasons why coral planulae have rarely been reported in tropical plankton studies. Perhaps the most common reason is that many of the previous studies (Table 1) had a different focus. Coral planulae were simply overlooked or ignored. At best, they may have been relegated to a "miscellaneous" category. However, this obvious explanation cannot be applied to the studies wherein planulae were actively sought, but were found to be exceedingly rare or unobtainable (Yamaguchi, 1972).

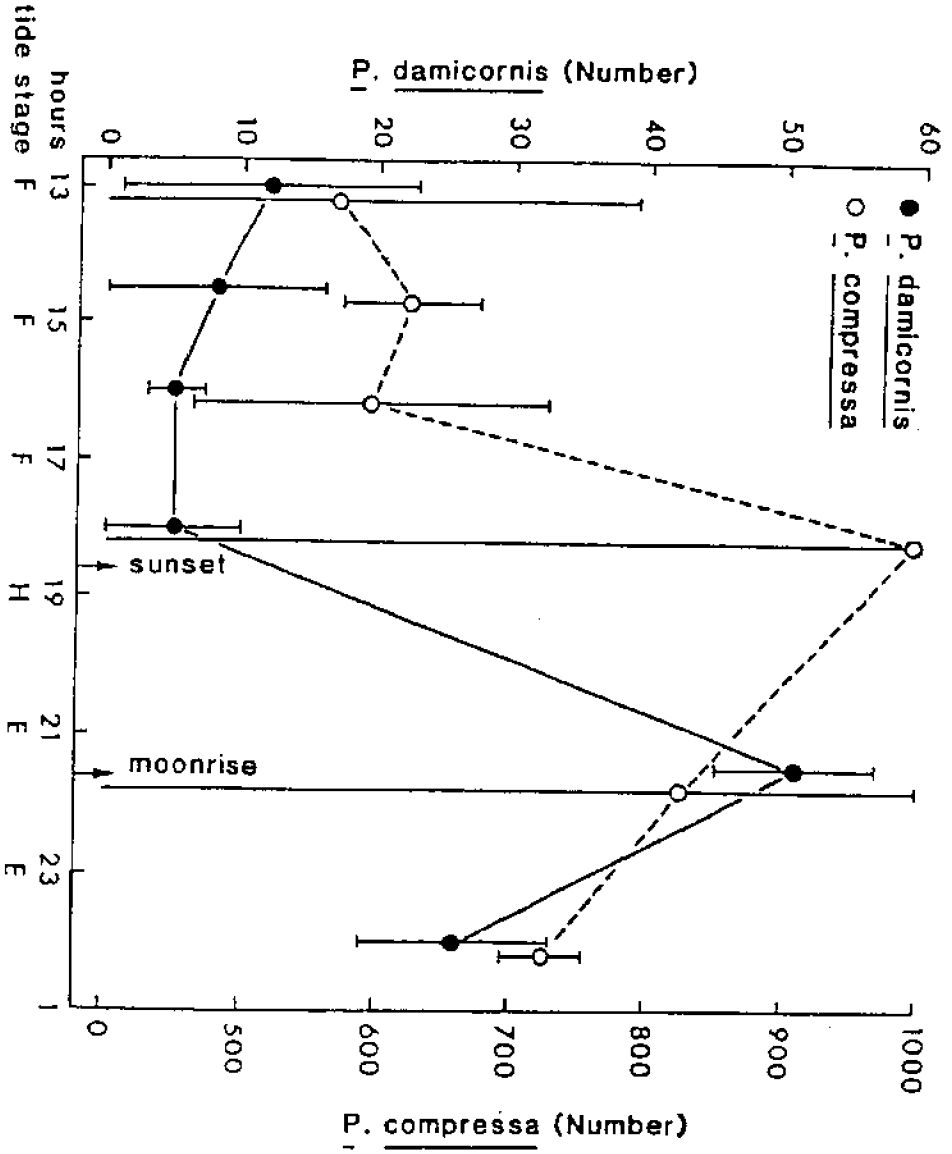

Fig 16. Average abundance of P. damicornis and P. compressa planulae over 12 hours

Table 4. Differences in the abundance of cnidarian larvae at 3 depths. Each number is an average abundance from 4 plankton tows normalized to the number per 100 m^3 of filtered seawater. Tows were made between 1440 h and 1610 h on 4 August along the seaward 10 m transect. Water depth there is approximately 12 m.

	No. of Larvae Recovered					
Depth Towed	Montipora dilitata	Semper's Type A	Semper's Type B	Porites compressa	Pocillopora damicornis	Fungia scutaria
Surface	103	8	34	47	0	4
1 m	183	8	9	64	5	15
5 - 6 m	200	10	6	63	0	6

The results of the present study indicate that the problem may be linked to the traditional procedure of adding buffered formalin to the plankton hauls "as soon as possible" (UNESCO, 1979) after they are brought in. The formalin kills the plankton which then settle to the bottom of the container. It has the secondary effect of rapidly bleaching any planulae white, and was also observed to disrupt the structural integrity of the delicate outer membrane of one and two day old P. compressa and M. verrucosa planulae. Following routine handling, (e.g. transfer of the samples into permanent storage jars) it was noted that many of these planulae had subsequently fragmented. This makes identification difficult if not impossible. Formalin does not appear to damage the larger forms such as P. damicornis planulae in this manner.

An alternative procedure which worked well in the present study is to allow the freshly caught plankton to settle in a bottle without adding a fixative or preservative. The most important benefit of this procedure is that most of the living coral planulae swim up towards the surface. Within a few minutes, the majority of the planulae will be found at the surface or just below the surface. There they can easily be observed with the naked eye as they swim about in the clear water. From there it is a simple procedure to collect them with a pipette for settling experiments. The remaining plankton can then be examined to find the injured or dead planulae which generally sink to the bottom (usually about one third of the total number). Few planulae will be found in the middle layers of clearwater above the settled mass of plankton. Only Semper's Type 1 and the red, sea anemone larvae were found more commonly on the bottom with the settled samples than at the surface.

The above discussion can adequately explain why coral planulae have been reported so infrequently. Additional problems which may have historically prevented the capture of planulae are: net mesh size too large, sampling at times when few corals were spawning or planulating, difficulties with identification, and as Kawaguti (1940) suggested, insufficient amount of water filtered.

When deciding what net-mesh size to use to trap planulae of a given size, one must bear in mind that the plankton netting will stretch under the pressure of incoming water. During a tow, this will effectively increase the mesh size. The combination of net stretch and the plastic body form of the planulae will most likely allow individuals of perhaps twice the dimensions of the mesh width (unstretched) or more to slip through.

Although several coral species have been reported to planulate or spawn during every month of the year in various parts of the world, many species appear to concentrate their reproductive activities during the summer months (Stimson, 1978; Harriot, 1983; Fadlallah, 1983). Therefore plankton tows taken outside of this period would presumably be less likely to contain planulae.

Distribution of Planulae

Planulae share a common feature with most plankton in that they exhibit a highly patchy horizontal distribution (Balachandran, 1973). Standard deviations were often as large as the mean in each set of 3 to 4 surface tows along a single transect, therefore they were not included in Figs. 6, 8, 10 and 13. Tows taken minutes apart along the same transect show a disparity of thousands of planulae per 100 m^3 of filtered seawater. The most obvious cause of a patchy distribution of planulae is the differential timing and location of release between colonies as suggested by laboratory observations on spawning and planulation. Numerous other potential biological and physical causes of plankton patchiness have been reviewed by Kinnerer (1980).

Despite this patchiness, several general spatial patterns of abundance are apparent. Overall, the lowest abundances of planulae were recorded from the reef flat and the channel transects. P. damicornis planulae were consistently more abundant along the seaward reef edge and 10 m seaward transects than along the others. Both P. compressa and M. verrucosa show an increasing abundance from the seaward reef edge to the 10 and 20 m seaward transects.

The interpretation of these data is complicated by the pattern of water circulation within the southeast basin which may tend to concentrate planulae in the waters adjacent to the study reef. Bathen (1968) has described the large counter-clockwise eddy centered in the basin and the overlying southwestward wind drift of the 0 to 2 m surface layer. During the study period, both of these currents were apparent. The counter-clockwise eddy would be expected to carry planktonic larvae located below 2 m depth away from the study area. These planulae might be dispersed to any location in the path of the eddy in the southeast basin. Perhaps some planulae would be carried back around to their point of origin. At the same time, the southwestward wind drift would tend to transport near-surface planulae across the basin, where they might be concentrated along northeast facing shores such as those of Coconut Island.

An additional complication precluding the simple interpretation of the data, is the presence of a submerged (3 - 5 m deep) patch reef (about 250 m long x 150 m wide), located 125 m east of the study reef. Short qualitative surveys of this patch reef revealed the presence of numerous colonies of M. verrucosa and P. compressa, but P. damicornis colonies were very rare. An attempt was made to determine the potential of the patch reef as a source of planulae by comparing the planula abundance upwind with that downwind of the patch reef. On 20 July, during the spawning period of M. verrucosa, plankton tows were taken upwind of the patch reef in addition to sampling along the normal (downwind) 5 transects. On this date, ten times the number of M. verrucosa planulae and eggs were recovered from the downwind tows (seaward 10 m and 20 m transects) than from those taken upwind, suggesting that the patch reef may be a large potential source of both P. compressa and M. verrucosa planulae. In this area, living coral is restricted to the upper 10 m depth range. The muddy lagoon floor is devoid of corals. There are no other possible sources of planulae in the vicinity.

The drogue and dye release experiments indicate that some of the planulae released from the north end of the patch reef would be carried directly over the study reef by the westward wind drift within about 2 h. If large numbers of M. verrucosa and P. compressa planulae are originating at the patch reef and being carried by the southwest wind drift towards the study reef, this provides a plausible explanation for the observed trend of increasing abundance of these planulae recovered from the seaward reef edge to the 20 m seaward transect. It may also clarify why the P. damicornis planula abundance distribution does not follow this trend, but in contrast, shows a peak abundance along the seaward reef edge and seaward 10 m transects. The majority of the P. damicornis larvae presumably originate from the study reef itself where this species covers almost 3 % of the outer reef flat.

In addition, the small gyre (noted previously) which exists during conditions of an incoming tide and normal trade winds (Fig. 4) could also increase the concentration of planulae off the study reef. The dye and drogue studies indicate that during these conditions the trade winds push the water over the study reef in a southwesterly direction until it reaches the reef edge. At this point it is redirected out into the channel and then back up to the north by the incoming tidal currents.

Vertical Distribution

Although no attempt was made to systematically determine the diurnal vertical distribution of the various species of larvae in the water column, the results of the two short sampling experiments at different depths raised interesting questions. The limited data on vertical distribution suggest that P. compressa and M. verrucosa planulae are in greater abundance at 6 m depth than at the surface during the day. The results of sampling at the surface over 12 h and 24 h periods indicate that more P. damicornis and P. compressa planulae are present at night than during the day (Figs. 15 and 16).

Taken together, this information could suggest a nighttime spawning and planulation peak, and/or the possibility that some species of planulae undertake a diurnal vertical migration. In 24 h laboratory tests Holloran, (this volume) found that P. damicornis colonies may reach their peak planulation at various times during the day or night. The timing of P. compressa spawning was also variable. In contrast, I observed M. verrucosa and M dilitata colonies to spawn only at night, usually several hours after sunset (also see Heyward, this volume).

Kawaguti (1940a), documented vertical migration of coral planulae in Iwayama Bay, Palau. The planulae were abundant at the surface at night, but absent from the surface during the day. During the daytime however, large numbers of planulae were netted from a layer 5 m below the surface. Another study which has noted diurnal migration is that of Balachandran (1973) who found that in the Indian Ocean, anthozoan larvae were present in 61% of nighttime oblique plankton hauls to various depths in the but in only 50% of daytime hauls. He concluded that night "seems to influence the upward movement of the larvae". Although a good deal of research has been devoted to the investigation of planula behavior of several species, it is difficult to extrapolate from studies carried out in small containers to the potential behavior of planulae in the field. However, these studies have at least shown that planulae respond to irradiance (Duerden, 1902; Edmondson, 1929; Abe, 1937; Kawaguti, 1941; Harrigan, 1972; Lewis, 1974), gravity and currents (Kawaguti, 1941), and, because of their gregarious settling behavior, chemical and tactile stimuli (Duerden, 1902, Edmondson, 1929, Kawaguti, 1941, Harrigan, 1972, Lewis, 1974). Planulae appear to have the ability to carry out a diurnal vertical migration. The swimming rates of several species of planulae were measured by Harrigan (1972) and Atoda (1953). They are too slow (2 to 3 mm sec^{-1}) to allow a planula to make headway against the more rapid horizontal currents encountered over the study reef or in the bay (5 to 15 cm sec^{-1}). However, this swimming speed would allow for substantial vertical migrations of up to 11 m h^{-1}.

An additional piece of evidence which appears to support the idea that some coral planulae undertake a daily vertical migration comes from the work of Kitalong (this volume). Prior to sunset on 15 July, she placed a demersal plankton trap over a P. compressa colony located on the same study reef used in the present work. The next morning the demersal trap was retrieved and the sample counted. Over 700 M. verrucosa planulae were recovered in this haul. One possible interpretation of this finding is that these planulae were seeking shelter or an appropriate settlement under the Porites head site during the day. After sunset, they may have detached from their temporary mucus strand attachments and were then caught in the plankton trap as they swam upwards.

Two coral species whose planulae have been intensively studied are Favia fragum (Lewis, 1974) and P. damicornis (Harrigan, 1972). The behavior of both F. fragum and P. damicornis planulae includes periods of crawling, temporary attachment, and preferential settlement in "dark" crevices. I observed M. verrucosa planulae to behave in a similar fashion when held in aquaria. A more detailed study will be necessary to ascertain if these planulae regularly congregate under coral colonies of various species during the day, and then return to the surface at night.

Export Of Coral Planulae From Kaneohe Bay

If large numbers of planulae are being released into Kaneohe Bay, it is possible that some of these may be exported out of the bay. In addition, if the numbers of planulae exported from the bay are large in comparison to local planula production at, for example, the reefs just outside of the bay entrance, the rate of coral recruitment on these reefs might be substantially increased by the "extra" Kaneohe Bay planulae.

In order to estimate the number of coral planulae which may be exported from the southeast basin, it is necessary to know the average density of the planulae in the water going out of the bay with the tide, and the daily gross outflow of water. According to Bathen's study (1968), most incoming tidal water is separated from the outflow. Since the density of planulae spawned outside the bay would presumably be greatly reduced by dilution from the ocean, the probability of these planulae being carried back into the bay is assumed to be negligible.

The average abundance of all types of coral planulae from all transects combined per day during the study was 328 planulae per 100 m^3. Several factors might affect the accuracy of applying this estimate to the entire southeast basin. The proximity of the plankton tow transects to potential sources of planulae, and their location in an area of probable planula concentration due to the action of wind and currents might indicate that this is an over estimate of the true planula density if applied to the entire southeast basin. However, if most planulae are undergoing a migration away from the surface during the day, the above estimate which is derived from daytime surface tows could be a considerable under-estimate of their true abundance in the basin. To what extent the above factors counteract each other is not known. A conservative estimate of planula density for the upper 5 m of the southeast basin during the study, is considered to be on the order of 1 planula per 100 m^3.

The average daily gross outflow (daily exchange transport) of water from the southeast basin has been calculated to be approximately 18×10^6 m^3 (Bathen, 1968). The majority of this water exits directly to the sea without passing via the north bay. About half of the gross outflow might not be expected to contain planulae if most planulae are concentrated above the 5 m depth range as indicated by Kawaguti's work (1940) in Palau. Given the conservative estimate of planula density of 1 planula per 100 m^3, and a gross outflow of planula-containing water of 9×10^6 m^3 d^{-1}, the average net export of planulae (assuming zero import) would be 90,000 planulae per day. Over the 44 d study period this totals 4×10^6 planulae. Whether this number of exported planulae has a significant effect on recruitment at reefs outside the bay, or even farther away, remains to be seen.

Despite the huge dilution factors involved, planulae may be expected to be recovered up to several miles from a reef. Russell and Colman (1934) netted several thousand coral planulae 3 miles east of the nearest reef (Low Isles, Great Barrier Reef, Australia) during the last two weeks of December, 1928. They made oblique, 30 minute tows to a depth of 23 m, using fine mesh (23 and 77 strands cm^{-1}), 0.5 m diameter nets. They probably filtered about 150 m^3 of water per tow.

Unfortunately, during the present study, rough seas during the periods of peak planula abundances prevented plankton sampling outside the "barrier" reef except on 3 days (Table 3). Only on 18 July were significant numbers of planulae (*M. verrucosa*) recovered. According to Bathen (1968), as water leaves the bay during an outgoing tide it sinks due to its higher density. He reports that three-fourths of the water leaving the bay exits below 3 m depth. This information suggests that future studies on the export of planulae from similar areas such as Kaneohe Bay, could concentrate their sampling at night and from the water column below the 3 m level outside the reef, as opposed to the daytime surface samples used in the present study.

Planktonic Lifespan of Planulae

It is tempting to infer a planktonic life span from the number of consecutive days a given planula type was recovered in plankton hauls. However the average residence time of the water in the southeast basin has been estimated to be 5 d (Bathen, 1968) and 4.5 d (Steinhilper, 1970). Theoretically, this means that every planula released on Day 1, and not settled by Day 5 will be exported out of the southeast basin.

Most *P. compressa* and *P. damicornis* planulae were recovered in plankton tows within 5 days after the last day of each spawning period. Possible explanations for these results are: 1) that the majority of planulae have been washed out of the study area as predicted by the average residence time estimates, 2) they have settled, 3) they are residing in the sub-surface layers, or 4) their numbers have been reduced by predation. However, *M. verrucosa* planulae were recovered up to 8 d after the last spawning observed in the field and laboratory.

This might indicate that certain groups of P. verrucosa colonies spawn slightly out of phase and later than the colonies I was observing, or that the planulae are being retained in the bay beyond the theoretical 5 d residence time. Several factors which might explain the latter hypothesis are abiotic effects such as gyres in the water circulation pattern which might retain planulae in a given locale, or biotic effects such as temporary settlement of planulae followed by their reentry into the plankton.

Several studies of the settling behavior of a wide variety of species of coral planulae indicate that provided a proper substrate most species of planulae can settle within a few days. When deprived of a suitable settling site, e.g. improper substrate or insufficient irradiance, the majority of planulae tested can survive several weeks without settling, and then successfully settle when a substrate is provided (Abe, 1937; Edmondson, 1929; Vaughan, 1908, 1910; Harrigan, 1972; Lewis, 1974). I observed that P. compressa and M. verrucosa planulae were able to settle on various substrates provided in indoor aquaria by Day 5, but some individuals existed for two weeks in the free swimming stage.

Considering the numerous potential factors affecting the number of consecutive days in which planulae of a given species are caught, it is clear that the present data cannot be used to judge the planktonic lifespan of these coral planulae.

Summary

1) A plankton sampling technique was designed to net coral planulae. The method is based on surface tows using a small, fine-mesh net, cooling the samples, and minimizing the time between collection and sorting, in lieu of using fixatives.

2) Over 100,000 cnidarian larvae were collected and sorted from a total filtered volume of approximately 5,300 m^3. Most of these were scleractinian planulae. Twelve types of cnidarian larvae were differentiated. Two have been tentatively identified as the Zoanthine larvae of the zoanthids Palythoa vestitus and Zoanthus pacificus. Six have been positively identified as the planulae of the scleractinian corals Pocillopora damicornis, Porites compressa, Montipora verrucosa, Montipora dilitata, Cyphastrea ocellina, and Fungia scutaria. The remaining planulae remain unidentified.

3) The horizontal distribution of P. damicornis, P. compressa, and M. verrucosa planulae among 5 plankton tow transects was studied. P. damicornis planulae were more commonly recovered directly along the study reef front, whereas more planulae of the other two species were caught along the transects further away from the study reef.

4) The spawning and planulation patterns of P. damicornis, P. compressa, M. verrucosa, and M. dilitata were followed by observing colonies held in the laboratory and in natural field populations. The peak recovery of the planulae of each species in the plankton tows generally occurred 3 - 7 d after the onset of spawning or planulation.

5) The planktonic lifespans of each planula species cannot be deduced from the plankton tow data due to various confounding biotic and abiotic factors.

6) Limited data suggest that some coral planulae may undertake a diurnal migration, spending the day at several meters depth and then migrating to near the surface at night.

7) The potential for the export of coral planulae from Kaneohe Bay is considered to be good, but whether this export is important to recruitment on reefs outside the bay remains to be seen.

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Direct retrospective analysis of the reef coral Porites compressa: evidence for sexual versus asexual origins of reef coral populations.

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Abstract

An attempt was made to determine the relative importance of asexual versus sexual reproduction in the reef coral Porites compressa in two different physical environments of the same reef, namely, the reef flat and reef slope. X-radiography is introduced as a method for determining coral colony origin, i.e. whether an existing colony is a product of a previously established colony. Radiographic studies of coral heads revealed a greater percentage of sexually derived colonies on the reef slope while colonies formed from asexual fragmentation formed a greater percentage of young colonies on the outer reef flat. As suggested in previous studies, the difference in mode of reproduction is attributed to the distinct physical characteristics dominating in each habitat.

Introduction

The formation of new colonies through settlement of planulae has long been considered to be the primary mode of reproduction among many species of reef corals (Marshall and Stephenson, 1933; Atoda, 1947a, 1947b; Harrigan, 1972; Connell, 1973; Endean, 1976; Kojis and Quinn, 1981; Rinkevich and Loya, 1979a). The production of new colonies by the fragmentation of established colonies has been shown to be an important alternative means of reproduction in reef corals (Stephenson and Stephenson, 1933; Cook, 1978; Tunicliffe, 1981; Highsmith, 1982; Jokiel et al., 1983; Nigel and Avise, 1983). This type of reproduction circumvents the high mortality rate of larvae and juveniles, and reduces the risk of mortality of the genotype (Cook, 1978; Highsmith, 1982). It may also allow the colonization of habitats unsuitable for the settlement of larvae (Highsmith, 1980; Sheppard, 1981). Previous studies have shown that fragmentation to be extremely important in the recolonization and recovery of coral reef systems after various natural and man-made disturbances (Maragos, 1972; Grigg and Maragos, 1974; Highsmith et al., 1980; Pearson, 1981; and Dollar, 1982).

Various methods for determination of colony origin have been developed. Stephenson et al. (1933), by inference, determined colony origin through observations of gross morphology of the coral colony. Highsmith (1982) noted the change in growth direction of the branches of a colony and whether or not they were attached. Others (Jokiel et al., 1983; Nigel and Avise, 1983) used immunocompatibility of colonies as evidence of common ancestry to a parent colony. Combinations of the above techniques have also been employed (Hunter and Kehoe, this volume).

The use of x-radiography to delineate high and low density growth bands in corals now enables us to study internal skeletal structure and determine past growth conditions (e.g. Knutson et al., 1972; Buddemeier, 1974; Buddemeier et al., 1974; Dodge and Vaisnys, 1975; Highsmith, 1979; Wellington and Glynn, 1983). The purpose of the present study was to apply this technique to the determination of colony origin in a natural population of the reef coral Porites compressa. Can x-radiography be used to reveal internal features of the skeleton that demonstrate origins of colonies? Can we see the remains of ancestral "seed" fragments within colonies? If so, we could use these data to determine the possible importance of asexual reproduction via fragments in various environments. It has been suggested that mode of reproduction in hermatypic corals may be related to habitat characteristics (Stimson, 1978; Kojis and Quinn, 1981). In the present study, an attempt was made to determine the relative importance of asexual (colonies derived from fragments) versus sexual reproduction (colonies derived through settlement of larvae on pre-existing substrata) for two environments (reef flat vs. reef slope).

Materials and Methods

Two collection sites were chosen on a natural reef located on the south leeward side of Coconut island, Hawaii (21° 29' 55" N, 157° 47' 43" W). The outer reef flat area immediately shoreward of the reef crest was the first study area. Water depth in the survey area ranged from 1.0 m to 1.5 m. This area was regularly subjected to turbulent water motion during storms. Hurricane Iva severely disrupted this area in November of 1982 (Bartlett, this publication). The substrate was mostly coral rubble with sand. The reef slope, immediately seaward of the reef crest was the second area sampled, ranging in depth from 2 m to 8 m. This area experiences less turbulence from wave action and has a substrate composed of coralline rubble.

Live coral heads of Porites compressa, 3 cm to 10 cm in diameter, were removed from both sites during August of 1983. These were sectioned with a diamond bladed rock saw. The 3 mm to 5 mm thick sections were cut through a plane intersecting the midpoint of the coral's base (i.e., the probable point of colony origin) and the point of highest relief on the colony.

X-ray exposures were made using a Faxitron 8050 Radiographic Unit and Kodak Industries Type AA x-ray film. The exposure setting was 50 KV for all sections, with exposure times varying from 1 min to 2 min depending on the specimen thickness. X-radiographs were viewed on a light table to reveal density bands and determine colony origin. Internal structure clearly showed that some colonies grew from broken branch fragments, while others originated as settlements on pre-existing substrata (Figs. 1 - 2). Percentage of "asexually" and "sexually" derived colonies were estimated for both areas of the reef and statistical comparisons were made (contingency tables using chi-square values and G-test of significance).

Results

X-radiographs of P. compressa colonies in the regions surveyed demonstrated their probable origins. In asexually derived colonies the outline of the broken ancestral branch could be seen in a horizontal position resting on the substratum. Regrowth of branches from the original fragment could be traced. Calyx walls were continuous. The change in direction of growth axis after the fragment fell to the substrata could be seen. This unusual orientation of growth bands is characteristic. These colonies were found unattached on the unconsolidated rubble or sand substrata. In contrast, colonies presumably derived from planula settlement show a different internal structure, with all growth bands radiating from a single point of original attachment on pre-existing coralline rock. A distinct discontinuity existed between the coral rock and the colony.

The data (Table 1) revealed a significantly greater ($p \leq 0.05$) percentage of sexually derived colonies on the reef slope compared to the outer reef flat. Colonies resulting from asexual fragmentation formed a significantly greater ($P=0.05$) percentage of young colonies on the outer reef flat. The physical characteristics predominant in each environment may explain the differing relative importance of asexual versus sexual reproduction in the two corals.

Table 1. Frequency of presumed "sexually" and "asexually" derived coral colonies. Numbers of colonies are listed followed by percent of total colonies that fell into each category.

Reef Site	Colonies Sampled	Sexually derived No.	% Total	Asexually derived No.	% Total	Undetermined No.	% Total
Flat	85	46	54%	36	42%	3	4%
Slope	70	54	77%	16	22%	0	0%

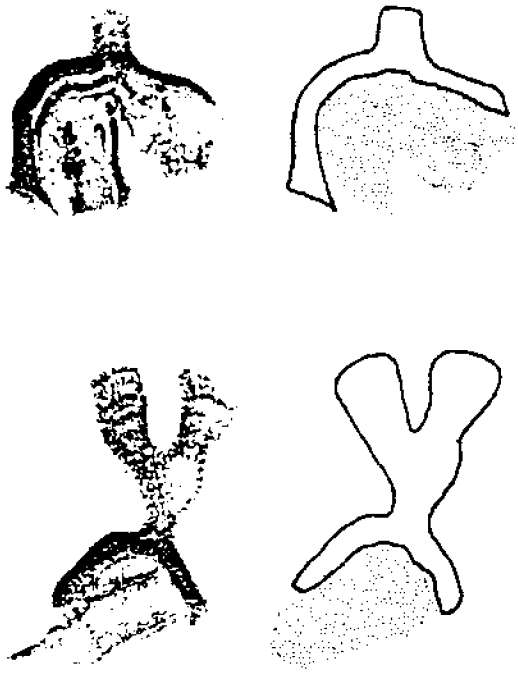

Fig. 1. Evidence for sexual origins in a colony of the "finger coral" Porites compressa. X-radiograph (positive print) indicates probable point of planula settlement (arrow) on pre-existing substratum (stipled area).

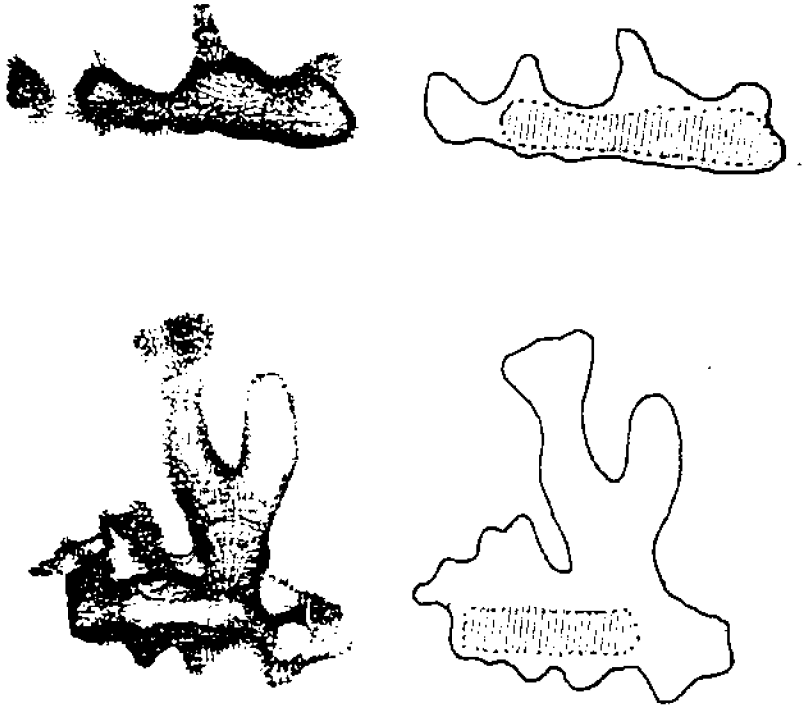

Fig. 2. Evidence for asexual origins in a colony of the "finger coral" Porites compressa. The original broken branch fragments (cross-hatched areas) are still apparent within the colony. Note the reorientation of colony growth direction radiating from the coral "finger".

Discussion

This study indicates that x-radiography can be a useful technique for the determination of colony origin in reef coral populations. X-radiography of Porites compressa colonies derived from sexual reproduction were characterized by growth bands oriented vertically, emanating from a single point of origin at the base of each colony (Fig. 1). They were formed usually attached on some form of hard substrate, e.g. pieces of coralline rubble, dead bioeroded coral colonies, rocks and even bivalve shells. The point of origin of the growth bands is considered to be the area on which the larvae first settled. These colonies are, therefore, considered products of sexually-derived larvae which require solid substrate for settlement (Harrigan, 1972; and Rinkovich and Loya, 1979b).

The outer reef flat in the present study is a turbulent environment created by waves breaking against the reef crest. Coral breakage, a common occurrence in the area of the crest, results in the movement of coral fragments downstream, increasing the frequency of fragments found on the outer reef flat. Transportation of coral fragments downstream has been documented by Highsmith (1982). Coral species that do not survive the breakage and transport processes become part of the sandy bottom and may become available as suitable substrate for the settlement of larvae. Fragments that do survive, however, re-establish themselves in the area, inspite of the soft, unconsolidated bottom. The greater wave energy and subsequent increase in the occurrence of coral breakage would explain the large percentage of asexually derived colonies in the outer reef flat. Because of the damaging wave stress and unsuitable soft substrate, the area becomes unfavorable for larvae settlement and asexual reproduction, i.e. fragmentation becomes a relatively more important mode of reproduction in the area.

In the reef slope area, seaward of the crest, water depth increases and wave action appears insignificant to cause breakage of established colonies. The area remains stable with respect to water movement. Settlement of larvae becomes a more significant mode of reproduction because of suitable hard substrate, e.g. boulders, old dead colonies, and coral rubble.

Undoubtedly, the relative importance of asexual versus sexual propagation of P. compressa varies widely between different environments. It would appear that the predominant mode of reproduction in this reef coral is affected if not determined by the surrounding physical environment. Wave energy and water turbulence have been shown in the past to control and limit the growth and distribution of many reef organisms (Yonge, 1940; Storr, 1964; Voshurgh, 1977). Roberts (1974) and Jokiel (1978) have demonstrated the effects of water motion on the growth, mortality and reproduction of reef corals. The free-living coral, Fungia scutaria has been shown to use the surrounding energy field of moving water to its advantage (Jokiel and Cowdin, 1976). Asexual reproduction in P. compressa may be an adaptation as Highsmith (1982) postulated. This would allow the coral to take advantage of wave stress to propagate asexually whenever possible and to release larvae when conditions are favorable.

X-radiography has been shown to be a direct, rapid and highly discriminating method that can be used to assess asexual versus sexual origins of reef coral populations.

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The role of fragmentation in the colonial, algal-bearing didemnid ascidian, Diplosoma similis

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Abstract

In many colonial invertebrates a successful genotype is often locally proliferated by fragmentation. Fragmentation is usually considered to be advantageous because it can decrease genet mortality. In this paper it is hypothesized that fragmentation may also increase genet fitness by stimulating genet growth rates and indirectly increasing genet fecundity. Fragmentation may stimulate genet growth rates by dividing the genet into smaller and proportionately faster growing ramets assuming that growth rates proportionately decrease as a function of ramet size. This hypothesis was tested by measuring the growth rates of genets of the colonial, algal-bearing ascidian, Diplosoma similis. As hypothesized, genets which fragmented more frequently had faster growth rates than more intact genets. Ramet (clone member) growth rates were also found to proportionately decrease as ramet size increased, supporting the proposed explanation for how fragmentation enhances genet growth rates. Ramet fecundity increased as a function of ramet size. Genet fecundity consequently should also increase as long as faster growth rates translate into larger-sized genets.

Introduction

The occupation of available space by colonial invertebrates is usually accomplished either through the recruitment of sexually produced larvae or by lateral vegetative spread (Jackson, 1977; Kay and Keough, 1981; Karlson and Jackson, 1981; Sutherland and Karlson, 1977). However, in many colonial invertebrates recruits are also generated by fragmentation and subsequent dispersal (Birkland et al., 1981; Highsmith, 1982; Jackson and Winston, 1981; Lasker, 1983; Millar, 1971). Of what additional selective advantage is fragmentation? The advantages which have been previously proposed are 1) rapid colonization of available space by a locally successful genotype (Bonner, 1958; Janzen, 1977; Maynard Smith, 1971, 1978; Williams, 1966, 1975), 2) increased probability of survivorship of the genet (sensu Harper, 1977, 1980; Cook, 1979), and 3) the ability to become established on substrata not directly colonizable by larvae (Highsmith, 1982). Another advantage which has not yet been considered is that fragmentation may also be a mechanism for stimulating genet growth rates which, particularly in encrusting colonial invertebrates, will be of vital importance in facilitating the occupation of space. If higher growth rates ultimately result in larger-sized genets, then fragmentation will also lead to an increase in genet fitness by indirectly enhancing genet fecundity.

As in other broad categories of reproduction, the mode of fragmentation among colonial invertebrates is highly variable. Fragmentation is commonly externally induced by both physical factors such as storm-generated waves (Bak and Engel, 1979; Bothwell, 1983; Connell, 1973; Glynn et al., 1972; Highsmith et al., 1980, Highsmith, 1982; Rogers et al., 1982; Tunnicliffe, 1981, 1983) and sedimentation (Hughes and Jackson, 1980; Lasker, 1983), and by biological processes including competitive overgrowth (Hughes and Jackson, 1980; Jackson and Winston, 1981), partial predation (Tursch and Tursch, 1982; Jackson and Winston, 1981), and boring by lithophagic organisms (Highsmith et al., 1980; Tunnicliffe, 1981). It may also be a natural developmental event as has been reported in the coral, Goniopora stokesii (Rosen and Taylor, 1969), the octocoral, Nephthea brasssica (La Barre and Coll, 1982) and many colonial ascidians (Birkland et al., 1981; Cowan, 1981; Millar, 1971; Oka and Usai, 1944). The net result of fragmentation is the division of the genet, or genetic individual derived from a zygote, into a clone of physically isolated daughter colonies or ramets.

The objective of this study was to test the hypothesis that active fragmentation can be adaptive (i.e. it may increase both genet growth rates and genet fecundity). The results of some preliminary experiments which were designed to test this hypothesis are then reported. The experiments were conducted using

the colonial, algal-bearing, didemnid ascidian, Diplosoma similis which appears to fragment as a consequence of natural developmental events.

D. similis is a green to blue-green, encrusting colonial ascidian approximately 2 mm thick which may grow as large as 3 cm^2 in area (Kott, 1980). It is commonly found on Hawaiian reefs growing on dead coral and attached rubble at depths ranging from 0 to -10 m. Living symbiotically with D. similis is the alga, Prochloron spp. which has been described by Lewin (1976) as a link between the Cyanophyta and the Chlorophyta. The association appears to be obligate, since D. similis dies if grown in the dark for more than a few days (personal observation). Colonies of D. similis are also capable of limited movement averaging 0.5 cm d^{-1} (Birkland et. al., 1981; Carlisle, 1961; Covan, 1981; Olsen, 1983; personal observation).

D. similis was chosen as the experimental animal because 1) fragmentation occurs frequently and colony growth is rapid insuring that the time span required to collect appropriate data would be short, 2) the products of fragmentation can be followed over time even though colonies are capable of movement whereas the fragments of colonial invertebrates are unpredictably and widely dispersed by wave action, and 3) large, lecithotropic larvae can be easily collected both in the laboratory and the field allowing accurate estimates of fecundity.

Hypothesis

Fragmentation in colonial invertebrates is hypothesized to be selectively advantageous because it stimulates genet growth rates and indirectly increases genet fecundity. Assuming growth rates proportionately decrease as a function of ramet size, genet growth rates are enhanced because, as a result of fragmentation, the genet is divided into smaller-sized ramets which proportionately have faster growth rates than the intact ancestral genet. In terms of absolute growth rates, collectively a fragmented genet will have a greater absolute growth rate than a similar-sized unfragmented genet. Since over time, higher growth rates potentially translate into greater surface area, and because fecundity has been reported in many colonial invertebrates to be positively correlated with genet size (Grigg, 1977; Jackson, 1979), fragmentation potentially will also indirectly increase genet fecundity.

Whether or not genet fecundity is actually enhanced by fragmentation will be dependent upon the shape of the size-specific fecundity and survivorship curves of the individual ramets. Because the ramets produced by fragmentation are relatively small compared to the parental ramet, there are potential costs to fragmentation, specifically increased mortality and lower fecundity. Fragmentation will be most advantageous when neither fecundity nor survivorship increases much between the size at which daughter ramets are produced and the original size of the parental ramets. As illustrate in Fig. 1, such a situation exists between the size ranges to the right of the intersection of the survivorship and fecundity curves. In this region, both survivorship and fecundity change very little as genet size increases.

Fragmentation may also entail a trade-off between genet fecundity and genet survivorship. For example, the production of ramets within the size-range to the left of the intersection of the survivorship and fecundity curves in Fig. 1 may increase genet fecundity, but will also probably substantially decrease genet survivorship. In this situation, for fragmentation to increase genet fitness, the advantage to the genet of increased fecundity must outweigh the cost to the parental ramet of lower survivorship.

The determination of whether fragmentation increases genet fecundity will therefore require that the demography of the ramets be documented. In particular, information must be collected on 1) the size at which a colony fragments, 2) the size of the colonies produced by fragmentation, and 3) the size-specific growth, survivorship, and fecundity schedule of the ramets. Size instead of age is specified here as the demographic classification factor, because for modular (sensu Harper and Bell, 1979) organisms such as colonial invertebrates and higher plants which exhibit plastic growth, the components of fitness are more closely related to size than age (Caswell, 1982a,b; Cook and Lyons, 1983; Harper, 1977, 1980; Hubbell and Werner, 1979; Hughes and Jackson, 1980; Jackson and Winston, 1981). To accomplish this goal it must be possible to either isolate genets or be able to identify them by some phenotypic character. Second,

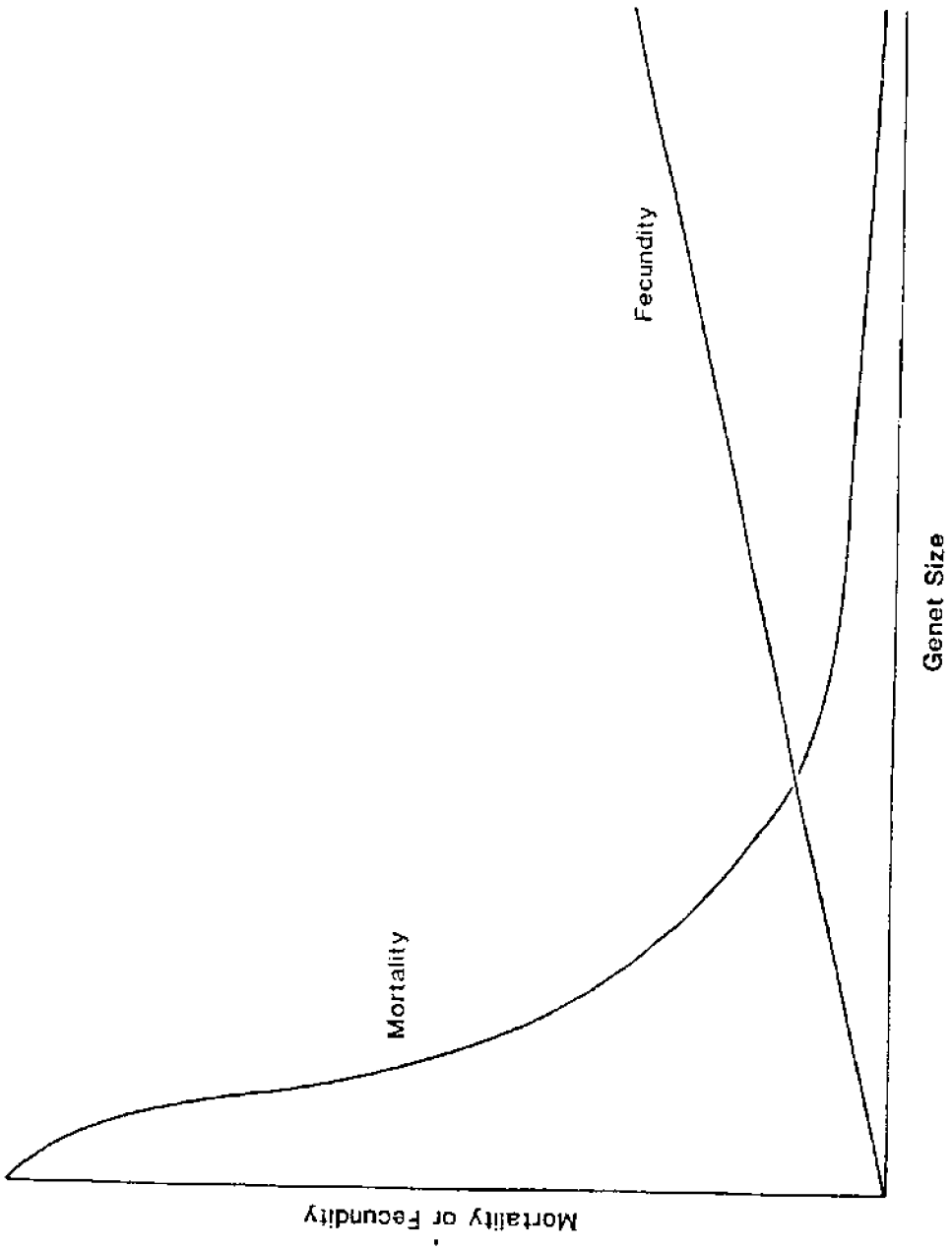


Fig. 1. Hypothetical plot of either probability of mortality or fecundity against genet size.

it must be possible to follow each member of a genet over time to measure fecundity and survivorship. Given these conditions, the fitness of a fragmented genet can then be directly compared to a similar-sized unfragmented genet. The fitness of the fragmented genet will be equal to sum of the fitnesses of all the ramets. In turn, the fitness of the ramets will be dependent upon the shapes of their size-specific fecundity and survivorship curves.

Materials and Methods

The experiments which are reported in this paper were carried out between May and August 1983. Colonies used for the laboratory growth and fecundity studies were collected from the reef crest (approximately 0-1 m deep at low tide) of the fringing reef located on the southwest side of Coconut Island, Kaneohe Bay, Oahu. The colonies were placed in buckets and immediately transported to shaded, aerated tanks at the Hawaii Institute of Marine Biology. These colonies were assumed to have different genotypes and were considered in the following experiments to represent the "ancestral" ramet, even though some are probably daughter ramets which were produced by fragmentation.

The hypothesis that fragmentation stimulates genet growth rates was tested by 1) comparing the growth rates of similar-sized genets which varied in the number of daughter ramets per genet and 2) by documenting whether relative growth rates of single colonies decrease with size. Size-specific ramet and genet growth rates were obtained by following the growth of a single ancestral ramet and all subsequent daughter ramets produced by fragmentation. The ancestral ramet was obtained be detaching single ramets of D. similis from their original substrata and then reattaching them to 6 cm^2 coral plates by loosely tying nylon filament lines around the ramets to hold them in place. Within 24 h the ramets had attached to the plates and the nylon line was removed. The coral plates were made from 1 cm slabs cut from massive blocks of Porites lobata collected from beaches along the northern coast of Oahu. Plates were individually suspended in seawater tanks by wire from a PVC frame to prevent colonies from escaping or moving to other plates during the course of the experiment. Water motion in the tanks was not as vigorous as in the natural environment nor was the turbidity as high. To correct for higher levels of light penetration due to the shallow depth of the tank and the associated increase in exposure to UV radiation (Jokiel, 1980), a 70% shade cloth was placed over the tank.

This growth study lasted 4 weeks from 15 June to 15 July. Genet and ramet size were measured at the beginning of the experiment, and at 1, 2 and 4 weeks and were measured in terms of zooid number, area and circumference. The number of zooids was determined visually under a microscope. Area and circumference were measured by tracing the outlines of camera lucid drawings with a Summagraphics brand x-y digitizer. Data on the size and number of daughter ramets produced between censuses, as well as genet survivorship were also collected.

The hypothesis that increased growth rates also leads to an enhancement of genet fecundity was partially tested by the determination of the size-specific fecundity curve for ramets of Diplosoma similis. Fecundity data for single ramets was obtained between 15 July and 20 August. The ramets were left on the original substrata and placed into small containers into which seawater flowed continuously. Water flowed out of spouts directly into a larval collector made from a piece of PVC open on top and covered on the bottom with 200 micron Nitex Brand mesh. The photopositive larvae, upon release, were washed out of the container and retained by the larval collector. Trial experiments where a known number of larvae were added to a container demonstrated that the larvae were unable to pass through the Nitex mesh.

Fecundity was measured in terms of the maximum number of larvae produced per day during the time interval each of the ramets was observed (3-30 d). The number of larvae produced was checked each day by visual examination of the larval collectors. One source of error in these measurements which may have introduced considerable variation in the data is the fact that fecundity was not measured at the same time of the month for all ramets. Ramet size was measured as described above.

The growth and survivorship of single ramets in the field was measured to determine the quality of the laboratory culture conditions and also to partially assess the potential cost of fragmentation and decreased genet survivorship. Field growth and survivorship rates were obtained by following ramets which had

settled on ten 20 cm^3 cement blocks over a 4 month period. The blocks were placed in the same location at which the laboratory colonies were collected, the southwest fringing reef off of Coconut Island. Ramet size was measured at monthly intervals by taking the blocks to the laboratory and examining each ramet with a microscope to determine the number of zooids per colony. The blocks were immersed at all times and were returned to the reef within 24 h. Only ramets on the vertical surfaces were monitored.

Records of the location of each ramet on the blocks were also kept to facilitate identification and to obtain data on recruitment and survivorship. The position of each colony was traced each month onto a transparent sheet of plastic, 20 cm^2 in area. Recruits were defined as any new ramets which appeared on the blocks, but were not located close to resident ramets. Survivorship was measured by following the fate of each marked colony over time under the assumption that the ramets in the field underwent very little movement between censuses.

Results

Laboratory growth rates of fragmented and intact genets were obtained from 30 genets which grew in culture for 4 weeks. These 30 genets plus three substantially large colonies were the only genets which remained healthy for the entire 4 weeks. Genets were classified as healthy if they averaged a monotonic growth rate of 1 zooid d^{-1} or more and never suffered the loss of a daughter ramet. As discussed later, the criterion of growth rate of 1 zooid d^{-1} was based on the fact that in the field most single ramets grew at a similar rate or higher. The three largest genets were also excluded from the data base because they represented too small a sample to make any firm conclusions about growth patterns within this size range or for the unsampled intermediate sizes.

The absolute growth rates (zooids) of all genets over 4 weeks increased linearly with initial zooid number which ranged between 8-90 zooids ($r=0.67$, $n=30$, $p<.001$) (Fig. 2). Growth rates varied between 50-200 zooids/4 weeks resulting in an average doubling rate of 2 weeks.

From a single ramet a mean of three (±1.8) and a maximum of seven daughter ramets were produced by fragmentation in four weeks and over 80% of these daughter ramets were 40 zooids or smaller in size (Fig. 3). The size range of daughter ramets produced from a single parental colony was constant over the entire distribution of initial genet sizes, except for parental ramets initially smaller than 60 zooids which produced on average smaller daughter ramets ($r=.01$, $n=47$, $p<.42$) (Fig. 4). However, the number of ramets produced per genet increased with increasing genet size ($r=.051$, $n=30$, $p<.001$) (Fig. 5). Thus, although the proportional investment per daughter ramet decreased as initial genet size increased, the total energy expenditure on asexual reproduction increased.

Growth in total zooids increased significantly as the number of daughter ramets per genet increased ($r=0.64$, $n=30$, $p<.001$) (Fig. 6). However, this correlation could be partly spurious due to the correlation between initial genet size and the number of daughter ramets discussed above. To test this possibility a multiple regression analysis was performed using initial genet size and ramet number as independent variables. Both independent variables were found to explain a significant portion of the variation. Colony number explained 20% of the variation explained by the full model which gave the following equation with a $r^2=0.62$, ($n=30$, $p<.001$):

$$Y=-0.418 + 1.510X1 + 16.956X2$$

where Y=growth (change in no. zooids d^{-1}), Xi=initial genet size, and X2=ramet number per genet Since zooid number and colony area are highly correlated ($r=0.98$, $n=20$, $p<.001$) (Fig. 7) the same relationships also apply with respect to increases in areal coverage over time.

The size-specific growth rates of single ramets was determined by measuring the growth of twenty-two of the thirty genets which remained intact for the first week. Due to the short time interval involved, conclusions drawn from these data should be considered tentative. Similar to the pattern for genets, larger ramets grew faster ($r=0.53$, $n=22$, $p<.01$) (Fig. 8), but the proportional rate of increase declined as initial colony size increased. T-tests applied to the regression equation revealed that the Y-intercept was not significantly less than one. The decline in the proportional rate of increase follows from the fact that such a relationship will always occur when the intercept of the re-

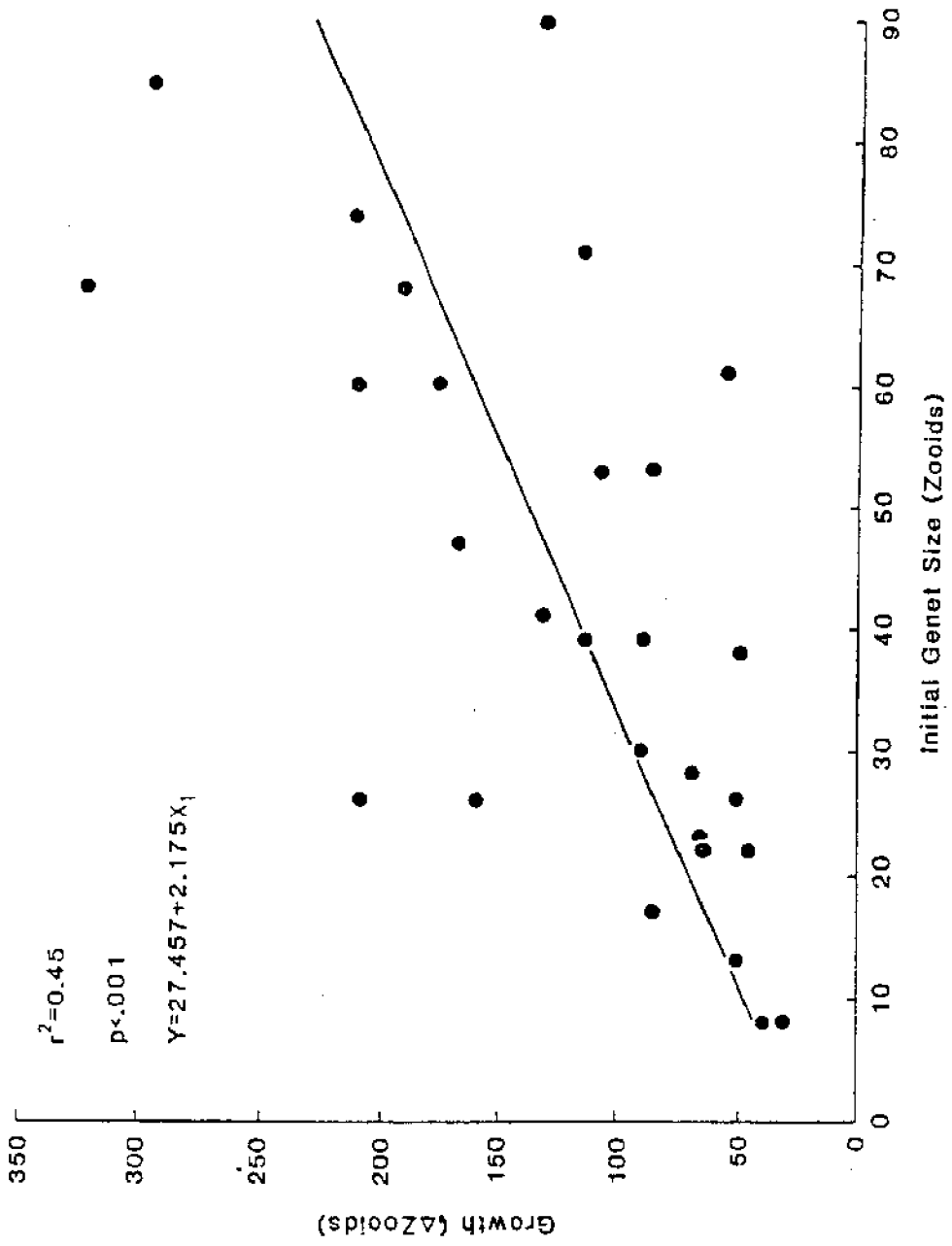


Fig. 2. A plot of growth in the laboratory, measured as the increase in zooids over four weeks against initial genet size. Genet size was measured by counting the number of zooids present in the entire genet.

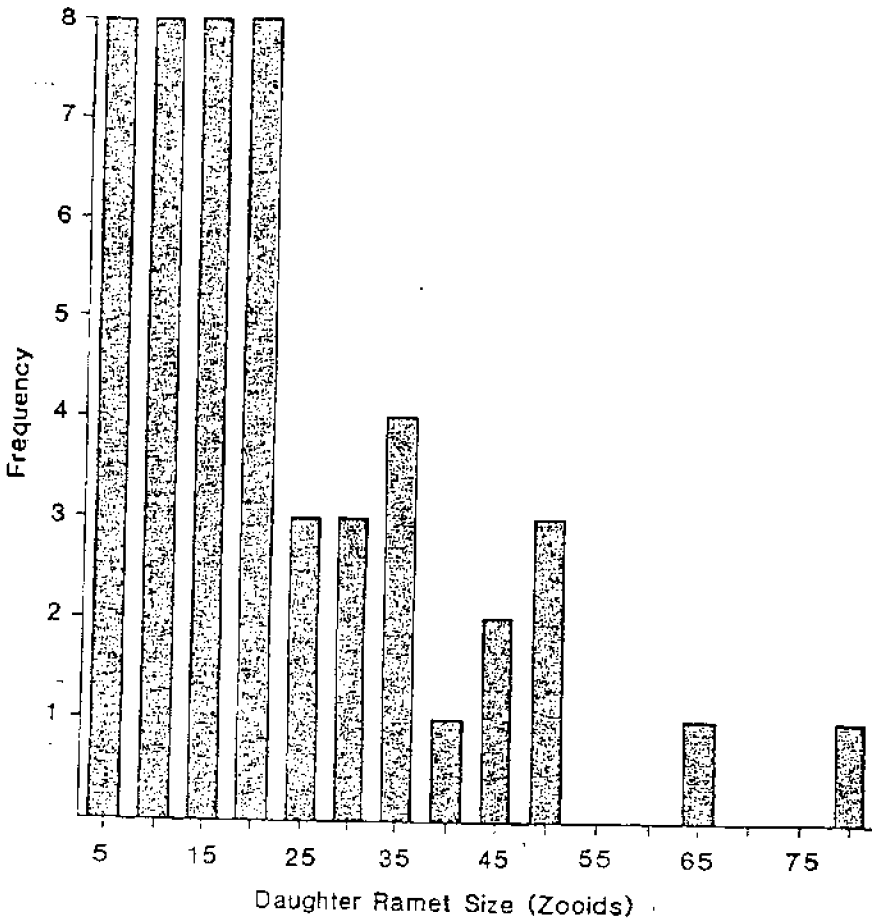


Fig. 3. Size-frequency histogram of daughter ramets produced by colony fragmentation.

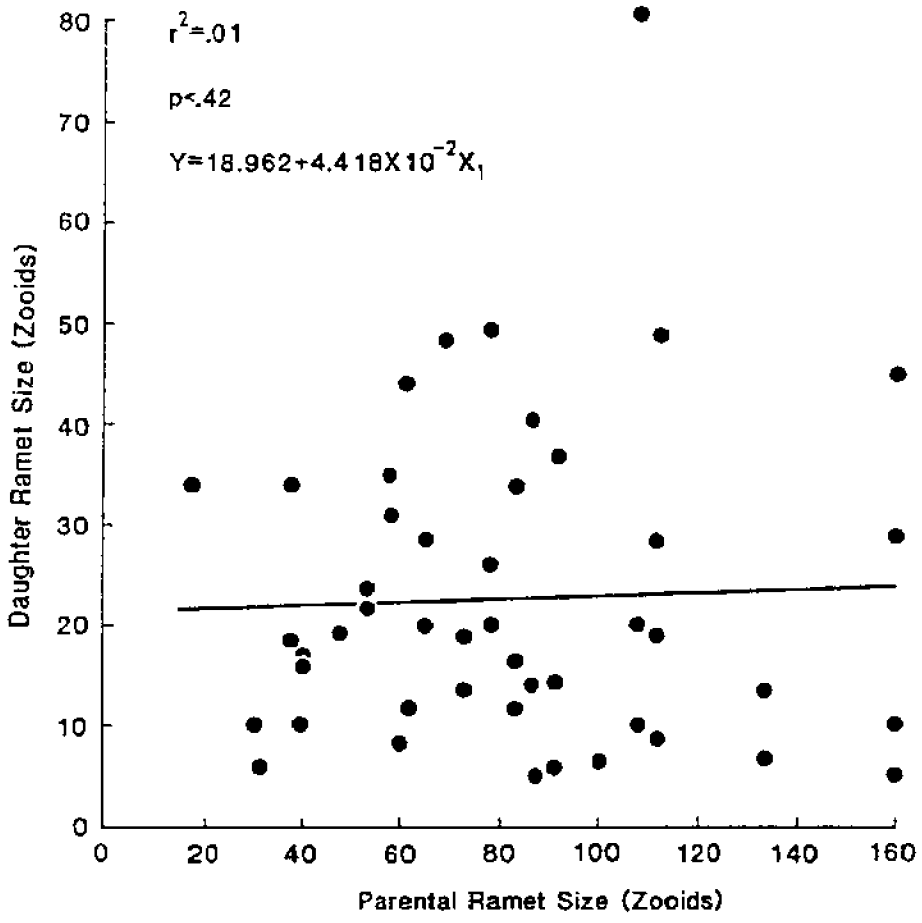


Fig. 4. A plot of the size of daughter ramets against the size of the parental ramets from which they were derived. Ramet size was measured by counting the number of zooids present per ramet.

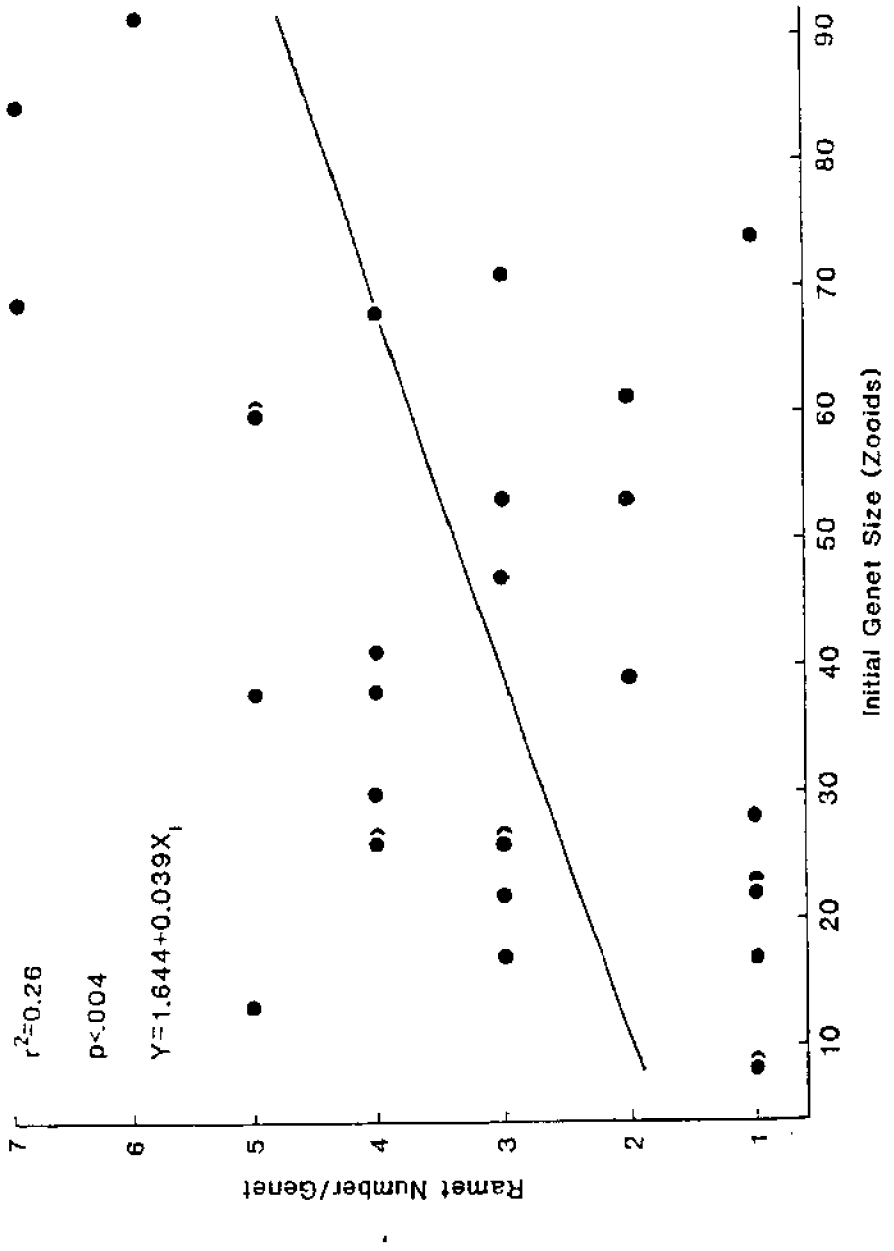


Fig. 5. A plot of ramet number against initial genet size. Genet size was measured by counting the number of zooids present within the entire genet.

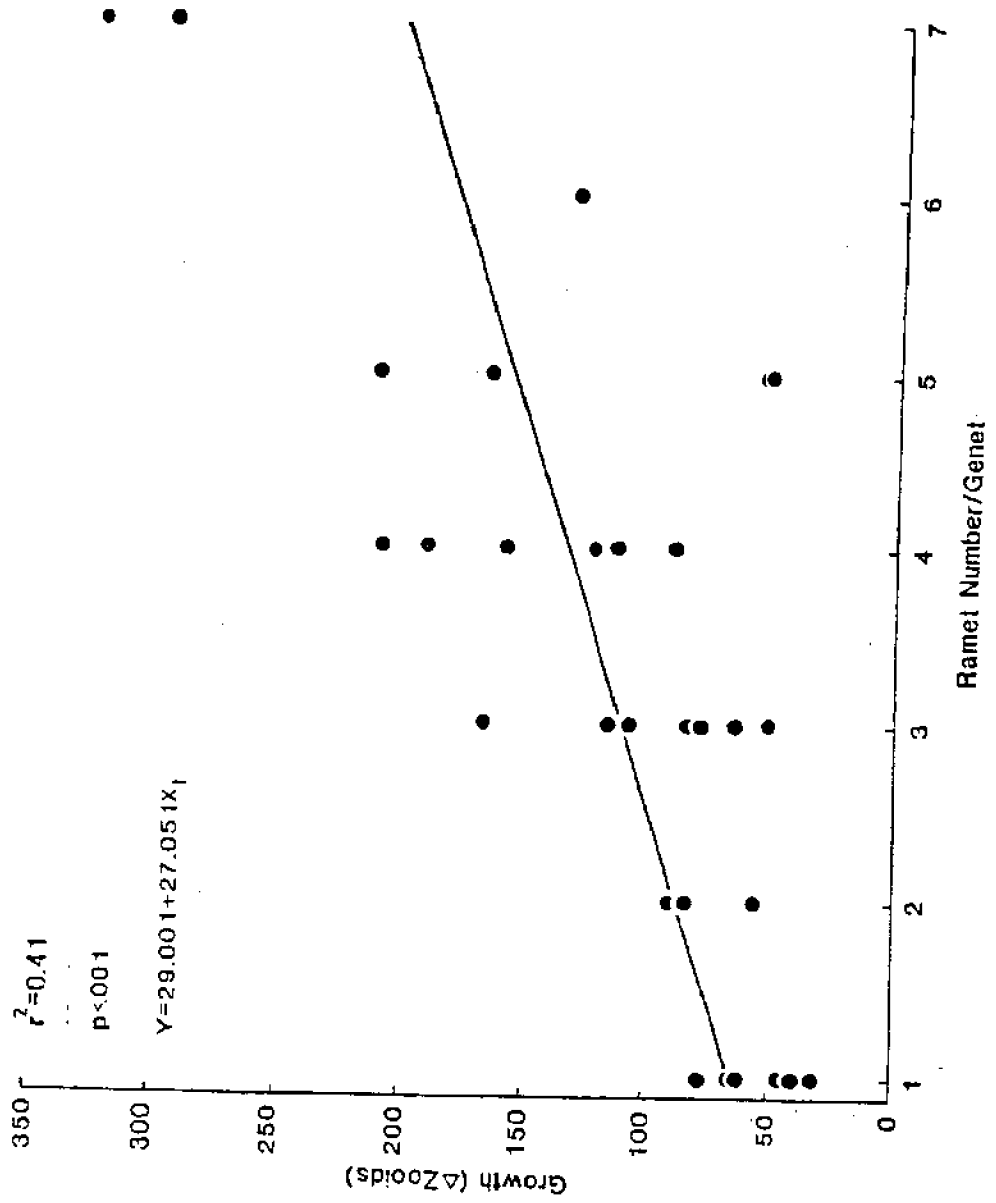


Fig. 6. A plot of the number of ramets per genet after four weeks against growth measured in the laboratory as the increase in zooids over four weeks.

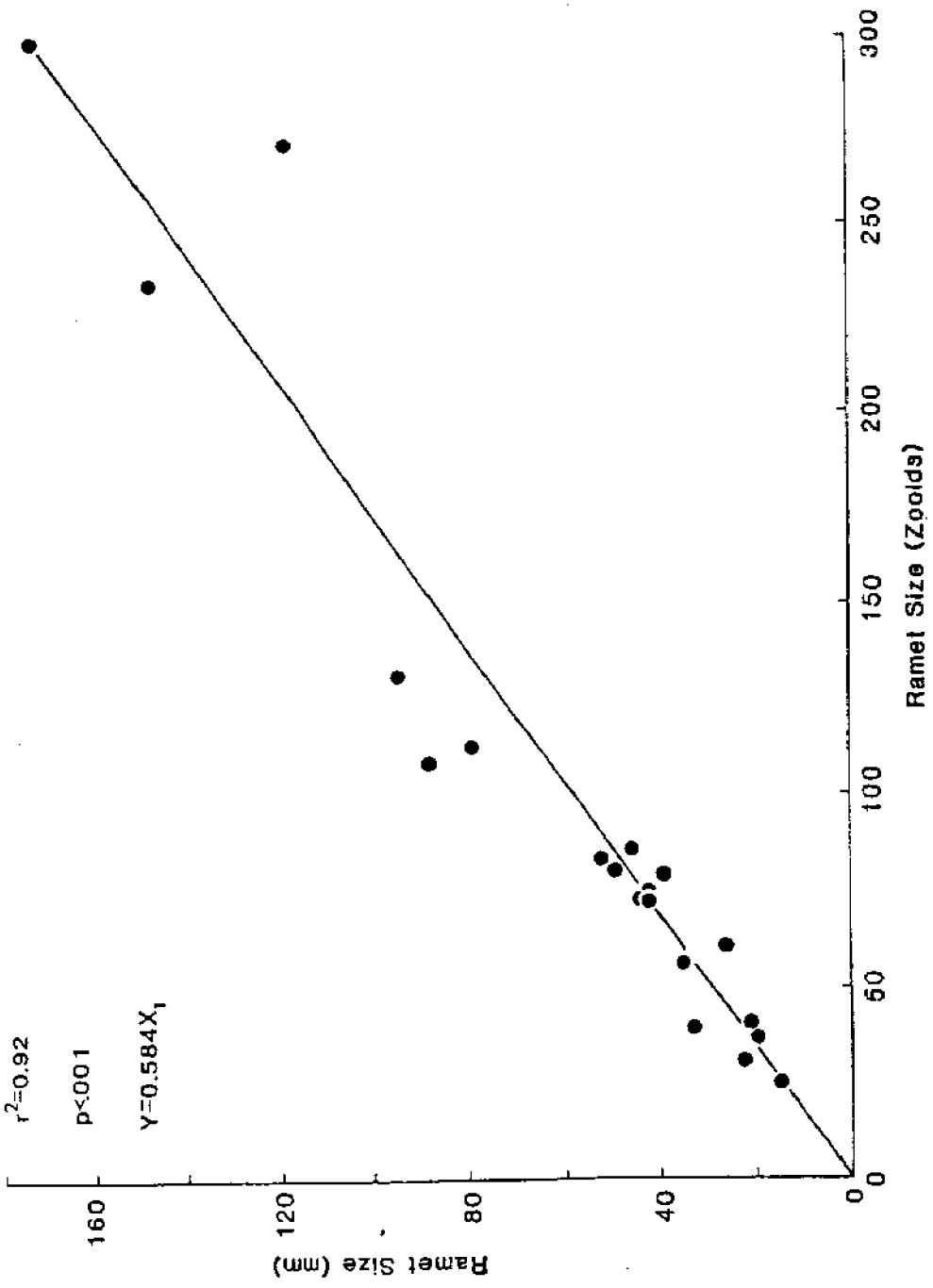


Fig. 7. A plot of area against zooid number, each of which were used as measures of colony size.

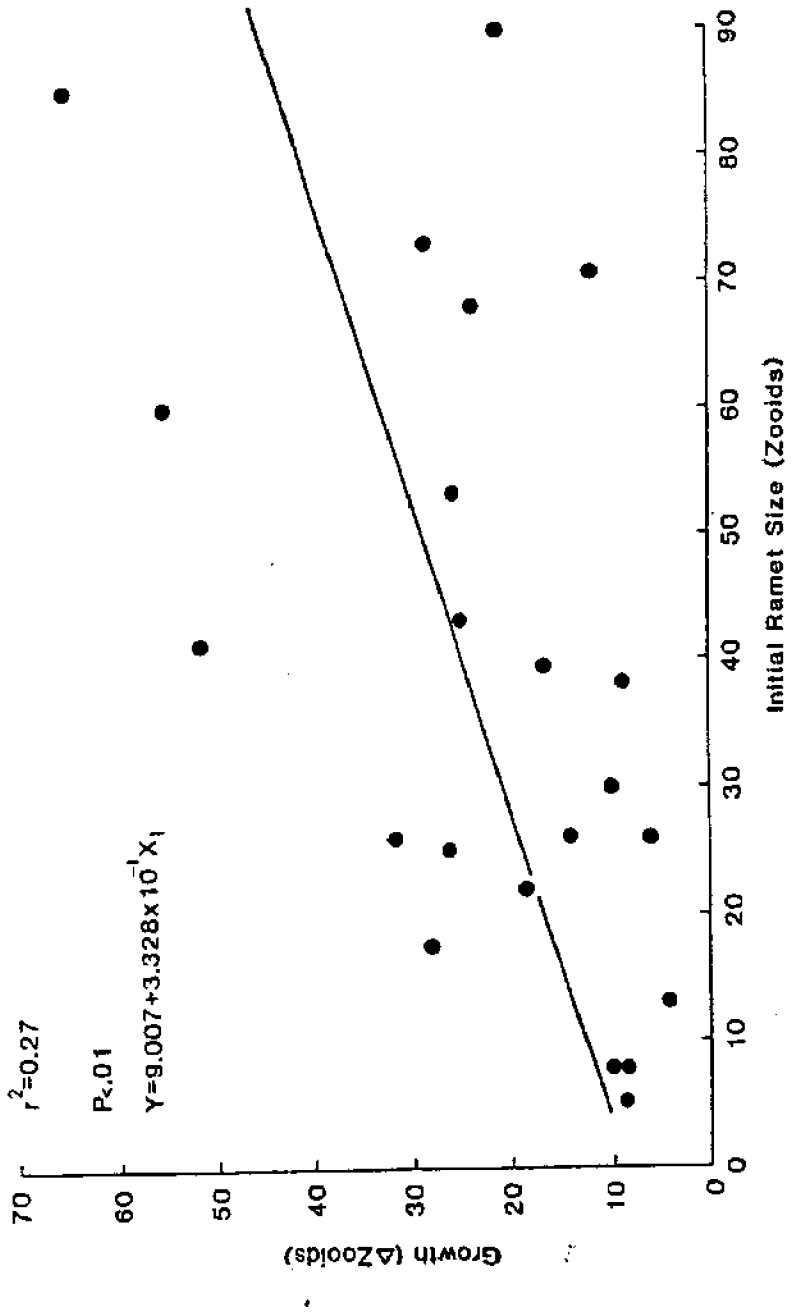


Fig. 8. A plot of growth measured in the laboratory as the increase in zooids over one week, against initial ramet size measured by counting the number of zooids per ramet.

gression equation is equal to zero, the absolute increase is linear, and the slope is less than one.

The correlation coefficient for the relationship between growth and initial colony size for ramets which grew in the field over a comparable 30 day period was r1 (n=12, p<.01)(Fig. 9). Ramets at the upper end of the size range exhibited lower growth rates than expected from the results of the laboratory growth studies, perhaps reflecting the action of external biological processes on growth. Except for the smallest ramets, all ramets which grew in the field had a growth rate greater than 1 zooid d^{-1}, but without exception, grew slower than similar-sized ramets which were raised in the field.

Survivorship rates in both the laboratory and the field suggest high mortality rates for small colonies (<40 zooids) and nearly constant low rates thereafter (Table 1). In the laboratory 41/58 (71%) of the genets less than 40 zooids which started out either died (14) or were classified as unhealthy (27) after 4 weeks as compared to 9/25 (36%) for colonies greater than 40 zooids. In the field, 22/51 (43%) of the colonies under 40 zooids died and most of these survived for less than one month. In constrast, only 2/16 (13%) ramets greater than 40 zooids apparently died. An alternate explanation for the difference in field survivorship rates between large and small ramets could be that the lower survivorship observed in small ramets may reflect a greater tendency for movement by smaller ramets. However, all except three ramets over 20 zooids were found for the first time on the last census at 4 months. If small colonies moved more frequently, then one would expect to find a greater number of large ramets appearing de novo at each census given an average growth rate of 2.220±.078 zooids d^{-1} (n=12).

Table 1. Size-specific mortality for laboratory and field populations.

	LABORATORY		FIELD	
Colony Size (#ZOOIDS)	Initial Frequency Distribution	Percent Mortality	Initial Frequency Distribution	Percent Mortality
0-19	29	83	40	45
20-39	29	59	11	36
40-59	9	56	13	0
60-79	10	30	4	50
80-99	2	0	6	0
100-119	0	0	4	0
120-139	2	50	1	0
140-159	0	0	6	0
>160	2	0	6	0

Fecundity increased linearly over the range (50-1500 zooids) of ramet sizes investigated (r=.84, n=32, p<.001)(Fig. 10), although the slope is quite gradual. The large observed variation in the fecundity of similar-sized colonies may be a consequence of ramets not being sampled at the same time of the month, particularly if the intensity of larval release is related to the lunar cycle.

Discussion

Previous quantitative studies on fragmentation in colonial invertebrates have been limited to an analysis of the effects of size and morphology on the probability of survivorship of randomly selected ramets (Bak and Engel, 1979; Knowlton et al., 1979; Tunnicliffe, 1981). These studies have assumed that at as long as survivorship is enhanced, fragmentation is selectively advantageous. The results reported in this paper represent the first documentation that genet growth and fecundity are also modified by fragmentation and that the extent to which they are modified is highly dependent upon both the frequency of fragmentation and the size of the fragments, which are generated by fragmentation. In

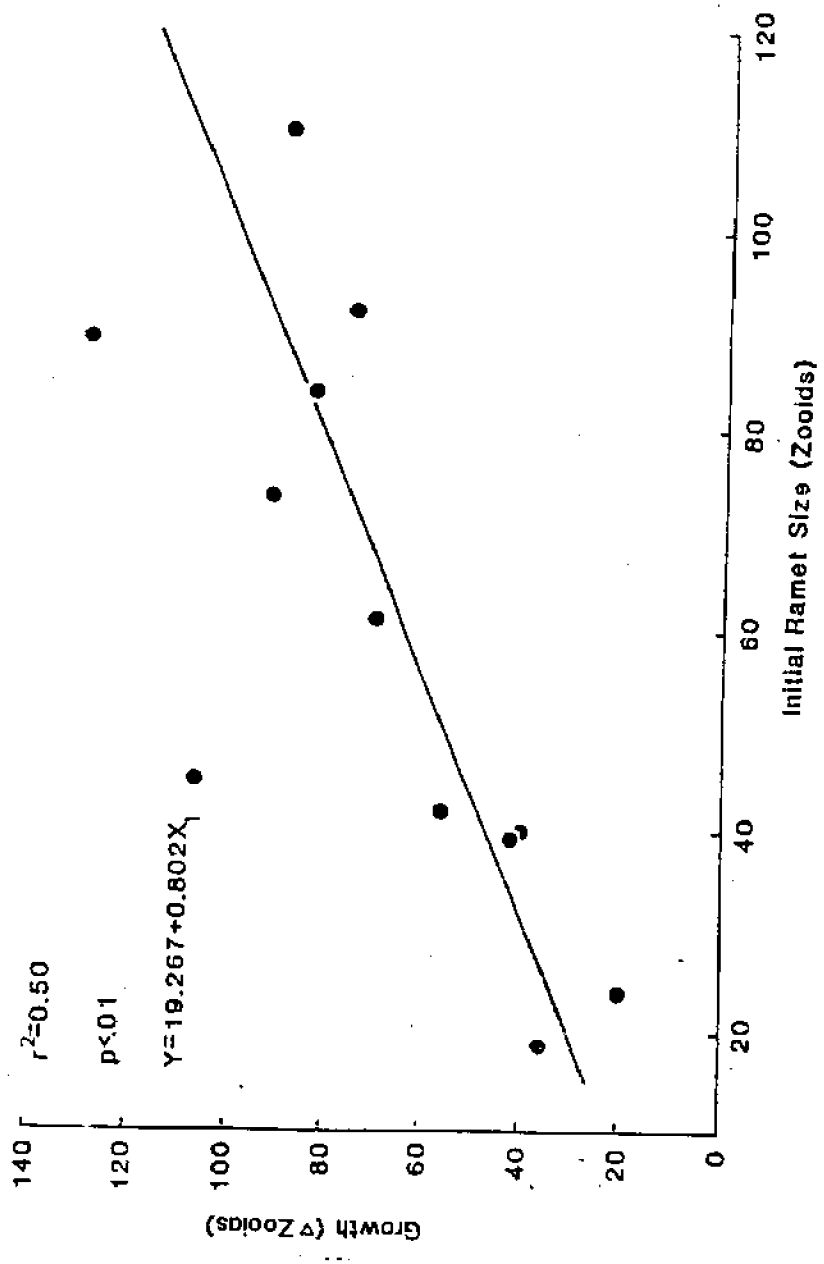


Fig. 9. A plot of growth measured in the field as the change in zooid number over 30 days against initial raset size measured by counting the number of zooids per raset.

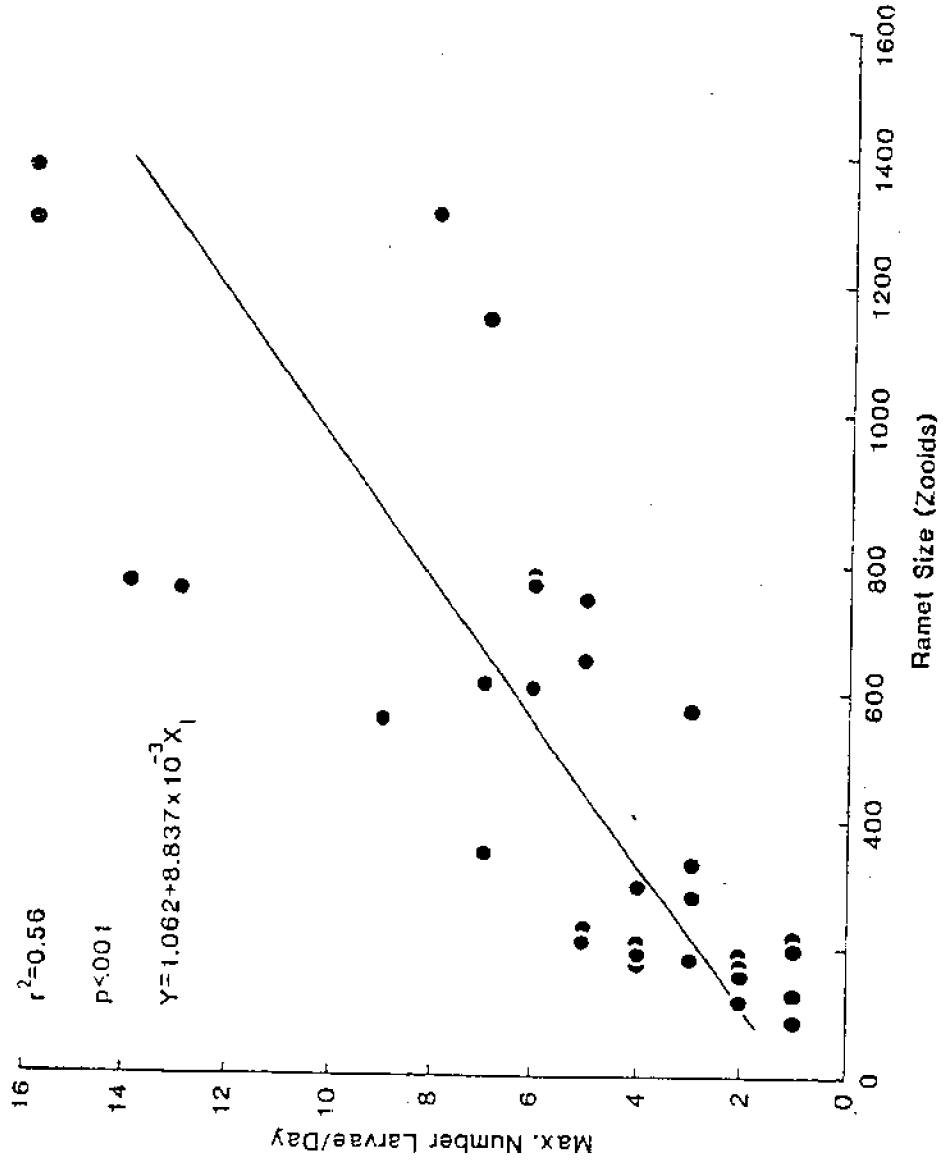


Fig. 10. A plot of the maximum number of larvae produced in one day by a single ramet in the laboratory against ramet size measured by counting the number of zooids per ramet.

light of these findings, future studies which attempt to examine the adaptive significance of variations in the pattern of fragmentation observed either within or between species must seek explanations which involve the optimization of both survivorship and fecundity. Optimally, these studies will be conducted such that the survivorship and fecundity of all the ramets within a genet are monitored.

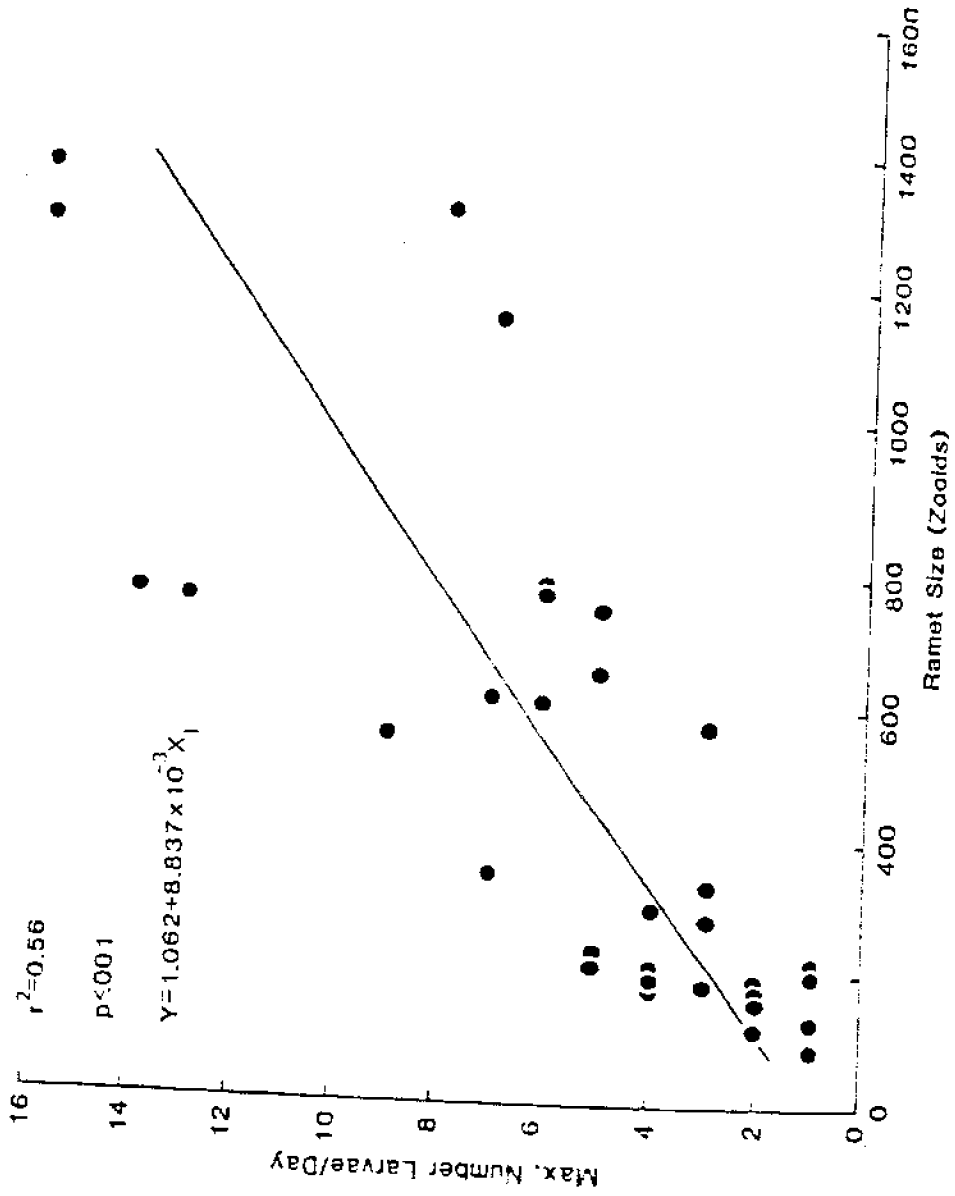
The size-specific growth and fecundity curves for ramets and genets of Diplosoma similis provisionally confirm the hypothesis that fragmentation provides a selective advantage by stimulating genet growth rates and indirectly increasing genet fecundity. The proportional growth rates of individual ramets were shown to decrease as a function of ramet size, because absolute growth rates appear to increase only linearly (Fig. 8). This suggests that fragmentation stimulates genet growth rates by dividing the genet into smaller units (ramets), each of which proportionately grows faster than the original intact genet. As a result, when comparing genets of equal size, the genet which consisted of the larger number of daughter ramet grew significantly faster than the genet which had fragmented less frequently.

Fragmentation may stimulate growth rates by increasing the genet surface area to circumference ratio. The ratio is highest in small ramets. Vegetative growth through the budding of zooids has been reported limited to zooids along the colony periphery in some colonial ascidians (Nakauchi, 1966a,b; Sugimoto and Nakauchi, 1974). By increasing the proportion of zooids within a genet which are located peripherally, fragmentation may also increase the proportion of zooids which are capable of budding. However, whether or not zooids of D. similis are similarly polymorphic is unknown. If smaller ramets are more mobile, they may also grow faster because they are better able to locate optimal habitats than larger colonies and can more rapidly escape from local environments which begin to deteriorate. Evidence for habitat selection comes from observations of ramets of D. similis moving in response to changes in light levels (personal observation). Living in an environment with appropriate light intensities is probably important to D. similis both to meet the photosynthetic requirements of its algal symbiont, Prochloron spp., and to avoid the potentially damaging effects of UV radiation (Griffin and Thinh, 1983; Olsen, 1983).

Clearly the realization of increased growth rates will depend upon a large fraction of the daughter ramets surviving. The laboratory and field survivorship data seem to suggest just the opposite, since the highest rates of mortality were recorded for ramets containing less than 40 zooids, the size of most of the daughter ramets produced by fragmentation (Table 1). However, this estimate of the magnitude of mortality may be too high. Much of the mortality in the laboratory may have been due to transplantation shock and the survivorship of newly settled colonies in the field may not be representative of survivorship rates for daughter ramets produced by fragmentation. Further research is needed to clarify this point.

If daughter ramets, in fact, experience high mortality in the field, then any advantage of fragmentation probably is derived from the production of large asexual propagules capable of dispersal. While it is known that ramets of D. similis are mobile, (personal observation), the distances over which they actually move in the field has not been determined. In the case of local disturbances, the further daughter ramets are potentially capable of dispersing, the greater will be the reduction in the probability of total genet mortality (Cook, 1979, 1983; Harnett and Bazzaz, 1983). The survivorship of even a few daughter ramets potentially could significantly increase genet survivorship. But increased survivorship will increase genet fitness, only if it also leads to an increase in lifetime reproductive success relative to a non-fragmenting genet.

The survivorship and fecundity curves further suggest that the costs of decreased fecundity and survivorship to the parental ramet as a result of fragmentation are low. The probability of survivorship of the parental ramet decreases very little as a result of fragmentation, since proportionately most daughter ramets represent only 20% or less of the parental ramet and additionally the probability of survivorship over a ramet size of 40 zooids is almost constant (Fig. 3 and Table 1). The frequent production of daughter ramets could slow down growth rates and hence decrease the fecundity of the parental ramet. But this cost may not be large in D. similis, since fecundity increases very gradually with increasing ramet size (Fig. 10). If a sufficient number of daughter colonies survive, because of their faster growth rates, they should be able to



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eventually surpass the production level of larvae which would have been achieved by an intact genet and hence increase genet fitness.

The length of the lag time before the daughter ramets compensate for the initial loss of fecundity experienced by the parental ramet is also a crucial factor. Young produced early in life contribute most to an individual's reproductive value (Hirshfield and Tinkle, 1975). Therefore, the longer the delay between the time fragmentation occurs and the resumption of sexual reproduction, the smaller will be the realized advantage of fragmentation. The laboratory data on fecundity provisionally suggests that ramets of less than 80 zooids were non-reproductive (n=12). For a daughter ramet starting at a size of 10-20 zooids, it would take 4-6 weeks to reach sexual maturity assuming a growth rate equal to the average growth rate measured in the laboratory. Since the doubling rate of D. similis is 1-2 weeks, this lag period could represent a significant cost to genets which fragment. However, the history of the 12 non-reproductive ramets is unknown. Daughter ramets derived from sexually mature parental ramets may remain reproductive. Bak et al. (1981) found that the daughter ramets of Trididemnum solidum, a Caribbean, algal-bearing didemnum ascidian, were still reproductive after fragmentation had occurred. The maintenance of sexual maturity would eliminate the hypothesized lag-time until the initial loss of fecundity to the parental ramet has been compensated.

If fragmentation increases genet fecundity, then the accepted idea that a trade-off between asexual and sexual reproduction must occur appears to be contradicted (reviewed by Abrahamson, 1980). The trade-off is presumed to occur because both sexual and asexual reproduction are assumed to share the same energy source and this energy source is limited. Therefore, energy expended on sexual reproduction is no longer available for asexual reproduction and vice versa (Abrahamson 1975, 1980; Harper, 1977,1980; Sarukhan and Harper, 1973; Williams, 1966). The contradiction may result because any short-term reductions in the amount of energy available per zooid for reproduction due to fragmentation are compensated for in the long-term by increased rates of zooid production. Although the fecundity of each individual zooid may be reduced, by increasing the number of zooids per genet, fragmentation contrary to expectations may actually enhance genet fecundity. Thus, at the level of the ramet the assumption that a trade-off exists between sexual and asexual reproduction may be valid. But at the level of the genet, instead of viewing fragmentation and sexual reproduction as alternative modes of reproduction, perhaps a more reasonable perspecitive is that fragmentation is actually a mechanism to increase sexual reproduction.

The importance of fragmentation within the life-cycle of D. similis still needs to be established for field populations. The life-history parameters reported in this paper only partially match the expected life-history attributes of an organism which predominantly reproduces by fragmentation. Organisms which reproduce asexually be fragmentation are usually characterized by rapid growth rates, relatively low energy allocation to sexual reproduction and are ecologically dominant space occupiers (Highsmith, 1982; Williams, 1975; but see Jackson and Winston, 1981; Winston, 1981).

The growth rate of D. similis was relatively slow compared to the growth rates for other subtropical to tropical colonial ascidians. The doubling rate reported for these species ranged between 1.5 to 10 days over the experimental phase of growth (Morgan, 1977; Sugimoto and Nakauchi, 1974; Yamaguchi, 1975), compared to a doubling rate of 1-4 weeks for D. similis. The daily output of larvae was also low (Fig. 10). Yet reproduction probably occurs year-round within populations from Kaneohe Bay (person observation), although it is unknown whether individual genets actually produce larvae all year as well. Recruitment onto new substrata by sexually produced larvae appeared to be uncommon. Recruitment of D. similis upon the ten 20 cm^3 cement blocks which were used to measure the growth of ramets in the field over 4 months averaged 1-2 ramets per block per month. Field observation on competitive interactions indicated that D. similis is seldom overgrown. On the other hand, D. similis has been observed to overgrow sponges, bryozoans, other tunicates and even some species of coral. However, frequently the organisms which are overgrown by D. similis did not suffer any damage.

The experiments reported in this paper suggest that fragmentation can potentially increase both genet growth rates and genet fecundity. Further work is needed to establish the extent to which colony fragmentation occurs in the field

and to obtain field estimates of genet growth rates, fecundity, and mortality in order to determine the extent to which fragmentation increases both genet survivorship and genet fecundity.

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Spatial variability in the recruitment of corals and other organisms in Kaneohe Bay, Oahu.

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Abstract

The colonization by corals and other organisms of concrete blocks and dead heads of the branching coral Porites compressa from seven different shallow water sites in Kaneohe Bay was investigated. Pocillopora damicornis was the only coral to recruit to either the blocks or the coral heads after three months. The mean number of corals colonizing both the blocks and the coral heads differed significantly between sites. Coral colonization of the two different types of substratum showed similar abundance trends at each site. Coral recruitment was highest on the windward edge of a patch reef where territories of the damselfish Stegastes fasciolatus are common.

After six months, two other species of coral, Cyphastrea ocellina and an ahermatype, ?Culicia sp. had also colonized the blocks. No recruitment by the two commonest corals in Kaneohe Bay, Porites compressa and Montipora verrucosa was detected. The mean number of corals per block was highest after six months on a windward reef flat. The mean number of corals present on the blocks increased between three and six months. At most sites the majority of individuals of Pocillopora damicornis were found on the inside uppermost surface of the blocks. The ahermatypic coral was only found on the undermost surface of the blocks.

Grazing fish were most abundant near the margins of reefs except where they were excluded by the territorial damsel fish, Stegastes fasciolatus. with low coral cover. At most sites, xanthid crabs were the most common motile invertebrates (1 cm. min. body dimension) colonizing the dead coral heads. At one site, however, hermit crabs were very abundant. Trochus intertus was the only motile invertebrate (1 cm. min. body dimensions) found on the concrete blocks. Outer surfaces of the blocks were covered primarily by algae at all sites but differences in the amount and type of algal cover probably reflected differences in fish grazing pressure n the sites. Sessile invertebrates such as tunicates, bryozoans and oysters were most common on the inner and bottom surfaces of the blocks but their relative abundances differed between sites.

Introduction

Artificial and natural substrata have been used to study coral recruitment in many different areas including the Eastern Pacific (Birkeland, 1977; Wellington, 1982); the Caribbean (Birkeland, 1977; Bak and Engel, 1979); the Great Barrier Reef (Connell, 1973; Bothwell, 1982; Wallace and Bull, 1982); Japan (Sakai, 1982) and Guam (Birkeland et al., 1982). In Hawaii, coral colonization of basalt and limestone has been recorded by Maragos (1972, 1983), Grigg and Maragos (1974) and Coles (1984). Coles also recorded coral colonization of concrete surfaces, and McVey (1970) recorded corals growing on plastic pipes. All these Hawaiian studies were performed on fringing reefs which may occasionally be exposed to strong wave action. None of these Hawaiian studies examined colonization during the first twelve months that the substrata were exposed.

Kaneohe Bay is the largest area of sheltered water in the Hawaiian Islands. Polachek (1978) recorded no coral recruitment after nine months on dead coral plates in northern Kaneohe Bay. Four species of coral: Pocillopora damicornis, Porites compressa, Montipora verrucosa, and Tubastrea aurea were recorded on P.V.C. plates after 15 months in central Kaneohe Bay (Lewis, 1980). Pocillopora damicornis were recorded by White (1980) on plates put out in some locations in Kaneohe Bay after only two weeks.

In this study, coral recruitment to two types of substratum on three patch reefs in Kaneohe Bay were compared after three months. Other organisms, both motile and sessile colonizing the substrata were also investigated.

Materials and Methods

Two types of substrata were used. The first type was concrete blocks with outer sides measuring 19.5 x 19.5 cm and inner surfaces measuring 19.5 x 11.5 cm. The second type of substratum was heads of the branching coral Porites compressa, that had been killed by exposure to the sun for 1-3 weeks. The coral heads were chosen to be similar in volume to the concrete blocks. Eight blocks and five coral heads were collected at each station three and six months after they were placed out in the field. Individual blocks and coral heads were placed in separate buckets in the field and transported back to the laboratory. The blocks were returned to the field. Colonization by corals on the blocks was recorded on eight surfaces - the top, the bottom, the two sides, the two inner vertical surfaces(inside sides) and the two inner horizontal surfaces(inside top and inside bottom). These surfaces were examined with a 10X hand lens, and the number of coral colonies on each surface was counted. The smallest corals counted were approximately 1 mm in diameter. The data for the two outer sides were pooled as were the data for the two inner vertical surfaces. The number of recruits setting on each type of surface was expressed as number of recruits/100 cm^2. Colonization by other sessile organisms on the blocks was recorded on the same surfaces as the coral colonies. No attempt was made to identify these organisms to species level. Instead, the abundance of broad taxonomic groups such as bryozoans or sponges were measured using 10 x 10 cm grid recording what type of organism intercepted 10 random points on the grid. Four blocks from each site were sampled at each time. These data were then expressed as percentage of the area covered by each taxonomic group.

To count recruits, the dead coral head was broken into pieces; and the pieces examined with a 10X hand lens. As the coral head was broken up, mobile invertebrates over 1 cm were collected and identified to species level if possible.

Nine concrete blocks placed in the field by D. Stoner in Spring 1983 were also examined. Three blocks were in cages constructed of 1 cm^2 were mesh. Three were under roofs constructed of the same mesh and three were placed directly on the reefs as controls. The blocks were examined after three and a half months exposure. Corals counted on top or on the two outer vertical surfaces (sides) were recorded as settling on exposed surfaces. Those settling on other surfaces (bottom, inside top, inside sides and inside bottom) were recorded as settling on shaded surfaces.

The nature of the substratum adjacent to where the blocks and coral heads were placed was determined using five 1 m^2 quadrats by recording what substratum type was present at 25 random points within each quadrat. The data was expressed as the percentage area covered by each substratum type that was recognized. Grazing fish at each site were counted by swimming along a 30 m stretch of reef adjacent to where the blocks were placed. All grazing fish within 2 m of the line were counted.

Study Sites

The blocks and coral heads were placed haphazardly at seven sites on three patch reefs (Heeia, Coconut Island and Urchin Reef) in Kaneohe Bay, Oahu (Fig. 1) between March 2 and April 21, 1983. The water depth at all study sites was between 1 and 2 m at high tide. Site 1 was on the windward reef edge of Heeia patch reef. There are numerous territories of the damselfish Stegastes fasciolatus at this site. Sites 2-6 were located around Coconut Island. They were located on: the windward reef edge (Site 2), the windward reef flat (Site 3), the leeward reef edge (Site 4), the leeward reef flat (Site 5) and the lagoon (Site 6). A few territories of Stegastes fasciolatus occur at Site 2. Site 7 was located on the windward side of the Urchin Reef which is so called because large numbers of Tripneustes gratilla were introduced there. The density of urchins on this reef (1.8/m^2) was much higher than at any other site. Stoner (this volume) describes where the cage blocks were placed.

Results

Coral Cover

Coral cover varied greatly between the sites from less than 2% at site 7 to approximately 70% at site 1 (Table 1). Porites compressa or Montipora verrucosa were the two most common corals at five of the seven sites. Pocillopora

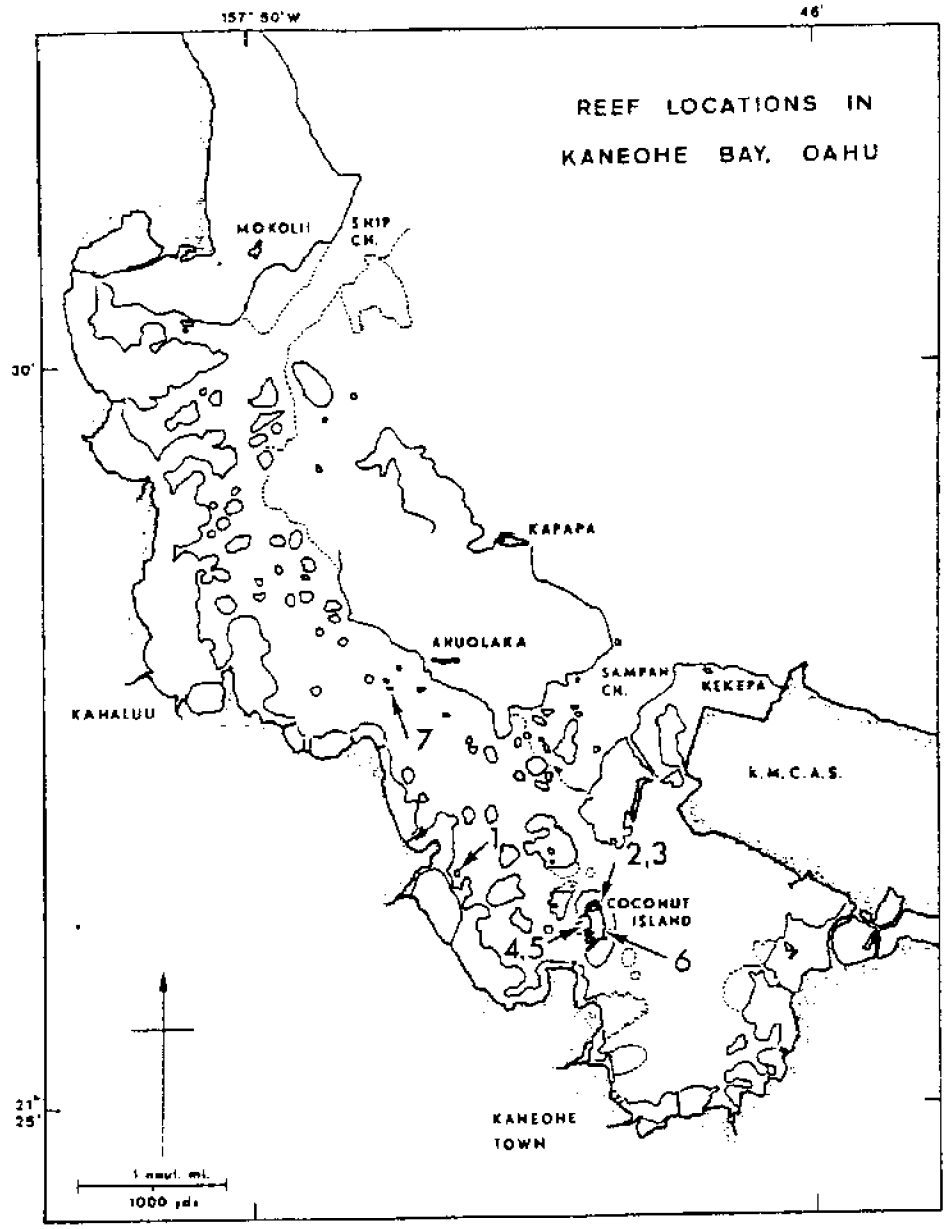

Fig. 1. Reef Locations in Kaneohe Bay; K. M. C. A. S. is the Kaneohe Marine Corps Air Station; dotted line represents reef areas below 10 feet; solid reef lines represent reefs at or near surface. Adapted from U. S. C. & G. S. Chart 4134 and aerial photographs.

damicornis was the most abundant coral at site 6. Maragos (1972) estimated that Porites compressa comprised about 85% of the total coral cover in Kaneohe Bay.

Table 1. Percentage cover estimates of coral and other types of substrata at the seven sites (mean).

	1	2	3	4	5	6	7
Total Coral	70.4	35.2	8.0	53.6	22.4	32.8	1.6
Pocillopora damicornis	25.6	6.4	1.6	1.6	0	15.2	0.8
Cyphastrea ocellina	0	0	0	1.6	0	0	0
Porites compressa	36.0	28.0	0	22.4	5.6	9.6	0.8
Montipora verrucosa	8.8	0.8	6.4	28.0	16.8	8.0	0
Coralline algae	24.8	48.0	16.8	18.4	3.2	0	0
Other algae	4.8	7.2	1.6	0	0.8	0	0
Sand	0	0	32.8	0	57.6	0	6.4
Rubble	0	3.2	16.0	28.0	16.0	67.2	92.0

Coral Colonization

After three months Pocillopora damicornis was the only coral to colonize either the concrete blocks or the dead coral heads. Recruitment rates to the two types of substratum were similar at each study site (Tables 2 and 3). No comparisons of recruitment rates per unit area to the two substrata were made since the surface area of the coral heads was not measured. Recruitment of P. damicornis to the coral heads was significantly more at site 7 than at any other site (Table 4).

After six months, two other coral species had also recruited to the blocks Cyphastrea ocellina and an ahermatypic species ?Culicia sp. The total number of corals colonizing the blocks differed significantly between three and six months as well as between sites (Tables 3, 5 and 6). At all sites except site 1, the number of corals present increased between three and six months.

Recruits of the ahermatypic coral were only found on the "bottom" or undermost surface of the blocks. Cyphastrea ocellina was found on both inner and outer surfaces of the blocks but too few colonies were present to determine if colonization was significantly higher on any particular type of surface. Pocillopora damicornis recruits were significantly more numerous per unit surface area on the "inside top" surface of the blocks except at site 1 after three months. At this site, initially the highest numbers of recruits per unit surface area were found on the outer sides of the blocks but by six months the density of recruits was highest on the inside top surface (Tables 3, 5 and 7). The percentage of Pocillopora damicornis recruits was far higher on caged blocks than on control or roofed blocks (Table 8).

Coral recruitment rates to the blocks were not strongly influenced by the amount of coral cover present at a site. After three months the highest colonization had occurred at site 1 which also had highest coral cover (approx. 70%), however, site 7, with the lowest coral cover (approx. 2%) had the second highest recruitment rates. After six months the highest numbers of corals were found on blocks from site 3 with only low coral cover (about 8%).

Grazing fish

Two species of acanthyrid (surgeonfish) and one species of scarid (parrotfish) were most abundant at sites 2 and 4. At site 1, the damselfish Stegastes fasciolatus was not able to exclude all grazers from the blocks. No grazing fish were observed adjacent to the blocks at site 7 (Table 9).

Motile invertebrates

Twenty seven species of motile invertebrates and two species of fish (1 cm min. body dimension) were collected from the coral heads (Table 10). Xanthid

Table 2. Recruitment of corals to dead coral heads (X±SE) after 3 months[1].

	SITE						
SPECIES	1	2	3	4	5	6	7
P. damicornis	20.80 ±8.87	0	1.40 ±0.51	1.60 ±0.75	2.20 ±0.80	1.40 ±0.68	3.80 ±1.47

[1] P. damicornis only species present.

Table 3. Distribution of coral settlements on cement blocks after 3 months.

A. Distribution of Pocillopora damicornis recruits (mean no. recruits per 100 cm² surface ± SE).

	SITE						
SURFACE	1	2	3	4	5	6	7
TOP							
Outside	1.05 ±0.75	0	0	0	0	0	0
Inside	0.73 ±0.48	0	0.45 ±0.22	1.12 ±0.60	1.12 ±0.48	0.22 ±0.12	1.51 ±0.17
SIDE							
Outside	1.79 ±0.63	0	0	0	0.02 ±0.02	0	0.10 ±0.07
Inside	0.14 ±0.07	0	0.03 ±0.03	0.08 ±0.06	0.20 ±0.14	0.03 ±0.03	0.50 ±0.13
BOTTOM							
Outside	0.56 ±0.20	0	0.20 ±0.10	0	0.07 ±0.04	0	0.69 ±0.27
Inside	0.14 ±0.07	0	0	0	0	0	0

B. Total all species[1] (Mean no. of recruits per block ±SE).

	SITE						
SPECIES	1	2	3	4	5	6	7
P. damicornis	22.13 ±8.23	0	1.88 ±0.83	2.88 ±1.42	3.75 ±1.13	0.63 ±0.32	9.13 ±1.75

[1] P. damicornis was only coral species present after 3 months.

Table 4. Analysis of variance for recruits on coral beads at seven different sites in Kaneohe Bay. Data were transformed using a square root transformation.

Source	DF	MS	F	p>F
Site	6	5.9544	5.39	0.0008
Error	28	1.1042		
TOTAL	34			

Results of Duncan's Multiple Range Test
Underlining indicates site means not significantly different p>0.05.

SITES	1	7	3	4	5	6	2

Table 5. Distribution of coral settlements on concrete blocks after 6 months.

A. Distribution of Pocillopora damicornis recruits.
(Mean no. recruits per 100 cm² surface±SE)

SURFACE	SITE 1	2	3	4	5	6	7
TOP							
Outside	0.30 ±0.31	0	0	0	0	0	0
Inside	1.56 ±0.58	0.28 ±0.19	2.68 ±0.57	0.95 ±0.33	1.84 ±0.52	1.00 ±0.28	2.12 ±0.22
SIDE							
Outside	0.71 ±0.17	0.12 ±0.12	0.41 ±0.11	0	0.07 ±0.03	0.02 ±0.02	0.15 ±0.05
Inside	0.42 ±0.29	0.06 ±0.04	0.59 ±0.17	0.08 ±0.08	0.47 ±0.09	0.03 ±0.03	0.73 ±0.16
BOTTOM							
Outside	0.56 ±0.31	0.10 ±0.07	0.69 ±0.22	0.26 ±0.17	0.16 ±0.09	0.07 ±0.04	0.92 ±0.33
Inside	0	0	0.06 ±0.06	0	0	0	0

B. Totals all species (Mean no. of recruits per block ±SE).

Species	SITE 1	2	3	4	5	6	7
P. damicornis	14.00 ±2.81	2.13 ±1.22	14.50 ±2.10	3.50 ±1.20	7.50 ±1.33	2.75 ±0.77	12.63 ±1.70
C. ocellina	0.25 ±0.16	0	0	0.63 ±0.33	0.38 ±0.26	0.13 ±0.13	0.13 ±0.13
Culicia sp.	0	0.88 ±0.61	3.38 ±1.57	1.63 ±0.65	0	0	0.25 ±0.16
TOTAL CORALS	14.25 ±2.88	3.00 ±1.20	17.88 ±3.01	5.75 ±1.21	7.88 ±1.43	2.88 ±0.77	13.00 ±1.78

Table 6. Comparison of the total number of corals on blocks from 7 different sites after 3 and 6 months. Data were transformed using a square root transformation.

Source	DF	MS	F	p>F
Site[1]	6	16.1195	16.08	0.0001
Rep(Site)[2]	49	1.0023	0.61	0.0500
Time	1	23.1916	25.39	0.0001
Site X Time	6	3.9342	4.31	0.0015
Error	49	0.9472		
TOTAL	111			

Results of Duncan's Multiple Range Test.
Underlining indicates stations whose means are not significantly different p>0.05.

a) sites 1 7 3 5 4 6 2

b. Times 6 months > 3 months

[1]error mean square is rep(site) [2]error mean square is true between site variance (time excluded from the model)

Table 7. Comparison of the total number of Pocillopora damicornis on different surfaces of blocks from 7 different sites after 3 and 6 months (ANOVA). Data were transformed using a square root transformation.

Source	DF	MS	F	p>F
Site[1]	6	0.9555	9.99	0.0001
Block(Site)[2]	49	0.0956	1.73	0.0028
Surface(Block Site)[2]	280	0.1255	2.28	0.0001
Time[3]	1	1.0050	14.65	0.0004
SiteXTime[3]	6	0.1993	2.91	0.0167
BlockXTime(Site)	49	0.0736	1.48	0.0273
Error	280	0.0463		
TOTAL	671			

Results of Duncan's Multiple Range Test.
Underlining indicates means not significantly different p>0.05.

a) SITES 1 7 3 5 4 6 2

b) TIMES 6 months > 3 months

c) Surfaces
Inside Top Bottom Inside Side Side Top Inside Bottom

[1]error term was block(site)
[2]error term was true between site variance (time excluded from the model).
[3]error term was blockXtime(site)

Table 8. Mean percentage of Pocillopora damicornis recruits on exposed surfaces of blocks (x±Se)

Treatment	% of Recruits on Exposed Surfaces
Control	2.0±2.0
Roof	2.0±2.0
Caged	43.7±8.4

Table 9. Grazing fish abundances at the different sites (X+SE).

SPECIES	SITE 1	2	3	4	5	6	7
Acanthurus triostegus	0	3.7±1.5	0.3±0.3	0	0	0	0
Carus sp.	10.0±7.2	54.7±11.6	2.0±2.0	29.3±8.9	2.0±0.6	3.0±1.5	0
Zebrasoma flavescens	0	1.3±0.7	0	0	0	0	0

Table 10. Motile invertebrates colonizing dead coral heads after 3 months: mean + SE (n=5) for sites 1-3,6,7: and range (n=2) for sites 4 and 5.

	SITE						
	1	2	3	4	5	6	7
PHYLUM ARTHROPODA							
Class Crustacea							
Family Xanthidae							
Carpilius convexus (Forskal)							0.2 ±0.2
Chorodiella laevissima (Dana)	6.4 ±2.7	3.8 ±0.9	1.6 ±0.7			0.4 ±0.2	1.8 ±0.7
Etisus laevimanus Randall			0.2 ±0.2	0-2 ±1.0		2.2 ±1.2	
Liomera bella (Dana)		0.2 ±0.2		1.0			0.2 ±0.2
Lophozozymes sp.	0.4 ±0.2						
Platypodia eydouxi (A. Milne Edwards)			0.2 ±0.2			0.4 ±0.2	1.0 ±0.3
Phymodius undulatus (A. Milne Edwards)	0.4 ±0.2	3.6 ±1.3	3.2 ±1.0	1-5	2.0	12.4 ±3.2	6.8 ±1.2
TOTAL xanthids	7.2 ±2.7	7.6 ±3.4	5.2 ±2.0	4-6	2.0	15.2 ±2.4	8.0 ±2.1
Family Portunidae							
Thalamita spiceri Edmondson					0-1	1.2 ±0.5	
Thalamita sp.						0.2 ±0.2	
Family Squillidae							
Goniodactylus falcatus (Forskal)	0.2 ±0.2	0.2 ±0.2	0.2 ±0.2	0-1	1.0		0.8 ±0.2
Family Diogenidae							
Calcinus latens (Randall)		1.4 ±0.8	1.2 ±0.8		0-1		30.2 ±16.2[1]
Family Alpheidae							
Alpheus gracilipes Stimpson	0.2 ±0.2	0.2 ±0.2	1.2 ±0.8		1-2		
Family Palaemonidae							
Palaemonella rotumana (Borradaile)		0.2 ±0.2	0.6 ±0.2		0-1		
PHYLUM ECHINODERMATA							
Class Asteroidea							
Family Asteridae							
Asterina anomala Clark						0.2 ±0.2	
Class Holothuroidea							
holothuroid sp. 1		0.4 ±0.4					0.2 ±0.2

Table 10 (cont.)

	SITE 1	2	3	4	5	6	7
Class Ophiuroidea							
ophiuroid sp. 1						0.6 ±0.6	
PHYLUM CHORDATA							
Class Pisces							
Family Blennidae							
Enchelyurus brunneolus Jenkins		0.6 ±0.2					
Family Bleotridae							
Asterropteryx semipunctatus Rüppell			1.0 ±0.6		0-1	0.4 ±0.2	0.2 ±0.2
PHYLUM PLATYHELMINTHES							
platyhelminth sp. 1							0.2 ±0.2
PHYLUM MOLLUSCA							
Class Gastropoda							
Family Trochidae							
Trochus intextus Reiner	0.4 ±0.2	2.4 ±1.5	1.0 ±0.3	0-1			
Family Triviidae							
Trivia sp.	0.2 ±0.2						0.2 ±0.2
Family Thaididae							
Drupella ochrostoma (Blainville)							0.2 ±0.2
Family Fissurellidae							
Diodora octogona Reeve		0.2 ±0.2					0.2 ±0.2
Family Mytilidae							
Brachidontes crebristriatus (Conrad)							0.2 ±0.2
Family Fasciolariidae							
Peristernia chlorostoma (Soverby)					0-1		
Family Mitridae							
Mitra assimilis Reeve		0.2 ±0.2					
Family Doridae							
dorid sp. 1		0.2 ±0.2					
PHYLUM ANNELIDA							
Class Polychaeta							
aphroditid sp. 1						0.4 ±0.2	

crabs were the most abundant invertebrates in the coral heads at most sites. Molluscs were relatively uncommon on the coral heads with the most common being Trochus intextus. There were differences in the abundance of invertebrate species between sites. For example, the hermit crab Calcinus latens was more than 10 times more abundant at site 7 than any other site.

Sessile organisms (Fig. 2a-g)

The top and two outer "sides" of the concrete blocks were covered predominantly by algae at all sites. On the top surface, the algae were often coated by a fine sediment coating particularly at site 6 and 7. At site 2, corallines and crustose red algae were most abundant on the top surface after three and six months. Heavy fish grazing at site 1 probably was responsible for the high cover of coralline algae at this site (Hixon and Brostoff, 1982). After three months, the outer surfaces of the blocks at most sites were covered by a short (<1 mm) algal turf of filamentous green algae such as Cladophora sp., brown algae such as Ectocarpus sp. and blue-green algae. At site 1 and 5 after three months, much longer filamentous algae including Ectocarpus were present. After six months at site 1, macroalgae such as Dictyosphaeria cavernossa and Gelidiella sp. had colonized the blocks. At site 7, after six months, long filamentous blue-green algae were present on the top surface of the blocks. At site 3 much of the algae cover after six months was made up of Acanthophora spiceri, Polysiphonia sp. and Ectocarpus sp.

Over 50% of the "bottom" surfaces of the blocks at most sites were covered only by a microbial film after three months. Bryozoans, tunicates or serpulid polychaetes covered the remaining area. At sites 2 and 7, invertebrates covered a higher proportion of the available area. After six months, bryozoans were the most abundant sessile animals at all sites except 5 and 6. At some sites (1,4,5, and 6) a large amount of the area available on the bottom of the blocks was still covered only by a microbial film. At site 7, the area on the bottom of the blocks covered by tunicate, principally Didemnum candidum, declined sharply between three and six months.

On the "inside bottom" surface of the blocks accumulation of large amounts of sediment occurred particularly at sites 3, 6 and 7 precluding successful colonization by most organisms. At sites 1, 2 and 4 recruitment of algae and invertebrates occurred on the inside bottom surface. With the exception of site 1, the amount of sediment present on the inside bottom surface increased between three and six months.

On the other inner surfaces after three months, very thin patchy algal films of diatoms and some Cladophora sp. covered much of the available surface area. Bryozoans and oysters were the most abundant invertebrates. The cover of bryozoans increased between three and six months at most sites. Some larger algae were present at sites 1, 3 and 7.

Discussion

Estimates of recruitment rates in the literature vary greatly. Wallace and Bull (1982) recorded up to 54 recruits/100 cm² after four months on pieces of dead coral. Polachek (1978) recorded no recruitment of corals to plates cut from dead corals placed out in Kaneohe Bay for nine months. Differences in recruitment rates between studies may reflect differences in techniques, variations in the time periods over which observations were made, and differences in the composition of the fauna in different localities. There is some evidence, however, that species may show different life history characteristics in different localities. Pocillopora damicornis planulates at different stages of the lunar cycle in different locations (Harriot, 1983; Richmond and Jokiel, 1984). In the Eastern Pacific, larval settlement of this species is extremely rare (Birkeland, 1977) but elsewhere in the Pacific it may be an opportunistic species (Maragos, 1972; Bothwell, 1982).

Common corals in Kaneohe Bay include those that spawn eggs and sperm, for example, Porites compressa, Montipora verrucosa and Fungia scutaria (Krupp, 1983; Heyward, this vol.); and those that release planulae, for example, Cyphastrea ocellina and Pocillopora damicornis (Harrigan, 1972; Stimson, 1978; Richmond and Jokiel, 1984; Wright, this vol.). The reproductive biology of the ahermatypic coral ?Culicia sp. is not known.

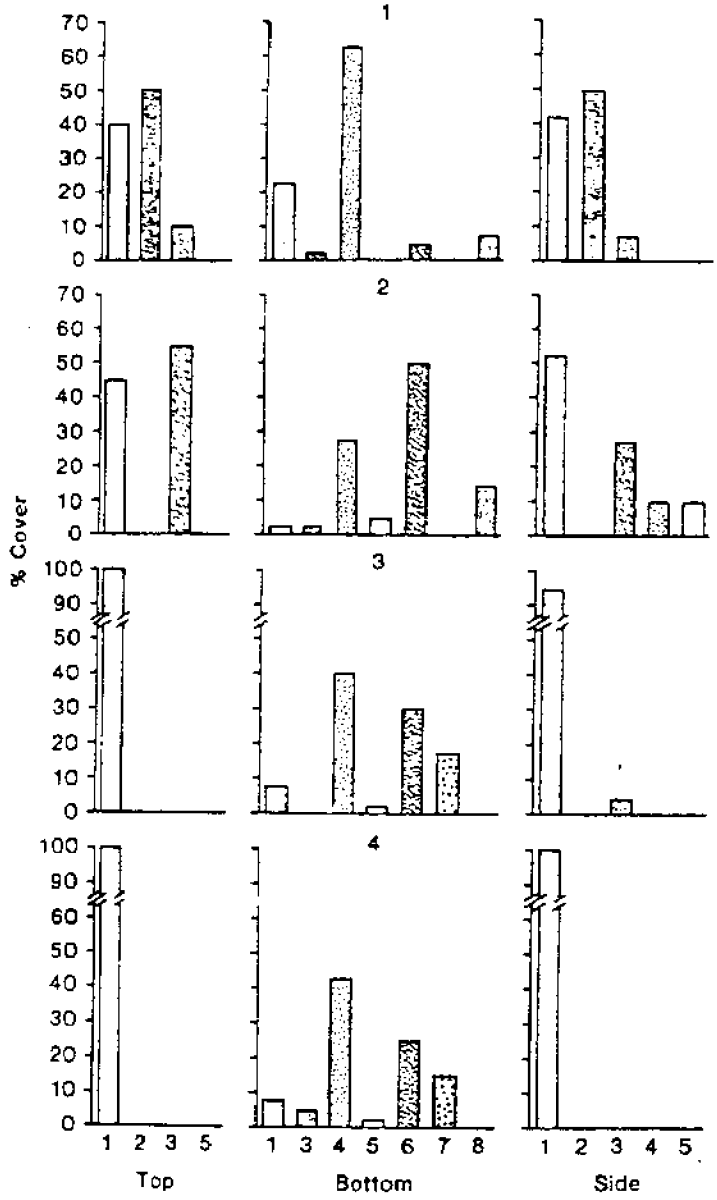

Fig. 2a. Percentage cover of different organisms on top, bottom and side surfaces of blocks after 3 months; from sites 1-4.
1=algal turf ≤1mm high, 2=macroalgae >1mm high,
3=coralline + red crustose algae, 4=microbial film,
5=oysters, 6=bryozoans,
7=tunicates, 8=polychaetes,
9=sponges, 10=anemones,
11=corals, 12=zoanthids,
13=sediment.

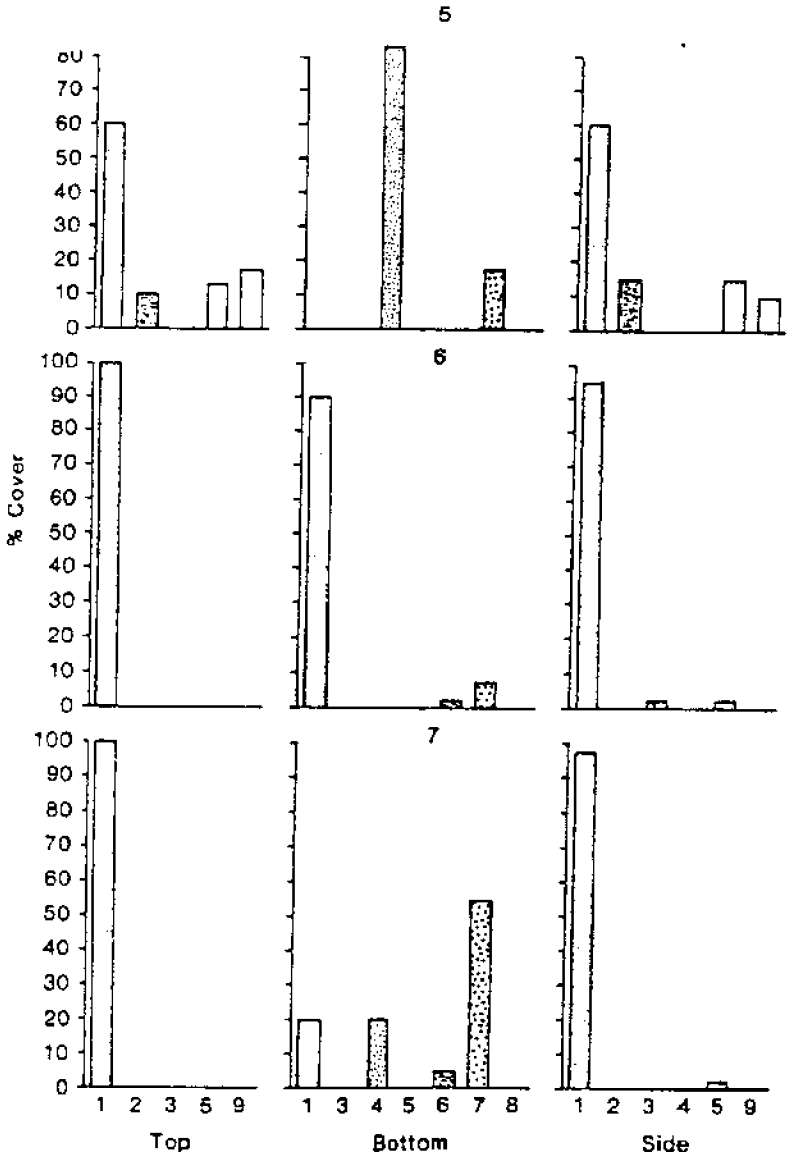

Fig. 2b. Percentage cover of different organisms on top, bottom, and side surfaces of blocks from sites 5-7 after 3 months. Key for organisms as in Fig. 2a.

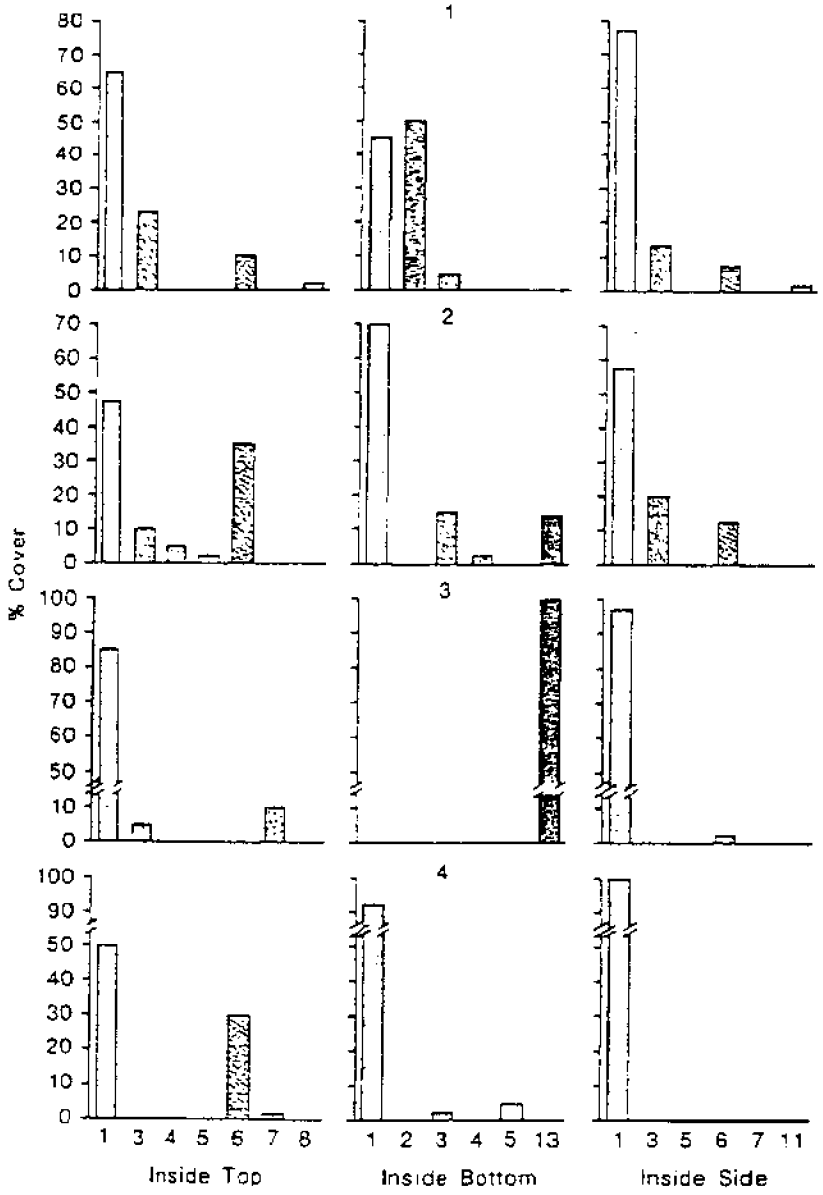

Fig. 2c. Percentage cover of different organisms on inside top, inside bottom, and inside side surfaces of blocks from sites 1-4 after 3 months. See Fig. 2a for key.

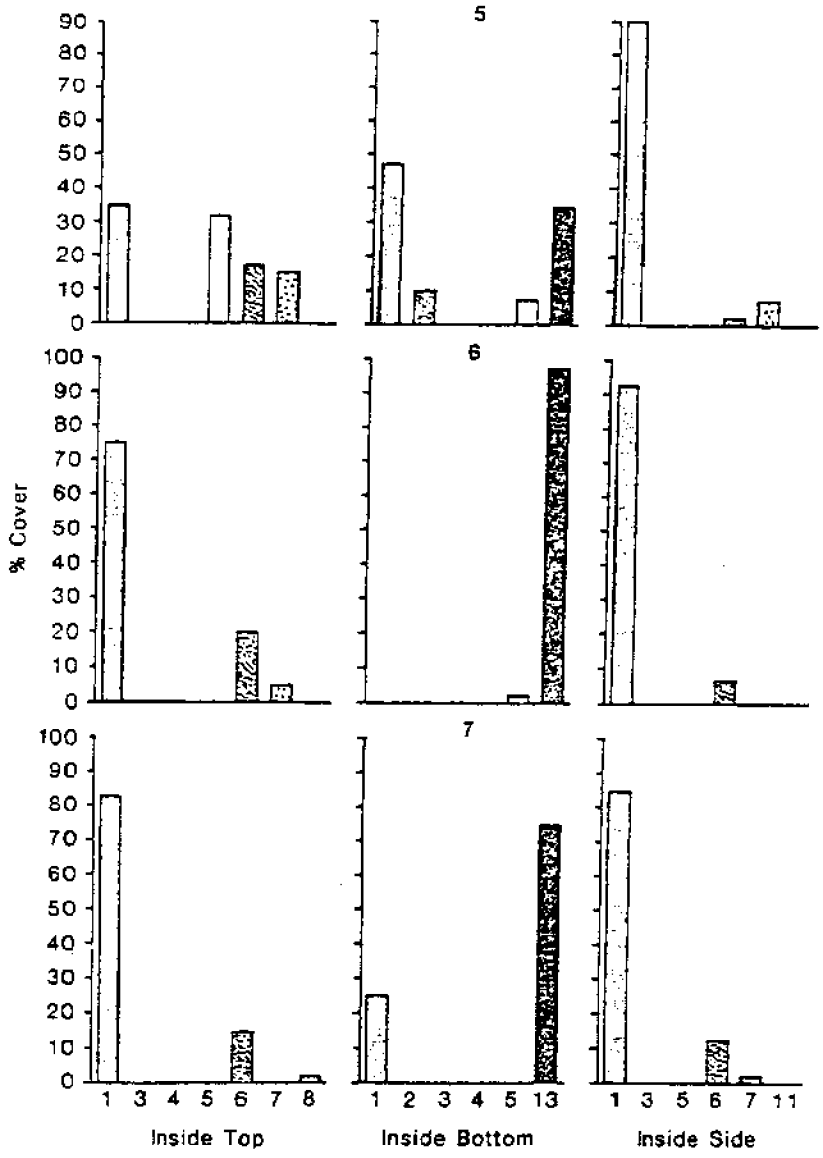

Fig. 2d. Percentage cover of different organisms on inside top, inside bottom, and inside side surfaces of blocks from sites 5-7 after 3 months. See Fig. 2a for key.

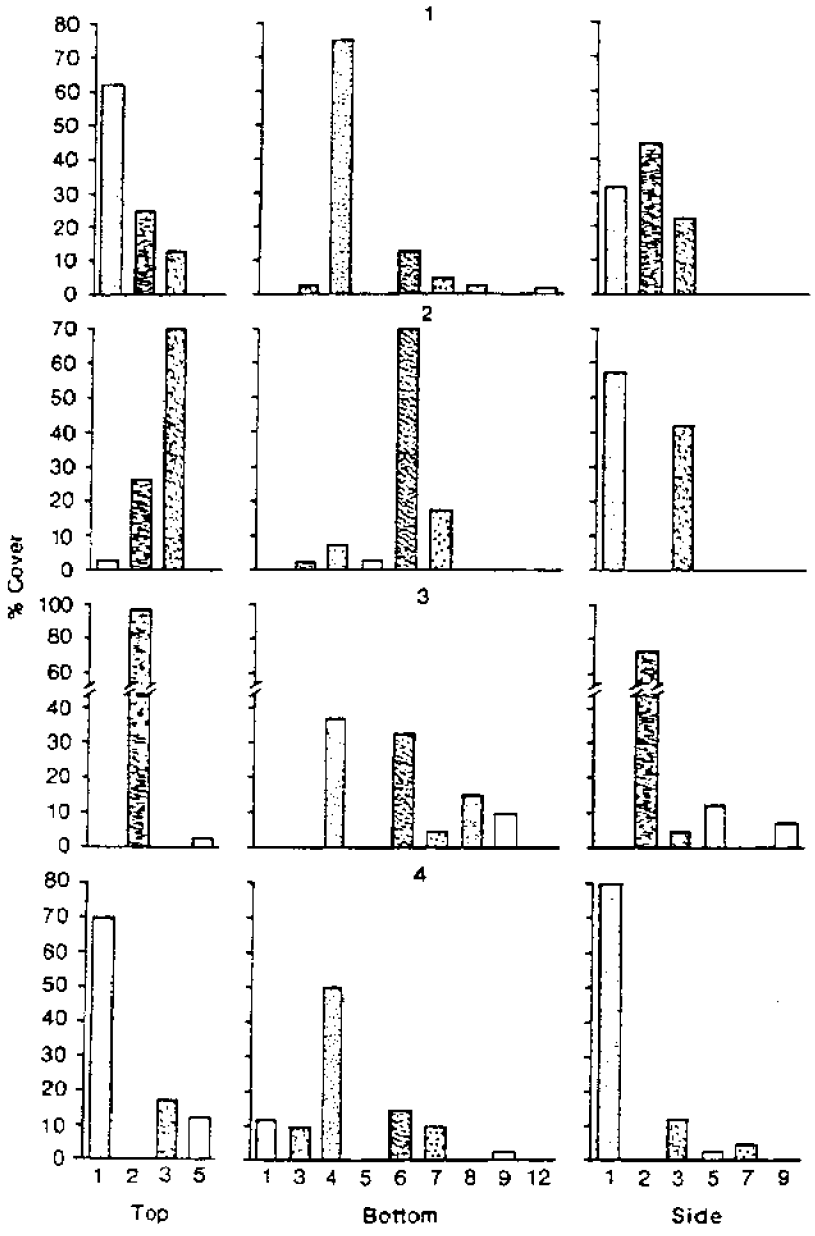

Fig. 2e. Percentage cover of different organisms on top, bottom and side surfaces of blocks from sites 1-4 after six months. See Fig. 2a for key.

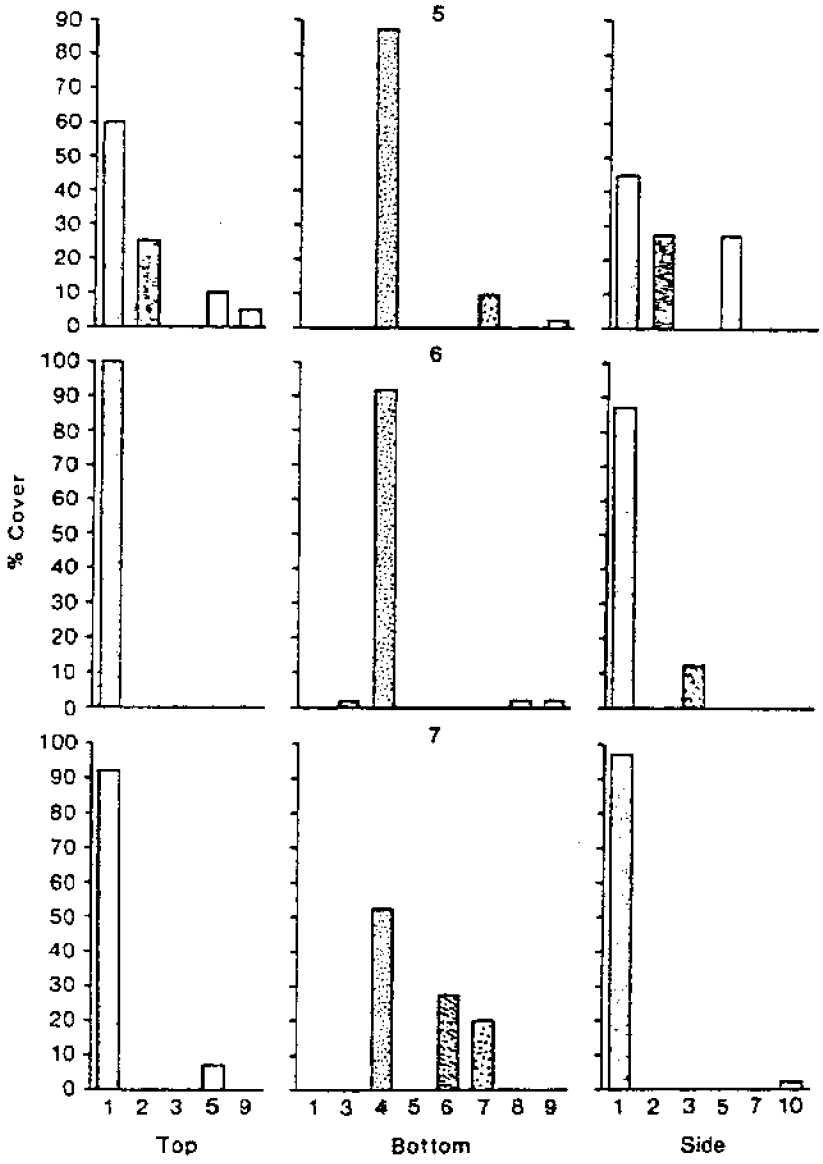

Fig. 2f. Percentage cover of different organisms on top, bottom, and side surfaces of blocks from sites 5-7 after 6 months. See Fig. 2a for key.

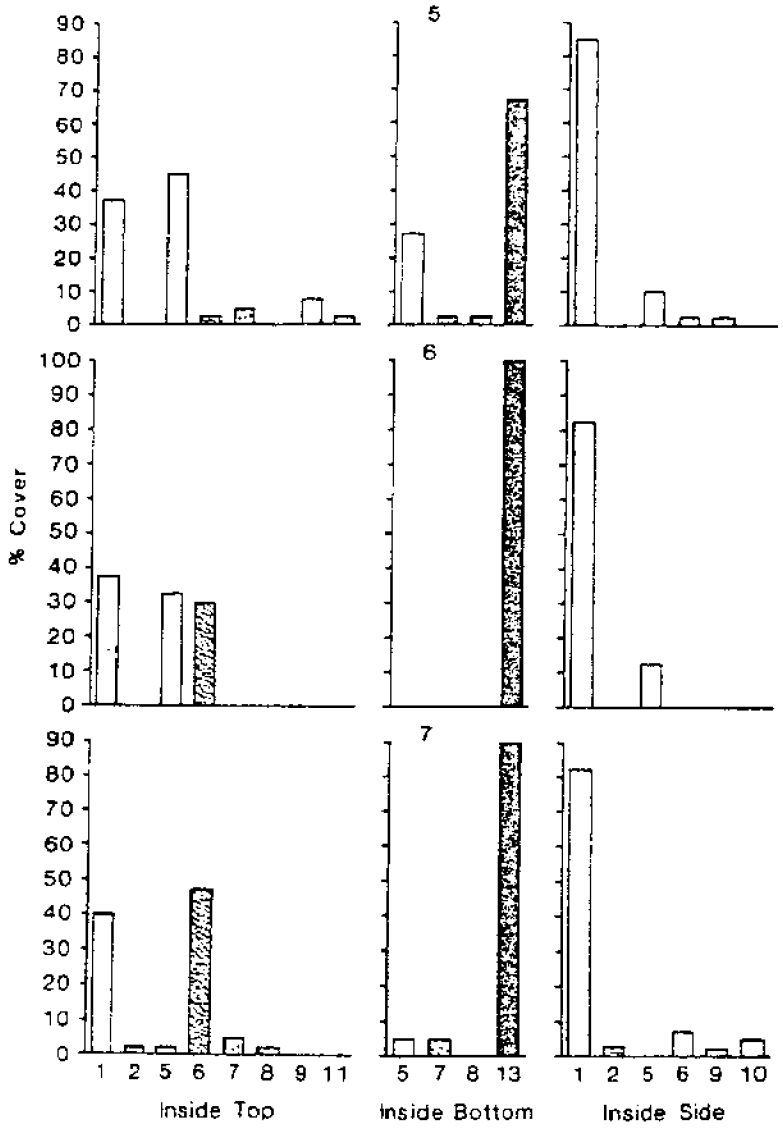

Fig. 2g. Percentage cover of different organisms on the inside top, inside bottom and inside side surface of the blocks from sites 1-4 after six months. See Fig. 2a for key.

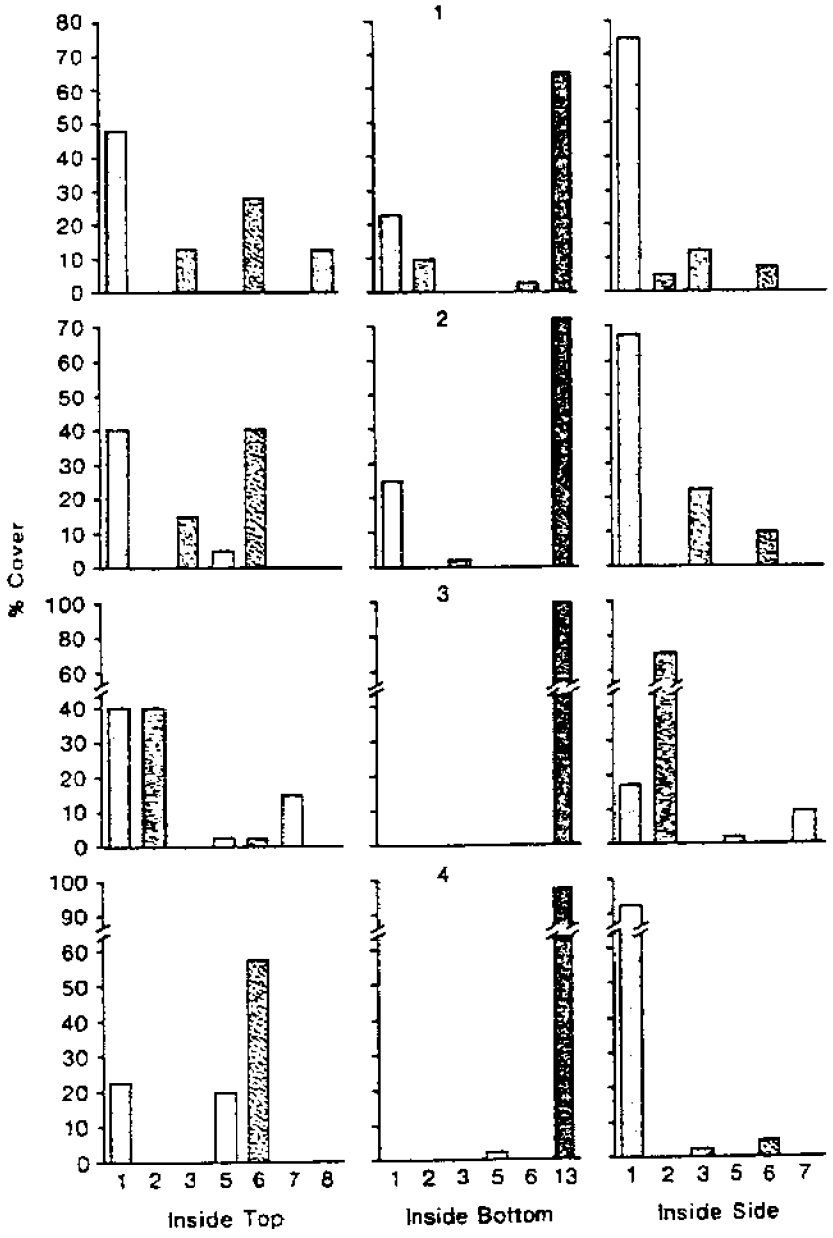

Fig. 2h. Percentage cover of different organisms on the inside top, inside bottom and inside side surface of the blocks from sites 5-7 after six months. See Fig. 2a for key.

The only hermatypic corals detected on the blocks after six months were both planulating species. One of them, Pocillopora damicornis has been recognized as an early colonizing species in Hawaii as well as other parts of the world (Maragos, 1972; Schumacher, 1977; Bothwell, 1982; Sakai, 1982). In Hawaii, most previous studies of coral colonization and community development have been carried out in more wave-exposed areas where another pocilloporid, Pocillopora meandrina is a conspicuous early colonist (Grigg and Maragos, 1974; Maragos, 1975; Coles, in press).

Spawning of many non-planulating species including Porites compressa and Montipora verrucosa occurred while the blocks were in situ (Heyward, this vol.), nevertheless, no recruitment by these species was detected on the blocks after six months' exposure. At the time of settlement Porites compressa and Montipora verrucosa larvae are significantly less than 1 mm (Hodgson, this vol.). The time taken for the larvae to reach 1 mm (the minimum size at which they could be detected in this study) is unknown. If growth rates of newly settled individuals of these species are slow it is possible that newly settled individuals of Porites compressa and Montipora verrucosa were overlooked in this study.

Coral recruitment rates were found to differ significantly between similar habitats on different patch reefs, as well as between different habitats on one patch reef. The number of recruits present on the blocks was the number of larvae that settled less the number that died after settlement. Hodgson (this vol.) found that coral planulae were distributed in patches. Some of the differences in recruitment rates recorded may be due to differences in the availability of larvae at the different sites. Regardless of these differences in larval availability at each site, early mortality of juveniles was probably high at all sites (Rylaarsdam, 1983).

After three months, coral recruitment was highest at site 1 where territories of the damselfish Stegastes fasciolatus form a continuous belt around the windward edge of the reef. S. fasciolatus actively excludes grazing fish such as scarids and acanthurids (Hixon and Brostoff, 1982, 1983). The higher recruitment rates at this site after three months may be attributable to the reduced grazing of the substrata in the damselfish territories. Sammarco and Carleton (1982) found recruitment rates to be five times higher in territories of the damselfish Hemiglyphidon plagiometophon than on substrata exposed to grazing fish. Territories of the damselfish Eupomacentrus acapulcoensis also act as refuges for juvenile Pocillopora damicornis.

By six months the number of juvenile corals at site 1 had declined. This may have been due to overgrowth by algae at this site. The sites with the highest number of juvenile corals present (sites 1, 3, 7) were sites either where grazing fish were rare or where damselfish were actively excluding them from the recruitment. Grazing fish have been shown to have a negative impact on coral recruitment (Brock, 1979; Neudecker, 1979; Sammarco and Carleton, 1982).

Damage to young corals by grazing fish is probably restricted to small individuals. Presumably, grazing fish such as acanthurids and scarids which are primarily herbivores can differentiate corals from preferred food items once the corals reach a threshold size of perhaps 3 to 4 mm (Birkeland, 1977; Brock, 1979). If a coral reaches this size it may escape further grazer damage. Corals that recruit to areas where there are few grazing fish may escape damage from grazers but in turn, may be overgrown by algae or more rapidly growing sessile invertebrates (Birkeland, 1977). Harriot (1983) found that the mortality of Pocillopora damicornis settling on algal covered blocks was much higher than on blocks relatively free of algae.

Urchins are capable of damaging newly settled corals (Sammarco, 1980, 1982; Rylaarsdam, 1983), however the role of other grazing invertebrates on coral recruitment has not been investigated. Hodgson (personal communication) has observed an unidentified xanthid crab dislodging newly settled corals. Xanthids may occur at high densities (Peyrot-Clausade, 1977). Their nocturnal behavior and cryptic habits make visual censuses difficult and probably explain why estimates of xanthid densities are much lower in studies that are based on visual estimates (Hatcher, 1982; Hayes et al., 1982). Trochus intextus, the largest grazing mollusc on the blocks and coral heads, has a robust radula (Hickman, personal commun.). It could perhaps damage newly settled corals in a fashion similar to that in which limpets damage newly settled barnacles (Stimson, 1970).

The majority of Pocillopora damicornis recruits were found on the inside top surface of the blocks at all sites except site 1 after three months. Previous studies have also found that juvenile hermatypic corals are more abundant on lower rather than upper surfaces of settling plates and vertical rather than horizontal upward facing surfaces in shallow water (Birkeland, 1977; Bak and Engel, 1979; Birkeland et al., 1982; Sato, 1982; Wallace and Bull, 1982). As Wallace and Bull point out, it is not clear whether the distribution of recruits is due primarily to differential mortality of recruits on different surfaces or if larvae are capable of selecting where they settle. Sato (1982) performed experiments to separate the effects of sedimentation, grazing and competition with algae on the survival of Pocillopora damicornis on different surface orientations and he concluded that P. damicornis survival was highest on downwards facing dishes. Corals that settle in shaded areas such as the inside top surface of the blocks may grow out into more well-lit areas (Birkeland, 1977; pers. obs.).

Sammarco and Carleton (1982) concluded that light rather than damage by grazing fish was important in determining the spatial distribution of corals since blocks shaded by a cage or roof had a higher proportion of recruits on exposed surfaces than unshaded blocks placed in or outside damselfish territories. This conclusion conflicts with results presented here in which only caged blocks and not those with roofs had a higher proportion of Pocillopora damicornis on the exposed surfaces. The high number of recruits on the outside of the blocks from site 1 may be related to the reduced fish grazing within Stegastes fasciolatus territories.

Sedimentation and competition with other organisms are two other causes of mortality that may influence the distribution of juvenile corals on the blocks. Sedimentation apparently prevented corals from surviving on the inside bottom surface of the blocks. Sediment also accumulated on the top of blocks with a thick algal covering. Corals less than 4 mm in diameter may be more susceptible to death from sedimentation than larger individuals (Bak and Engel, 1979).

Depending on which surface of the block a coral settled on, it was likely to encounter different types of organisms with which to compete for space. The type of organisms present were influence by the grazing regime present at that site (Sammarco and Carleton, 1982). Overgrowth of corals by a variety of organisms occurs (Bak and Engel, 1979; Sammarco, 1980). It is however difficult to asssess the true frequency of overgrowth since it may occur rapidly, for example, in less than one week an oyster had totally overgrown a juvenile Pocillopora damicornis (Fitzhardinge, pers. obs.). Bak and Engel (1979) were only able to determine the cause of juvenile coral death in less than 50% of the cases although they monitored the corals fortnightly.

Acknowledgements

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Larval release in the sponge Callyspongia diffusa

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Abstract

Release of larvae from Callyspongia diffusa was noted in early August, 1983, at Coconut Island in Kaneohe Bay, Hawaii. The larvae swam about a finger bowl propelled by their surface cilia for about 16 h and were found settled on the bottom of the bowl the following day. Histological observations of the larvae forming within the parent sponge were more consistent with that of embryo development than that of gemmule formation.

Introduction

Sponges are known to have several means of reproduction. Sexual reproduction in the development of a ciliated swimming larvae as has been demonstrated for several marine sponges (Wilson, 1894; Okada, 1928). Several types of asexual reproduction in sponges have also been noted. Asexual gemmules arise from an aggregation of disorganized choanocytes and/or mesohyl cells usually located in the basal portion of the adult sponge. The surface epithelial cells of these forming gemmules secrete a capsule or acellular layer which acts as protection against adverse conditions. When the adult sponge dies and degenerates due to the changing environment, the gemmules are either left in place to regenerate the original sponge, or are separated and dispersed by the water currents. When a batch of gemmules originating from the same adult sponge hatch, they release cells that intermingle and form a functional adult sponge capable of filter feeding and growth (Hartman, 1958; Rasmont, 1962; Connes, 1975). Alternatively, a gemmule can release a ciliated larvae that can swim, choose an appropriate settling habitat, attach to the substrate, spread, metamorphose, and finally begin to pump water and filter feed as a small adult (Wilson, 1894). Therefore, ciliated larvae can originate from either sexual or asexual reproduction and can appear identical in gross anatomy. The larvae released from Microciona prolifera, as noted by Warburton (1966), were only assumed to be a result of sexual reproduction since histology of the sponge tissue was not done to determine the origins of the embryos. Another method of asexual reproduction is by fragmentation; the breaking apart of an adult sponge with the resulting fragments reattaching to the substrate establishing viable sponges (Jokiel et al., 1982; Neigel and Avise, 1983). Encrusting sponges can spread over the substrate in many directions. Tissue death in central portions often produces separate sponges that grow independently but share the same genotype (unpublished observations of Hymeniacidon sinapium). Budding is a form of controlled fragmentation often seen in Tethya species (Wilson, 1894; Bergquist, 1978; unpublished observations of Tethya auratium).

The immune system of Callyspongia diffusa, a purple-colored branching sponge found on reef crests in Kaneohe Bay, Hawaii, has recently been a subject of investigation (Hildemann et al., 1980; Bigger et al., 1981, 1982; Johnston et al., 1983). In conjunction with original (Hildemann et al., 1980), and cellular studies (Johnston and Hildemann, 1983), genetic patterns of the population structure were examined using allograft acceptance and rejection (Jokiel et al., 1982). Those observations suggested fragmentation to be one mode of reproduction for Callyspongia. The closer together the sponges were located on a reef, the greater chance that subsequent parabioses would result in fusion of paired sponges. Production of sexual larvae was assumed to be taking place in Callyspongia but had not been observed in the Kaneohe Bay animals. It is important to understand all the reproductive capabilities and strategies of a poorly understood species before using data from wild populations to generate theories of the genetics underlying a measurable histocompatability system. Fragmentation has been documented as effecting the genetics of the Callyspongia population structure (Jokiel et al., 1982). This paper will describe the presence of embryos within the tissues of the adult sponge, the release of ciliated larvae and their post-release behavior.

Observations

In early August, 1983, a variation in the gross tissue morphology was noticed in some of the sponges. The internal core of the branches showed cords or tracts of lighter colored tissue as compared to the rest of the animal. Higher magnification from a dissecting microscope revealed many small lavender spheres embedded in the light colored tissue tracts (Fig. 1). One animal was induced to release its larvae by leaving it overnight in a finger bowl of unaerated seawater. At mid morning the following day, the larvae were being ejected out of the oscula and carried several inches from the adult in the excurrent water stream. Following their release, the larvae swam about the bowl at or near the surface of the water. They were 220 microns x 280 microns, covered with cilia except for the dark purple-colored posterior pole which had none, but which was encircled with much longer cilia (Fig. 2). By the next morning, the larvae had altered their swimming pattern, settled on the bottom of the bowl, and begun to spread out. Similar behavior has been reported for the larvae of Microciona prolifera (Warburton, 1966). Sections of the adult sponge containing embryos showed the embryonic cells to be large, homogeneous and densely packed with a thin covering of epithelium. A few spicules were present. No capsule or secreted acellular layer was evident (Fig. 3).

Discussion

Sponges are known to produce sexual as well as asexual larvae (Wilson, 1894; Bergquist et al., 1970) and an understanding of the larval type produced by Callyspongia should be important for future studies of the population structure. Sivaramakrishnan (1951) investigated an Indian Ocean population of Callyspongia diffusa and reported that asexual larvae were produced from gemmules. Although the present study did not address this question, some observations and comparisons to other studies may be pertinent. What may have been eggs and sperm were noted on occasion in dissociated cell preparations from Callyspongia (unpublished observation), and appeared very similar to that of Halichondria panicea (see Fell, 1974, Fig. 8, page 73). This might suggest sexual reproduction, but alternatively these cells could have entered the animal through the aquiferous system and not be of Callyspongia origin.

Gemmules are protected packets of cells produced by the adult sponge for the purpose of over-wintering. They are typically found flattened against the substrate to which they continue to adhere during adverse conditions when the adult sponge dies and disintegrates (Fell, 1974). Gemmules have been noted in marine species (Hartman, 1958) even though they are more commonly found in fresh water forms (Rasmont, 1962). The observations made here for Callyspongia and those reported by Sivaramakrishnan (1951) describing the reproductive bodies do not correlate to that of a gemmules. They are not clustered at the base of the animal but are found throughout the tissues. They do not appear to be produced for over-wintering purposes, but are ultimately released as free swimming larvae. The adult animal is healthy and thriving rather than disintegrating due to adverse conditions. The illustrations of gemmules by Sivaramakrishnan are very similar to the embryos shown here in section (Fig. 3), and to the oocytes and embroyos of Haliclona echasis (see Fell, 1974, Fig. 5, page 69). In no case was a thick protective covering noted. Sivaramakrishnan only describes a thin envelope in his text that is not obvious in the photographs. Perhaps Sivaramakrishnan is describing the development of embryos forming ciliated larvae to which he is erroneously applying the term "gemmules". His description of their formation even correlates to oogenesis where the oocyte is surrounded by and engulfs nurse cells followed by the cleavage and development of the embryo (Fell, 1974).

The ciliated, actively swimming larvae of Callyspongia that is ejected from the adult results in the dispersal of the species to settlement areas distant from the adult. This is unlike larvae that may only crawl on the substrate and settle short distances from the parent (Mileikovsky, 1971). The distances and directions that these larvae travel will depend on the length of time that the larvae spend swimming at the surface, the wind direction, water currents and tides. An 8-12 h planktonic period (assumed from larval behavior in a finger bowl) is sufficient time for released larvae to be carried from the nearby environment of the parent and perhaps be removed from the Coconut Island reefs.

This observation of a dispersal mechanism bears on the population genetics of the species, but unanswered is the question of whether the larvae are sexual or

Fig. 1. Adult Callyspongia that contains larvae. (L=larvae)

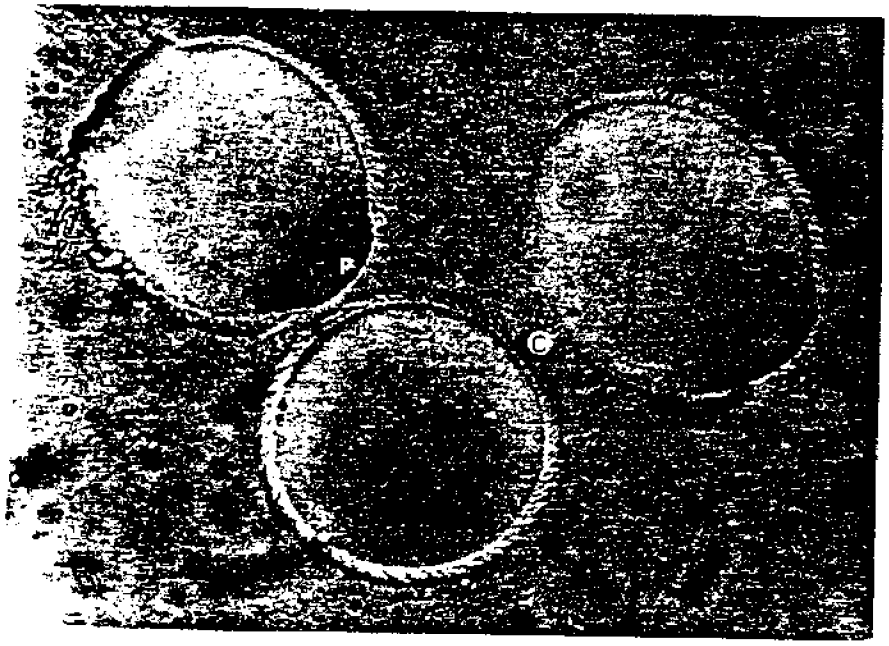

Fig. 2. Callyspongia larvae a few hours after release. Note the darkly pigmented posterior pole and the surrounding cilia. (C=cilia; P=posterior pole)

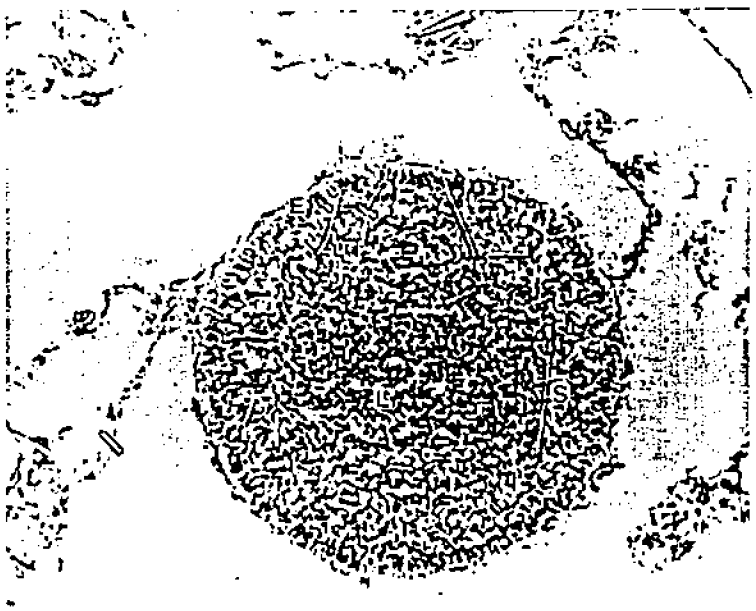

Fig. 3. A hemotoxylin and eosin stained paraffin section of a Bouin's fixed sponge containing larvae that shows the larval cells to be homogeneous in the interior with a covering layer of thin epithelial cells. Note the spicules. No capsule or acellular layer is evident. (L=larvae; S=spicules; E=epithelial cells)

asexual. In a benign environment to which the animal is well adapted it may be advantageous to produce identical copies of a successful genotype, but in a changing or changeable habitat, sexual offspring with the chance of enhanced adaptability have obvious advantages. The answer to the question of larval origin may be obtained most easily by using graft acceptance or rejection as a measure of genetic identity. The parabiosis of offspring from the same or different parents should show the following. When larvae or newly metamorphosed sponges from genetically different parents can be shown to reject, this will indicate the age of immunocompetence for this species of sponge, and will act as a positive control. Subsequently, if offspring from the same parent fuse, this will indicate genetic identity of the larvae and they can be assumed to be asexually produced. If offspring from the same parent reject, this will indicate genetic nonidentity, and the larvae can be assumed to be products of sexual reproduction. Past work on adult Callyspongia where over 750 parabioses have resulted in rejection (Hildemann et al., 1980; Bigger et al., 1981,1982) would predict that Callyspongia probably produces sexual larvae.

Acknowledgements

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Symbiosis in coral reef communities: a review

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Abstract

Symbioses, close heterospecific associations, are particularly numerous in coral reef communities. These associations represent results of the evolution of many types of adaptive interactions, including coevolution. Although many can be classified according to the traditional categories of parasitism, commensalism, and mutualism, others are difficult to categorize, especially since little is known about their biology. Of special significance are the wide variety of symbioses involving reef corals as hosts for symbionts.

Introduction

The establishment of a close association between two species as an alternative to direct competition is an important "strategy" for survival in biotic communities. This can be especially significant in highly diverse communities, such as coral reefs, where selection for survival in the face of strong competition is at a premium. The term symbiosis is used here to designate these close heterospecific associations irrespective of harm or benefit to the partners. This designation is in accordance with the original definition of the term by de Bary (1879) as "different species living together." Unfortunately, the term has also been used as a synonym of mutualism, which is only one of several types of heterospecific associations.

Coral reef communities represent the largest assemblage of symbiotic associations in the marine environment and possibly in the biosphere. Reef corals themselves are hosts to a variety of symbionts, from obligate zooxanthellae crucial to the survival of the host to numerous types of external associates. Corals provide a large surface area, shelter among branches, potential food (tissue, mucus and its associated detritus, food caught by ciliary-mucoid activity) and a hard skeleton for burrowers and gall-forming forms. The defense mechanisms of the coral hosts (especially nematocysts and extruded mesenterial filaments), although a barrier to symbionts particularly during larval settlement, may be used by established symbionts to their advantage. Although dead coral colonies are utilized as temporary habitats by a diverse group of non-specialists, only live corals provide a more stable environment to symbiotic specialists (see Coles, 1980).

The Meaning of Symbiosis

Symbioses are perhaps best recognized as a broad category of heterospecific associations embracing various degrees of adaptive interaction. The nature and significance of the interactions between the partners are very diverse and difficult to categorize. As a result, numerous terms and definitions have been coined to describe symbioses. The literature abounds with discussions of the terminology used in designating these associations (for example Baer, 1952; Caullery, 1952; Cameron, 1956; Dogiel, 1962; Lincicome, 1963; Geiman, 1964; Croll, 1966; Henry, 1966; Cheng, 1967; Nicol, 1967; Matthes, 1967; Scott, 1969; Read, 1970; Odum, 1971; Olsen, 1974; Starr, 1975; Odening, 1976; Nobel and Nobel, 1982; Lewin, 1982). Unfortunately, some disagreement still exists, especially regarding the use of the term symbiosis.

In 1937 the American Society of Parasitologists recommended the use of the term symbiosis as a collective category that includes parasitism, mutualism, and commensalism (Hertig et al., 1937). Although the term was used in this context by de Bary (1879), it remained associated with his investigations of the mutualistic relationship between algae and fungi in lichens. This misinterpretation has been responsible in part for the use of symbiosis as a synonym of mutualism.

Predator-prey relationships should not be considered as instances of symbiosis. Predators can be differentiated from symbionts (parasites) by their momentary association with a smaller prey and by their rapid and destructive consump-

tion of whole individuals or fragments (see Cheng, 1967 and Nobel and Nobel, 1982). An absolute demarcation between predation and parasitism, however, is sometimes impossible, and some authors prefer not to make a distinction (Watt, 1968; Gilbert et al., 1976). Instances of such intermediate situations among marine organisms are the "micropredatory" gastropod molluscs associated with cnidarians (Graham, 1955; Rees, 1967; Robertson, 1970; Salvini-Plawen, 1972; Yonge, 1974; Hadfield, 1976).

The adaptive interaction between the members of a symbiosis results in the establishment of a dynamic equilibrium between the partners. Relative benefit or harm is the consequence of such interaction. Symbioses have, therefore, been classified according to the presence or absence of harm or benefit in the partners. Parasitism has been traditionally said to occur when the larger member of the association (the host) is harmed, mutualism when both members obtain benefit, and commensalism when no harm or benefit to the host occurs. The use of these criteria in categorizing symbioses, however, has been unfortunate. The concepts of benefit and harmfulness tend to be anthropomorphic in their interpretation and are usually difficult to analyze. Furthermore, very little is known about the biology of most symbioses and first-hand observations of the presence of harm or benefit may be deceptive. On the other hand, "benefit" as an outcome of a heterospecific interaction may be useful in understanding the evolution of symbioses.

A more recent concept used in categorizing symbioses is the presence or absence of metabolic dependency, an idea developed by Cameron (1956) and Smyth (1962). Parasites are accordingly defined as being metabolically dependent on their host, whereas commensals are associated with their host without exhibiting any metabolic dependency. Mutual metabolic dependency is characteristic of mutualism. Metabolic (biochemical) dependency in the form of nutrients, enzymes, or even developmental stimuli (Cheng, 1967) can be experimentally demonstrated or quantified and used in a more objective context. Unfortunately, our inadequate knowledge of most symbioses (particularly the commensal associations) prevents the application of these criteria to all heterospecific associations. It is also difficult to apply this concept when dealing with symbioses where behavioral (rather than biochemical) adaptations are predominantly involved.

Relative fitness, although difficult to quantify, may be useful in categorizing symbioses (see Roughgarden, 1975). In this context a commensal can be considered an associate which increases its fitness as a result of the symbiosis without changing the fitness of its host, a parasite as an associate which likewise increases its fitness while decreasing that of its host, and a mutualistic associate as that which increases its fitness as well as that of its host.

A growing number of investigators has opted to surmount the difficulties of categorizing symbioses by minimizing the need of classifying the association in question and merely referring to it as an instance of symbiosis. This is obviously advantageous in those cases where the association is not adequately understood.

Parasitism

Parasites exploit their host not only as a habitat but as a source of nutrition and other essential metabolites. The evolution of this type of relationship necessitates the establishment and maintenance of a dynamic equilibrium between the partners. Although the adaptive significance to the parasite is obvious, the host is not necessarily "harmed" as a result of the association. Lincicome (1971) has presented evidence which suggests that some parasites even contribute to the well-being of the host.

Parasitism is a widespread phenomenon in the marine environment. Most major groups include species considered to lead a parasitic existence and all free-living species most probably serve as hosts to parasites at one time or another. General reviews of parasitism among marine animals, including those inhabiting coral reefs, have been given by Hopkins (1957), Nicol (1967), and Bohde (1982). Cheng (1967) has extensively surveyed the parasites of numerous marine molluscs. In addition, instances of parasitism among coral reef organisms are included in several general surveys (Baer, 1952; Caullery, 1952; Cheng 1973; Nobel and Nobel, 1982).

Protozoa. Numerous species of protozoans have been recorded as external or internal parasites of marine animals and plants (Baker, 1969). Flagellates, amoebas and ciliates are common associates of the digestive tract of most coral reef animals. Although some are considered to be parasites, the significance of most of these associations remains unknown. All protozoans traditionally classified as sporozoans are parasites. Gregarines, a group of sporozoans, are common parasites of cells and body cavities of invertebrates. Marine vertebrates, especially fishes, are parasitized by numerous species of coccidians, microsporidians, and myxosporidians. The first two groups are also found in invertebrates.

Platyhelminthes. The phylum includes the trematodes (flukes) and cestodes (tapeworms), two large and important groups of parasites of vertebrates. Most monogenetic trematodes are ectoparasites (skin and gills) of bony fishes but some species parasitize elasmobranchs, crustaceans, and cephalopods (see Hargis, 1969). Digenetic trematodes are second only to the nematods as the most common helminth parasites of marine vertebrates and are probably found in most if not all coral reef fishes. Their complex life cycle always involves a first intermediate host (a mollusc, rarely a polychaete) but larvae may develop in other intermediate hosts before invading the definitive host where they reach sexual maturity. The vast literature on the systematics and biology of digenetic trematodes has been reviewed by several authors (Yamaguti, 1971; Erasmus, 1972; Cable, 1974). All cestodes (tapeworms) are intestinal parasites of vertebrates and may be found in coral reef fishes (Yamaguti, 1959). Their larval stages can be found in molluscs, crustaceans, and other groups (Cheng, 1967). Although most turbellarians are free-living predators, numerous species are associated with echinoderms, molluscs, crustaceans , and other coral reef invertebrates. A few species have been recorded from fishes. Some symbiotic turbellarians inhabit the body cavity or digestive tract of their hosts and are, therefore, regarded as parasites by some workers (see review by Jennings, 1974).

Nematoda. Nematodes, commonly known as round worms, are ubiquitous parasites of many marine groups. They encyst in tissues (including those of algae) or inhabit the digestive tract, body cavity, gills, blood vessels, and other organ systems of the hosts. The life cycles may involve larvae developing in intermediate hosts. Thousands of species are known but many more remain undescribed. Parasitic nematodes are particularly common in fishes (see reviews by Margolis, 1970 and Yamaguti, 1961). Various aspects of the biology of nematodes have been reviewed by Lee (1965), Crofton (1966), and Croll (1977).

Annelida. All myzostomid annelids are associates of echinoderms, especially comatulids in coral reefs (general treatment by Prenant, 1959). Some species form galls on the body wall of the host while others invade the coelomic cavity or digestive tract. Several species of polychaetes and leeches have been described as parasites of other marine invertebrates and fishes (see Baer, 1952 and Clark, 1956).

Mollusca. Numerous species of prosobranch gastropods show various degrees of adaptive interactions with coelenterates, including reef corals (Graham, 1955; Rees, 1967; Robertson, 1970; Salvini-Plawen, 1972; Yonge, 1974; Hadfield, 1976) and echinoderms (Baer, 1952; Caullery, 1952; Robertson and Orr, 1961; Lützen, 1968). These range from predators to highly specialized endoparasites. Some of the bivalves associated with invertebrates have been classified as parasites (Boss, 1965).

Crustacea. The parasitic way of life has evolved in a wide variety of marine crustaceans, including coral reef forms. Baer (1952), Caullery (1952), and Green (1963), among others, have reviewed the occurrence of parasitism in the Crustacea. Numerous species of copepods, for example, are associated with most marine groups. Many are loosely associated with the external surfaces of the host and show few specializations to their symbiotic way of life (Dudley, 1966; Humes and Stock, 1973). A gradation between predation, commensalism, and parasitism, however, is observed in many families of copepods (Bocquet and Stock, 1963). Some have even become highly specialized endoparasites. Parasitic copepods are associated with many groups of coral reef animals, but molluscs, echinoderms, and fishes are among the most common hosts. Similar adaptations from predation to endoparasitism are observed among isopods associated with other crustaceans and fishes . Barnacles often live on the surface of a wide variety of invertebrates and vertebrates without showing any apparent specializations for a parasitic existence. Many species, however, show a high degree of host

specificity and some even appear to absorb nutrients from their hosts. The highly specialized ascothoracic cirripedes parasitize soft corals and echinoderms; the rhizocephalids are even more specialized and are responsible for parasitic castration in decapod crustaceans (Reinhard, 1956). Parasitism among the decapod crustaceans has been described only in brachyuran crabs. All members of the family Pinnotheridae (pea crabs) are symbionts of molluscs, echinoderms, and other invertebrates in coral reefs (see review by Schmitt et. al., 1973). The symbiosis between eumedonids, a group of parthenopid crabs, and their echinoderm hosts in coral reefs can be best described as instances of parasitism (Castro, 1971).

Other Animal Groups. Stages in the life cycle of some hydroids and sea anemones appear to be parasites of other cnidarians. Dales (1957) lists several hydroids which appear to be parasites of fishes. Rees (1967) reviews symbioses between cnidarians and molluscs, some of which may be parasitic in nature. Several nemerteans (ribbon worms) are commonly referred to as parasites of bivalves. Cheng (1967), however, reviews these associations and classifies them as commensals. Nemerteans belonging to the genus Carcinonemertes inhabit the egg masses and gills of coral reef crabs (see Humes, 1942). Very little is known about the biology of marine rotifers associated with crustaceans and echinoderms, some of which have been regarded as parasites (see Hyman, 1951). Carapid (pearl) fishes, inhabitants of the body cavity of sea cucumbers, sea stars, tunicates, and bivalves are sometimes classified as parasites due to their ingestion of some host tissue (see review by Trott ,1981).

Microorganisms. Viruses, bacteria, and fungi are most probably found in association with all marine plants and animals. All three groups are known to be responsible for numerous types of diseases in molluscs, crustaceans, and fishes (see Snieszko, 1970).

Algae. Very little is known about the biology of parasitic algae, also known as alloparasites. This term is usually restricted to the red algae which are epiphytes or endophytes of other algae and which show a reduction in size as well as in the amount of pigment in their tissues (Setchel, 1918). The relatively few investigations which have been undertaken on parasitic algae in temperate regions have demonstrated metabolic interactions between the algae and their hosts (see Goff, 1979a; 1979b). A number of algae have been reported from the surface of marine animals but the nature of these associations remains unknown.

Commensalism

Instances of commensalism are possibly the most difficult to demarcate among the three major categories of symbiosis. Borderline cases between parasitism and commensalism can be easily recognized in numerous symbioses. Many symbionts have been classified as commensals on the assumption that there is no metabolic dependency on their host or that the host does not appear to be harmed by the symbiont. Our knowledge of most of these associations, however, remains restricted to descriptive accounts of the distribution, morphological adaptations, and general behavior of the partners. It will not be surprising to find that metabolic dependency in one or both partners has evolved in many commensal associations.

Most commensals inhabit the surface of their host. The sharing of food by both partners can be a further adaptation, hence the literal meaning of commensalism as "eating at the same table." Several authors have made a distinction between commensalism and associations where no food appears to be shared. These associates are often described as phoretic, epizoitic, or epiphytic. These terms are often restricted to facultive, non-host specific inhabitants of the external surfaces of animals and plants. The term endoecism has been used to describe associates which inhabit the burrows, tubes, or shelters of their host, whereas, inquilinism describes associates which find shelter within the body of the host. Synoecious associates have been described as those inhabiting the surface or shelter of their hosts, a combination of phoresis and endoecism. Discussions of the terminology which has regrettably been used in the classification of commensalism have been given by several authors (Caullery, 1952; Henry, 1966; Matthes, 1967; Gotto, 1969).

As expected, there is a great diversity in the types of commensal symbioses found in the marine environment. General reviews of commensalism among marine organisms have been given, among others, by Dales (1957, 1966), Nicol (1967) and

Gotto (1969). Table 1 summarizes references which list, catalogue, review, or discuss commensal symbioses among inhabitants of coral reefs.

Mutualism

It can be hypothesized that commensal or even parasitic symbioses may evolve toward a mutual exchange of metabolites or an increase in the fitness of both partners as a result of their association. Such is the case of mutualism, the "symbiosis" of most European workers. In endozoic algae associated with invertebrates as well as in other mutualistic symbioses the host not only provides a habitat to the symbiont, but there is a mutual metabolic dependency which is often obligatory in nature. Although a similar exchange of metabolites has been used by some to define parasitism (Smyth, 1962; Lincicome, 1971), the possible utilization of metabolites by the parasitized host is a transient, non-obligatory by-product of the parasite.

Classified here under mutualism are also associations where behavioral rather than physiological adaptations dominate the interaction between the partners. Cleaning symbiosis, for example, had been traditionally classified as mutualistic due to an apparent benefit to the associates. Although food and even other metabolites are sometimes part of these associations (see Trager, 1970), it is difficult to apply the concept of metabolic dependency in their classification. An increase in the fitness of the partners as a result of the association, however, may be used to consider them as mutualistic.

Algae-Invertebrate Mutualism. Various groups of algae are mutualistic associates of marine invertebrates. The taxonomy, distribution, and morphology of these algal symbionts have been discussed in numerous reviews (Yonge, 1957; Droop, 1963; Büchner, 1965; McLaughlin and Zahl, 1966; Taylor, 1973a, 1973b, 1973c, 1974; Muscatine, 1974; Trench, 1979). A mathematical analysis of algal symbioses is presented by Hallock (1981). The most common are the zooxanthellae, the name commonly given to a heterogeneous group of endozoic dinoflagellates, cryptomonads, and diatoms. These symbionts are apparently restricted to the marine environment. Zooxanthellae are predominantly associated with cnidarians, especially reef corals, but are also found in other invertebrates such as protozoans, sponges, turbellarians, and bivalves. Green unicellular algae, the zoochlorellae, are the most common endozoic algae of fresh water invertebrates. Similar algae, however, have been found in association with sea anemones and marine turbellarians. Cyanellae, endozoic cyanobacteria (blue-green algae), have been identified as the symbiotic algae in numerous sponges and in echinoid worms (Fogg et al., 1973; Sarà and Vacelet, 1973). Various prokaryotic green algae (genus Prochloron) are symbionts of didemnid ascidians (Lewin, 1976; Kremer et al., 1982). Various saccoglossan gastropods retain the chloroplasts of ingested green algae as symbiotic organelles (Taylor, 1970; Greene, 1974). Filamentous green algae and red algae have also been reported in association with sponges, bryozoans, and other invertebrates.

Some of the algae-invertebrate symbioses in coral reefs have been widely studied. The translocation and utilization of carbon and nitrogen compounds from the symbiont to the host has been demonstrated in most of the symbioses thus far investigated; the algae may also utilize the nitrogenous waste products of the host (see reviews by Smith et al., 1969; Muscatine, 1971, 1974; Muscatine et al., 1975; Schoenberg and Trench, 1976; Trench, 1979; Muscatine, 1980a, 1980b; Felbeck et al., 1983). Of special interest is the symbiosis between zooxanthellae and reef corals (see Yonge, 1963; Goreau et al., 1971; Taylor, 1973b; Muscatine, 1973; Muscatine and Porter, 1977; Muscatine et al., 1981). In addition to providing the host with nutrients, the algae play an important role in the deposition of the calcium carbonate skeleton of the host (Pearse and Muscatine, 1971; Vandermeulen and Muscatine, 1974).

Behavioral Symbioses. Complex behavioral interactions have evolved in fishes which remove ectoparasites, injured tissues, and food particles from other fishes, mostly in coral reefs (Feder, 1966; Losey, 1971, 1972). Similar patterns have been studied in several cleaner shrimps (Limbaugh et al., 1961). Visual communication between cleaners and their hosts allows the cleaners to derive nutrition as well as a relative immunity to predation. Physical contact during interactions is transitory. It represents, however, a symbiosis between populations rather than between individuals. A similar communication between symbiotic partners has evolved in the associations between some alpheid shrimps and gobiid fishes (Karplus et al., 1972a, 1972b; Preston, 1978) and between several pomacentrid fishes and sea anemones (Mariscal, 1971; Allen, 1972; Roughgarden, 1975; Schlichter, 1976).

Table 1. Summary of reviews of commensal symbioses in coral reefs.

Commensals	Host	References (Remarks)
Most groups	Most groups	Caullery, 1952; Dales, 1957 Dales, 1966; Nicol, 1967 Gotto, 1969; Read, 1970 Hopkins, 1957 (Survey of parasites which includes commensals)
Many groups	Sponges	Fishelson, 1966; Westinga and Hoetjes, 1981
Most groups	Hydroids	Dales, 1957 (Table by C. Hand)
Most groups	Corals	Patton, 1976 (Associates of live corals)
Most groups	Molluscs (commercial species)	Cheng, 1967 (Survey of parasites including commensals)
Many groups	Sea cucumbers	Changeux, 1960
Protozoans	Crustaceans	Sprague and Crouch, 1971
Cnidarians	Molluscs	Rees, 1967
Hydroids	Hermit crabs	Mills, 1976
Sea anemones	Hermit crabs brachyuran crabs	Dales, 1957 (Table by J. W. Hedgepeth; (also see section on mutualism-- behavioral symbioses) Ross, 1967; 1974 (Also see section on mutualism - behavioral symbioses)
Sea anemones	Molluscs	Ross, 1967
Turbellarians	Most groups	Jennings, 1974
Sipunculans	Corals	Rice, 1976 (Associates of coral skeleton)
Polychaetes	Most groups	Clark, 1956
Molluscs	Cnidarians	Rees, 1967 (Includes micropredatory associates)
Gastropods	Corals	Robertson, 1970 (Includes micropredatory associates) Radfield, 1976 (Includes micropredatory associates)
Bivalves	Most groups	Boss, 1965; Purchon, 1977

Table 1 (continued).

Commensals	Host	References (Remarks)
Bivalves	Corals	Morton, 1983
Crustaceans	Most groups	Balss, 1956; Patton, 1967
Crustaceans	Sponges	Arndt, 1933
Copepods	Most groups	Humes and Stock, 1973; Gotto, 1979 (Includes parasitic associates)
Copepods	Sea anemones	Humes, 1982 (Includes parasitic associates)
Copepods	Stony corals	Humes, 1979 (Includes parasitic associates)
Copepods	Holothurians	Humes, 1980 (Includes parasitic associates)
Barnacles	Stony corals	Ross and Newman, 1973 (Associates of coral skeleton) Newman et. al., 1976 (Associates of coral skeleton)
Amphipods	Molluscs	Vader, 1972
Caridean shrimps	Most groups	Bruce, 1976a; 1976b
Pontoniine shrimps	Most groups	Holthius, 1952; Miyake and Fujino, 1968
Pontoniine shrimps	corals	Bruce, 1972; 1977 (Associates of live corals)
Pontoniine shrimps	Gorgonians	Bruce, 1970
Pontoniine shrimps	Sea urchins	Bruce, 1974
Pontoniine shrimps	Crinoids	Bruce, 1971
Alpheid shrimps	Gobiid fishes	Harada, 1969 (Also see section on mutualism--behavioral symbioses)
Brachyuran crabs	Scleractinian corals	Castro, 1976 (Many species most probably metabolically dependent on live coral hosts)
Pinnotherid crabs	Most groups	Schmitt et. al., 1973 (Some considered parasites)
Echinoderms	Most groups	Clark, 1976 (Non-specific external associates)
Pomacentrid fishes	Sea anemones	Allen, 1972 (Also see section on mutualism--behavioral symbioses)

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A guide to animals symbiotic with reef corals in Hawaiian waters

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Abstract

The macroinvertebrates and fishes that are symbiotic with Hawaiian reef corals are reviewed. Symbiont species are briefly described and the nature of their respective relationships with coral hosts are discussed.

Introduction

Reef corals support a wide variety of invertebrates and fish which live symbiotically with the coral hosts, many of which appear to rely on the corals for at least part of their trophic requirements. These close heterospecific associations are referred to as "symbionts" without implication of benefit or harm (Cheng, 1967; Castro, 1976). The associations range from loosely formed relationships where the symbionts benefit by using the coral as a habitat which may provide protection from predators to obligate specific associations where coral tissue or mucus is the prime food source of the symbiont. Corresponding with the limited number of Hawaiian coral species the number of species in symbiotic association with reef corals is more restricted in Hawaii than in more tropical areas of the western Indo-Pacific. Most of these associations in Hawaii are with corals belonging to the genus Pocillopora which have a branching structure, in contrast with other Hawaiian reef forming species.

The following descriptions summarize the organisms associated with Hawaiian reef corals with special attention to the trophic relationships. The organisms described do not include demersal reef fishes (see Hobson 1974) or macroinvertebrates (e.g. Acanthaster planci) that are predatory on coral tissue, but is confined to organisms which reside on corals or their skeletons. Two approaches are possible for describing these organisms and their symbiotic relationships: 1) a phylogenetic approach listing pertinent symbiont species with reference to their host and the relationship type (Table 1), or 2) descriptions of the species associated with specific host corals. Since the latter approach corresponds more closely to the manner in which the investigator will become acquainted with coral symbionts and the number of species of coral in Hawaii is low, the host-symbiont approach will be emphasized in this presentation, beginning with the coral species which have the greatest variety of associated organisms.

Descriptions of the Symbionts

HOST: Pocillopora meandrina Dana

In Hawaii P. meandrina is common in open areas where wave action is unrestricted. It is an erect, branching coral with a dense skeleton which enables it to withstand substantial wave energy. It grows to nearly 40 cm in diameter in hemispherical to hemi-ellipsoid shape with meandering open spaces approximately 2 cm wide within its branched structure. The open area within the branched structure is utilized by a variety of symbionts, especially decapods, and more particularly, crabs of the family Xanthidae. The P. meandrina symbiont community was described by Barry (1965) and Coles (1980), and conspicuous species of Trapezia in this community were studied by Preston (1971, 1973) and Huber (1983).

Family Xanthidae

Genus Trapezia

Five species of Trapezia occur on P. meandrina : T. intermedia, T. wardi, T. ferruginea, T. flavomaculata, and T. digitalis. Edmondson (1962) gives descriptions of these species under the names of T. cymodoce intermedia, T. cymodoce maculata, T. cymodoce ferruginea, T. flavopunctata and T. digitalis respectively. The names used here correspond to those to be used in the revised Reef and Shore Fauna of Hawaii (Eldredge, unpublished ms.) and are based on a provisional key to all the Trapezia species (Serène 1969).

Table 1. Summary of animal species reported to be symbiotic with Hawaiian corals. Abbreviations for coral hosts genera: M= Montipora, Poc= Pocillopora, Por= Porites, T= Tubastrea, P= Fungia.

CLASSIFICATION	HOST(S)	RELATIONSHIP	REFERENCE
Phylum PLATYHELMINTHES			
Class Turbellaria			
Order Polycladida			
Family Prosthiostomidae			
Prosthiostomum			
P. montiporae	M. verrucosa	Parasitic	19
Phylum MOLLUSCA			
Class Gastropoda			
Order Mesogastropoda			
Family Architechtonicidae			
Phillipia radiata		Predatory	15,21,27,28
Family Epitoniidae			
Epitonium ulu	P. scutaria	Predatory	3,15,28
Order Neogastropoda			
Family Muricidae			
Druppella elata	Poc. sp.,	Predatory	14,15,20,28
=D. cornus	Por. compressa		
Family Magilidae			
=Coralliophilidae			
Quovula madreporarum	Poc. meandrina	Commensal	2,20,28
=Rhizochilus madreporarum			
Order Nudibranchia			
Family Cuthonidae			
Phestilla melanobranchia	T. aurea,	Predatory	15,16,21
	Dendrophyllia sp.		
P. sibogae	Por. lobata,	Predatory	15,16,21
	Por. compressa		
Phylum ARTHROPODA			
Class Crustacea			
Order Decopoda			
Family Xanthidae			
Trapezia			
T. digitalis	Poc. meandrina,	Parasitic	2,7,9,13,
	Poc. eydouxi	Parasitic	19,22,24,25
T. intermedia	Poc. meandrina, Poc.	Parasitic	2,7,9,13,
	eydouxi, Poc. damicornis	Parasitic	19,22,24,25
T. wardi	Poc. meandrina,	Parasitic	2,7,9,13,
	Poc. eydouxi	Parasitic	19,22,24,25
T. ferruginea	Poc. meandrina,	Parasitic	2,7,9,13,
	Poc. eydouxi	Parasitic	19,22,24,25
T. flavopunctata	Poc. meandrina,	Parasitic	2,7,9,13,
	Poc. eydouxi	Parasitic	19,22,24,25
Domecia hispida	Poc. meandrina,	Parasitic	2,7,9,13
	Poc. damicornis		

Table 1 (continued).

CLASSIFICATION	HOST(S)	RELATIONSHIP	REFERENCE
Actaea speciosa	Poc. meandrina, Poc. damicornis	Parasitic	2,7,9,13
Haldiria trisanguculata	Por. lobata	Commensal	10
Family Hapalocarcinus			
H. marsupialis	Poc. meandrina, Poc. damicornis	Commensal	7,11,18,26
Pseudocryptochirus			
P. kahe	Poc. meandrina	Commensal	23
P. crescentus	Poc. eydouxi, Pavona duerdeni	Commensal	11,12
Family Alpheidae			
Alpheus lottini	Poc. meandrina, Poc. damicornis	Parasitic	1,2,5,9
Synalpheus charon	Poc. meandrina, Poc. damicornis	Parasitic	1,2,5,9
Alpheus clypeatus	Poc. meandrina	Commensal	1,4
Alpheus deuteropus	Por. lobata, Por. evermanni, M. verrucosa	Commensal	6,30
Family Pontiniidae			
H. depressus	Poc. meandrina	Parasitic	2,7,9
Family Portunidae			
Charybdis hawaiensis	Poc. meandrina	Commensal	pers. obs.
Phylum ECHINODERMATA			
Class Stelleroidea			
Order Ophiurida			
Family Ophiocomidae			
Ophiocoma pica	Poc. meandrina	Commensal	2
Phylum CHORDATA			
Class Osteichthyes			
Order Scorpaeniformes			
Family Caracanthidae			
Caracanthus maculatus	Poc. meandrina	Parasitic	2

References: 1. Banner (1953), 2. Barry (1965), 3. Bosch (1965), 4. Bowers (1970), 5. Bruce (1976), 6. Castro (1971), 7. Castro (1976), 8. Castro (1978), 9. Coles (1980), 10. Coles (1982), 11. Edmondson (1925), 12. Edmondson (1933), 13. Edmondson (1962), 14. Fankboner (1970), 15. Hadfield (1976), 16. Harris (1971), 17. Harris (1975), 18. Hiro (1937), 19. Huber (1983), 20. Jokiel and Townsley (1974), 21. Kay (1979), 22. Knudsen (1967), 23. McCain and Coles (1979), 24. Preston (1971), 25. Preston (1973), 26. Potts (1915), 27. Robertson (1970a), 28. Robertson (1970b), 29. Robertson et al. (1970), 30. Vaughan (1973).

With the exception of T. digitalis, which has a less prominent epibranchial tooth on the anterolateral edge of its carapace, all the Trapezia species are morphologically similar, but they are easily distinguished by their color patterns.

Trapezia intermedia Miers

This is the most common Trapezia species and is generally the first of this genus to colonize a growing P. meandrina colony. T. intermedia is the only symbiont commonly found on P. meandrina heads less than 5 cm diameter, and it can be found on heads up through maximum coral size. The crab ranges up to 15 mm carapace width and is characterized by pale reddish spots on a light brown background on the carapace, cheliped, wrist and walking legs and a network of reddish-brown lines covering the surface of the cheliped palms.

Trapezia wardi Serène

This species is the closest of the remaining species to T. intermedia in size, shape and coloration. It also has reddish spots on a light brown background, but in this case the spots extend to the cheliped palm and are generally redder and more distinct from the light brown background than is the case for T. intermedia.

Trapezia flavomaculata Eydoux and Souleyet

This species is also spotted, but is strikingly different from T. intermedia and T. wardi in that the spots are white or yellowish and larger, approximately 18 being required to cover the crab carapace. Also, the walking legs are striped with white and reddish brown, and the spines on the anterior margin of the carapace are generally more heavily developed. This is the largest of the Trapezia species found in Hawaii, ranging up to 25 mm carapace width, and this species is generally found along with Trapezia wardi on larger P. meandrina colonies.

Trapezia ferruginea Latreille

This species is similar to T. intermedia in body shape and size range, but has no spots on its carapace or legs, appearing solid pale-brown in coloration. Its epibranchial tooth at the antero-lateral margin of the carapace is less developed and less acute than T. intermedia, T. wardi or T flavomaculata.

Trapezia digitalis Latreille

T. digitalis is the most distinctive of the five species, having a deep brown coloration, and development of the epibranchial tooth is reduced to the point that the tooth appears only as a bump. Adults grow to a carapace width of about 15 mm and are generally found with T. intermedia on small to intermediate size P. meandrina colonies. The carapaces of juvenile T. digitalis often have half of their carapaces with the dark brown color characteristic of the adults, with the remaining half colored white.

Other Xanthids.

Two other species of xanthid crabs occur symbiotically with P. meandrina, but neither resemble any of the Trapezia species and both are apparently independent of the interspecific interactions that determine the composition of the Trapezia community.

Domecia hispida Eydoux and Souleyet

The more commonly encountered of the two species in this group is D. hispida, which ranges up to about 15 mm carapace width and, like the Trapezia species, generally occurs in mated pairs on the coral host. It is similar in general body shape to T. digitalis, but its drab, brownish-yellow carapace and chelipeds are covered with small denticulations, and the upper surface of the cheliped and anterior border of the carapace bear small black spines. Barry (1965) found no evidence for mucus feeding by this species (based on gut analysis). A relative of this species, D. acanthophora, is symbiotic on Acropora corals in the Caribbean (Patton, 1967), and another species, D. glabra, is symbiotic on Indo-Pacific Acropora (Patton, 1966).

Actaea speciosa Dana

This is the least common crab occurring on P. meandrina, and is also the most distinctive. Its robust carapace legs and chelipeds are covered by pink and white bead-like denticulations which are separated by numerous furrows. Like D. hispida and the Trapezia species it usually occurs as mated pairs, and its first walking leg is modified to enable mucus feeding similar to Trapezia spp. Barry (1965) reports that the size of individuals of this species and D. hispida tend to increase with increasing size of their coral host.

Family Hapalocarcinidae

Hapalocarcinid crabs have undergone major changes in their body structure and behavior which indicate their close symbiotic association with reef corals. No member of this family lives independently of a coral host, and habitation of corals occurs in two distinct ways: 1). A crab causes the host coral to form a gall-like structure around the crab, or 2). A crab occupies a pit or burrow which may extend well into the coral skeleton. P. meandrina is host to two haplocarcinid species representative of both types of dwelling.

Hapalocarcinus marsupialis Stimpson

This is the most common hapalocarcinid crab occurring on Pocillopora, and its presence is clearly marked by the presence of characteristic galls in various stages of development. It was first described by Stimpson from specimens taken from Hilo Harbor (Potts, 1915). Galls are usually occupied by females and at one time males were thought to be free living, but Fize (1956) has noted males (which are much smaller than females) occurring in small open galls. Potts (1915) and Patton (1966) provide excellent descriptions of this species and its habitat. Female crabs are colorless when small to dark grey when large and are highly modified for their existence in a confined space. Females occupy a coral branch at the juncture of a forming bifurcation and, through movement of water by the crabs's mouthparts and appendages, induce coral growth to form a chamber around the crab. Larger galls are two-chambered, a smaller chamber marking the point of the original crab settlement, leading to a larger chamber which is formed by subsequent coral growth. This larger chamber begins as two leaf-like or shell-like valves which gradually grow together and fuse, except for a number of small holes which allow water to pass in and out of the gall. Ultimately, even these holes can be overgrown by the coral skeleton, killing the crab which has long since been trapped inside.

Since the female crab is resident within its gall and ultimately trapped there, males must be much smaller than females and move from gall to gall to accomplish fertilization. Females occupying the larger chamber of the gall are almost always egg bearing, and young are probably produced and released continually from the time of sexual maturation. Adult crabs probably feed on small plankton trapped by the mouthpart setae. Patton (1976) has, however, noted crabs in opened galls to pick at coral tissues with their chelae and transfer material to their mouthparts.

Pseudocryptochirus kahe (McCain and Coles)

This species is the only burrowing hapalocarcinid that utilizes pocilloporid corals as habitat. Its presence is indicated by openings 2 to 3 mm in diameter in the tips or sides of P. meandrina branches. Chamber openings are usually circled by violet rings which contrast with the medium brown coral tissue. Openings lead to cylindrical chambers 3 to 8 mm deep, the bottom of which is usually spheroid and smooth. Chambers almost always contain a female P. kahe, and occasionally two females occupy a single chamber. Approximately 20% of the chambers have females and males, the male occupying the brood pouch on non-ovigerous females. As in H. marsupialis, males are substantially smaller than females, and apparently migrate from chamber to chamber to fertilize sexually mature females.

Crabs range up to 4-5 mm carapace width and are drab brown in color. The carapace is elongate and highly tuberculated, especially in larger specimens, and is strongly depressed anteriorly. Often, the dorsal surface of the crab can be observed on living corals at the entrance of the crab chamber, resembling a sort of operculum to the chamber's opening. The crab strongly resembles, both in physical characteristics and burrow formation, other species of Pseudocryptochirus which inhabit a variety of species of massive corals from

many families. P. kahe may be synonymous with Cryptochirus dimorphus described by Henderson (1906) from specimens obtained in the Andaman Islands.

Family Alpheidae

Alpheids, commonly known as snapping shrimp because of the noise they make with their large cheliped when disturbed, are very common in coral reef rubble. Two Hawaiian species have become adapted for obligate symbiotic association with live pocilloporid corals, and a third species utilizes a specialized habitat within algae growing on a dead P. meandrina bases.

Alpheus lottini Guérin

This species occurs throughout the Indo-Pacific from the Red Sea to the Gulf of California. A mated pair of this colorful species is almost always found in live heads of P. meandrina on the larger branches near the base. It is described by Banner (1953, under the synonym Crangon ventrosa) as the "most spectacular, both in color and size of the Hawaiian alpheid shrimps". Body length from rostrum to telson ranges up to 45 mm, with a massive large cheliped about one third as long as its body. Color is bright orange-red on the upper surface with red longitudinal stripes along the carapace and abdomen and red spots on the upper portions of both chelipeds.

Like the trapeziids, A. lottini appears to have an obligate dependence on coral mucus for at least part of its diet, and to have morphological adaptations for mucus feeding consisting of setae clumps on its third maxillipeds and chelae of its second legs (Patton, 1974). Gut analyses have indicated mucus-like material (Barry, 1965; Patton, 1974). Patton (1974) observed a starved specimen to scrape the surface of Pocillopora with one of its second legs and then clean this appendage with its mouthparts.

Synalpheus charon (Heller)

This species is in many respects similar to A. lottini in that it is an obligate symbiont of pocilloporid corals, where it almost always occurs in mated pairs. It differs from A. lottini in its smaller size, with a maximum length of about 20 mm, and its coloration, which is a solid brilliant orange-red. S. charon is an early colonizer of small Pocillopora heads and dominates, along with T. intermedia, the symbiont community of small host corals. Although a trophic dependence on the coral host might be anticipated, Barry (1965) found no mucus or other coral-derived materials in S. charon gut analysis.

Alpheus clypeatus Coutière

Although this species is not a symbiont of live Pocillopora corals, it is included here because it is often found on the bases of P. meandrina colonies where it constructs tubes in mats of the filamentous algae Acrochaetium sp. (Bowers, 1970). A. clypeatus is similar in size to S. charon and shows similar heterosexual pair formation and agonistic behavior to non-mate conspecifics as occurs in many pair-forming obligate symbionts of coral hosts. Because agonistic encounters decrease with the amount of algae available as habitat, more than one pair of A. clypeatus are often found on P. meandrina, which have substantial algal mats growing at their base. A. clypeatus constructs tubes in the algal mats with its second periopods and also utilizes the algae as food.

Other Symbionts

Three other species have been noted to be commensal with Pocillopora meandrina and two of these are considered obligate symbionts.

Quoyula (=Rhizochilus) madreporarum (Sowerby)

This species is a member of the mollusc family Coralliophillidae whose members, as the name implies, are all associated with soft or stony corals. Q. madreporarum is a gastropod with a limpet-like shell and a pink foot, and it is found attached to branches or bases of the coral. Removal of the animal from the coral reveals a scar outlining its former attachment position, indicating that Q. madreporarum remains fixed in a single position throughout most of its adult life. Shell size ranges 1 - 12 mm along the long axis, and as many as 65 individuals have been found on a single host colony (Coles, unpublished). No information is available concerning trophic dependence of the symbiont on its

host. However, since O. padreporarum occurs only on corals of the family Pocilloporidae (Maes, 1967) throughout the Indo-Pacific (Robertson, 1970b), some trophic relationship may be assumed. Robertson (1970b) proposes that all coralliophillids feed suctorially on their hosts' tissues and mucus. However, there is no indication that O. padreporarum affects its host beyond the symbiont's point of attachment.

Ophiocoma pica Muller and Troschel

Little information is available regarding this brittle star which may be commensal with P. meandrina. O. pica is dark brown to black on the arms with a central disc up to 25 mm in diameter. It is found wrapped around the base and branches and in the rubble at the base of P. meandrina heads. Although this species was listed by Barry (1965) as a P. meandrina commensal, no information exists as to its host specificity or degree of trophic dependence on its host. It is likely that its requirements, if any, are limited to the type of physical space afforded by the branches of P. meandrina.

Caracanthus maculatus (Gray)

This small fish appears to be the only fish species in Hawaii that is an obligate commensal of a reef coral. It is oval in outline and extremely compressed, with the entire body except the fins covered with small, velvet-like papillae. Its coloring is bluish-gray with prominent dark reddish spots over most of its body. Maximum size is about 40 to 45 mm standard length. Although the trophic relationship of this species with its host is not established, it is likely that it consumes coral mucus, because the fish is never observed outside of P. meandrina coral heads.

A number of other species of fish utilize the space within P. meandrina heads as both habitat and refuge from predators, although their association is not obligatory. Most common of these transient species is the white-spotted damselfish Dascyllus albisella. Groups of these fish hover above coral and retreat within a head when disturbed. Other species which can often be found with P. meandrina are the scorpionfish Scorpaena cornigera, the hawkfishes Paracirrhites arcatus, Cirritops fasciatus and Amblycirrhites bimacula, the four-lined wrasse Pseudocheilinus tetrataenia and juvenile eels of the genus Gymnothorax.

Other Pocilloporid Hosts:

Pocillopora damicornis (Linn) and P. eydouxi (Milne, Edwards and Haime)

No comprehensive studies of the organisms symbiotic with P. damicornis have been performed in Hawaii. Preliminary observations (Coles, unpublished) of the organisms occurring with P. damicornis sampled from Kaneohe Bay indicate this community to be a somewhat restricted version of the P. meandrina symbiotic community described above. Trapezia intermedia, Alpheus lottini, Synalpheus charon and Harpiliopsis depressus are the dominant ectocommensals, and Hapalocarcinus marsupialis galls can be very abundant on a single coral head. Such relatively few numbers of species occuring with P. damicornis are in marked contrast with results of studies of the P. damicornis symbiont community made elsewhere. Abele (1976) and Abele and Patton (1976) found 55 decopod crustaceans on live P. damicornis in Panama, while Austin et al. (1980) described up to 101 species to be symbiotic with P. damicornis from the Great Barrier Reef.

Even less information is available for the symbionts that occur with P. eydouxi. This coral species is similar to P. meandrina except that it is larger, more erect and the internal spaces defined by its branching arms are more open. Therefore, the habitat space afforded within its structure is less protective. Field observations suggest that its symbiont community is very similar to that of larger P. meandrina.' In addition, a species not found on P. meandrina commonly occurs on P. eydouxi. This is the portunid crab Charybdis hawaiiensis Edmondson which is found as mated pairs on the coral. This crab ranges up to 5 cm carapace width and is brown-orange in coloration, with prominant spination on the antero-lateral edge of its carapace and on the upper surface of its chelipeds. Dactly of the chelipeds display distinctive orange, white and brown bands. Although pairs of this species commonly occur on the relatively rare P. eydouxi the commensal association is apparently not obligatory. For example, C. hawaiiensis is one of the most common organisms sampled in the impingement catches at the Kahe Power Station at Kahe Point, Oahu (Coles and

Fukuda, 1983), indicating that it probably also resides in macroalgae and within fouling communities, as well as within interstices of the general coral reef.

Other Coral Hosts

Because of the internal habitat space provided by their branching structures, species of the coral Pocilloporidae are host to most of the reef organisms in Hawaii that have developed symbiotic association with hermatypic corals. However, a few other symbiotic associations exist with reef corals having non-branching colony forms. Generally these associations are trophic and obligatory, unless the symbiont has developed a means of constructing a habitat within the coral's skeleton.

Host: Pavona duerdeni Vaughan

P. duerdeni is a massive coral with starlike and symmetrically arranged calyces. This species usually is found in turbulent, shallow water along leeward coastlines. It is host to a single symbiont Pseudocryptochirus crescentus (Edmondson).

P. crescentus' presence is indicated by crescent-shaped openings on the surface of P. duerdeni which lead to chambers up to 2 cm deep within the coral skeleton. The chambers are crescent shaped in cross-section, conforming with the crab's carapace. The animal is small, up to 2.5 mm carapace width by 3 mm length. The carapace is drab brown, its surface roughened with small tubercles and its anterior position bends downward strongly. Superficially this species strongly resembles a small P. kabe. However, males and females occupy separate chambers and the differences in size between sexes are not as extreme as for P. kabe. P crescentus has also been reported on another species of Pavona in the waters of Clipperton Island (Garth, 1968).

Cryptochirus minutus Edmondson is another chamber-forming hapalocarcinid that has been reported to reside on the reef corals Cyphastrea ocellina and Leptastrea purpurea in Hawaii (Edmondson, 1933). This species is similar to P. crescentus. It is likely that further investigations will reveal more new species or new habitat reports in Hawaii for members of this cryptic crab family.

Host: Porites lobata Dana

P. lobata is a massive lobate or encrusting species which dominates the coral cover in most nearshore areas in Hawaii. It is host to four symbionts: two decapod crustaceans and two gastropod molluscs.

Family Xanthidae

Maldivia triunguiculata (Borradaile)

This small brown xanthid crab occupies chambers remarkably similar to those of hapalocarcinid crabs such as Pseudcryptochirus kabe. Its habitat is readily recognizable as crescent-shaped openings on a P. lobata surface (Coles, 1982). Breaking the coral open reveals a pit or chamber which can extend into the coral to a depth of over 5 cm. The chambers are usually occupied by a single female M. triunguiculata, less frequently by a single male or occasionally the chamber may be found empty. The crab can sometimes be observed at the opening to its burrow with its chelipeds and anterior carapace slightly protruding. It seldom exceeds 5 mm in carapace width and its dimensions closely correspond to the cross-sectional dimensions of the chamber opening. The crab lacks distinctive markings or spination, and its chelipeds are massive relative to its body and are unequal in size.

No information is available concerning trophic relationship to the host, but it is likely that the association is non-trophic, since crabs have been found within dead coral reef and within dead P. meandrina skeleton. Habitation of empty chambers may occur sequentially, with larger crabs expanding the cross-sectional area of the chamber.

Alpheus deuteropus Bilgendorf

This alpheid shrimp is a close counterpart of M. triunguiculata in that it forms burrows in P. lobata where it occurs in mated pairs. The presence of the

symbiont is indicated by black fissures up to 25 cm long by a few cm deep on the surfaces of P. lobata. The fissures may be simple or branched. At or near the deepest part of the crevice may be found the openings of one or more burrows which are oval in cross-section. A. deuteropus reside within the burrows typically with their heads positioned outwards and their chelae pointed outward and spread to fill the burrow and the channel. Most crevices have two burrows: a male in one and a female in the other. Densities of A. deuteropus within live P. lobata can be very high, up to 50 per square meter, and increase with increasing live coral coverage (Vaughan, 1973). This species can also be found inhabiting burrows of Porites evermanni, which is superficially similar to P. lobata and in Montipora verrucosa. Therefore the association with reef coral is non-specific and facultative, but A. deuteropus seldom inhabits burrows in dead reef material.

The shrimp is a moderately large (up to 3.5 cm) alpheid, mostly transparent in life except for small red chromatophores on the body and a greenish cast to the chelae. The large chela is rather distinctive in having a small dactylus which rotates to close laterally across the end, and the chelae are densely covered with bundles of setae. Although the chelae are strong enough to break bits of coral and usually show sign of abrasion, given the consistent outward-facing position of the shrimp, it is unlikely that the chelae are used in burrow formation. Vaughan (1973) found evidence of calcium carbonate crystals within the burrows not deposited by coral growth, suggesting a chemical mechanism for dissolving coral skeleton by the shrimp to form and extend the burrow. Algae and hydroid growth at the lip of the crevice may also act to maintain the crevice opening against coral overgrowth.

Family Architectonicidae

Phillipia radiata (Roding)

This gastropod, rather than relying on a coral for habitat, resides in sand or rubble near live P. lobata and emerges to feed at nighttime on the coral's polyps. The spiral shell of the adult is approximately 1 cm in diameter and is white with brown markings. It feeds with a highly extendible proboscis containing a radula on its tip which it everts to feed on P. lobata and possibly P. compressa polyps. This then is a case of predation on coral tissue rather than parasitism on coral mucus as is the case for pocilloporid symbionts. In addition to simple food requirements P. radiata requires host tissue to be able to complete its development either beyond the larval stage (Hadfield, 1976) or subsequent development beyond the arrested growth stage of the post larvae (Robertson, 1970: Robertson, et al., 1970).

Family Cuthonidae

Phestilla sibogae Bergh

This member of the nudibranch suborder Eolidadea, which includes many coelenterate feeding species, feeds on the tissues of the corals Porites lobata and P. compressa. Although P. sibogae is seldom observed in the field, Porites colonies in aquaria or seawater tables will become infested with numerous P. sibogae which rapidly feed on available coral tissue and lay egg masses under the host coral colonies. It is likely, therefore, that P. sibogae populations are controlled under natural conditions by fish feeding. P. sibogae ranges up to 30 mm length and the patterns produced by the numerous cerata covering its dorsal surface resemble the polyps of its coral host. This camoflauge effect is enhanced by the symbiont's color being provided by the zooxanthellae from its host's tissue. Similar to Phillipia radiata, P. sibogae requires a substance from the live host to complete metamorphosis from larva to adult (Hadfield and Karlson, 1969).

Similar in appearance and lifestyle to P. sibogae is Phestilla melanobranchia Bergh which requires the abermatypic coral Tubastraea coccinea for its food source. This species is distinctive in having coloration which is usually bright orange, but may be pink or black depending on the color of their individual host coral.

Host: Porites compressa Dana

Drupella elata Blanville

Very little information is available concerning this gastropod parasite of P compressa and Pocillopora. All published accounts refer back to an unpublished study by Fankboner (1979) who described the animal's feeding process. Feeding involves "spitting" a saliva on the coral tissue, followed by rasping and sucking on the partially digested flesh. The gastropod digests coral tissue and zooxanthellae, but passes nematocysts through the gut undischarged.

Host: Fungia scutaria Lamarck

F. scutaria is a solitary coral with individual coralla containing a single oral cavity from which radiate numerous septa. The aboral surface is covered with small projections which also radiate from the center. This species is host to a single species of mollusc that utilizes it as a food source.

Epitonium ulu Pilsbury

This is one of the five species of Epitonium that feed on coelenterates in Hawaii, the other four being predators of sea anemones. This gastropod is small up to 15 mm diameter, with an elongate cone-like white shell. Small ridges ascend the outside of the shell like a small spiral staircase. Like other coral-feeding symbionts, this species does not become abundant on its host unless transferred to a laboratory environment where the normal population of natural predators is absent. The adult animals live on the periphery or lower surface of the host coral, feeding and depositing eggs. Guinther (1970, cited in Hadfield, 1976) has noted that E. ulu never crawls directly on the flesh of the coral host, but rather moves on a grid of secreted mucus strands that are cemented to the coral.

Host: Montipora verrucosa (Lamarck)

M. verrucosa is a reef coral with a very plastic growth form that prospers under low and high turbidity conditions. It is host to a single organism which is a polyclad platyhelminth worm.

Prosthiostomum montiporae Poulter

This flatworm ranges in length 4 - 15 mm and is much longer than it is broad. It is difficult to observe under field conditions, but careful examination of M. verrucosa heads which show localized areas of tissue loss near cryptic areas in the skeleton will often produce individuals of this species (Jokiel and Townsley, 1974). The worm is translucent, but shows the red-brown color characteristics of the host's tissue located in the worm's gut. The dorsal surface therefore appears to have a light brown stripe flanked by darker brown, while the ventral surface is white. The anterior portion of the head has numerous marginal eyespots lying in front of a triangular pattern of cerebral eyespots.

The flatworm feeds on the coral host beginning in circular patterns within the coenosarc and spreading to polyps, resulting in strips and blocks of coral skeleton appearing pale pink where superficial tissue has been removed. Feeding begins in cryptic areas of the coral. On heavily infested corals where the flatworm is not controlled by predators all external tissues can be eliminated within days. Experiments have shown that starved P. montiporae will not feed on corals of other genera, but will feed on other Montipora species (Jokiel and Townsley, 1974). In so doing, it will take on the color of the host which can even be bright blue in the case of Montipora flabellata.

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The effects of predation on growth and competition in the corals *Montipora verrucosa* and *Porites compressa*

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Abstract

A series of experiments was designed to evaluate the effects of predation by a selective corallivore (the one-spot butterflyfish *Chaetodon unimaculatus*) on growth and competition between the corals *Montipora verrucosa* and *Porites compressa*. Caged colonies of *M. verrucosa* had a vertical growth rate of 9.71×10^{-3} cm d^{-1}. Uncaged colonies of this species that were exposed to predation had a vertical growth rate of only 3.92×10^{-3} cm d^{-1}. In the caged treatments *M. verrucosa* killed and overgrew *P. compressa* tissue, as predicted from laboratory experiments. In the uncaged pairs, however, several colonies showed a reversal of dominance, with *P. compressa* killing branches of *M. verrucosa*. There is a caging effect on growth rate, as shown by comparison of caged and uncaged colonies in an environment free of *C. unimaculatus*. The effect of caging is slight, and insufficient to account for the extreme decrease in growth rate of *M. verrucosa* in the presence of predation by the selective corallivore.

Introduction

Competition for space between corals has been postulated to be a major force controlling community structure in stable environments (Connell, 1978; Sheppard, 1981). Corals can compete for space by rapid growth rate, overtopping morphology and direct aggressive interaction (Lang, 1973; Richardson et al., 1979; Sheppard, 1979). However, the outcome of competitive interactions may be modified by other factors including the delayed development of sweeper tentacles (Wellington, 1980), the site of the interaction (Bak et al., 1982), or activities of the epifauna present (Bak et al., 1982).

Corallivores have been found to depress growth rates of corals (Glynn et al., 1972; Neudecker, 1979), and may also affect outcomes of competition for space. However, the impact of corallivores on growth and competition of corals may depend on feeding preferences shown by the corallivores. Studies of the effect of herbivores on marine algae (e.g. Lubchenco and Gaines, 1981) suggest that feeding preferences for the competitively dominant species prevent monopolization of space by those species. In contrast, when competitively inferior species are the preferred foods, those species may be eliminated from the community.

Coral cover is very high on patch reefs in the northern end of Kaneohe Bay, Oahu. At the primary study site, patch reef #42 (Fig. 1), coral coverage on the top of the patch reef approaches 100%. The reef flat is dominated by two coral species: *Montipora verrucosa* and *Porites compressa*. The slope is constructed primarily of large colonies of *P. compressa*. A chaetodontid corallivore, the "one-spot butterflyfish" *Chaetodon unimaculatus*, is abundant on this reef. These fish form aggregations at the perimeter of the reef and make feeding forays onto the reef flat. *C. unimaculatus* is a selective corallivore, preferring *M. verrucosa* in both laboratory and field feeding observations (Cox, 1982).

In Kaneohe Bay, both *M. verrucosa* and *P. compressa* have similar growth rates, (Table 1), and colony morphologies. *M. verrucosa* displays a unilateral xenogeneic incompatibility against *P. compressa* (Hildemann et al., 1977); i. e. *M. verrucosa* was able to kill tissues of *P. compressa* it came in contact with, similar to aggressive encounters of the type described by Lang (1973). Other researchers have noted that *M. verrucosa* has the ability to overgrow *P. compressa* (Branham et al., 1971; Maragos, 1972; Dollar, 1975). Polacheck (1978) characterized 51 naturally occurring interfaces between *M. verrucosa* and *P. compressa* on patch reef #42. He classified *M. verrucosa* as the dominant coral in 14% of the interactions, a standoff in 84% of the interactions and subdominant to *P. compressa* in 2% of the interactions. If *M. verrucosa* is the competitively dominant species in laboratory encounters, then why is there a high proportion of standoffs between *M. verrucosa* and *P. compressa* on the reef? This may result

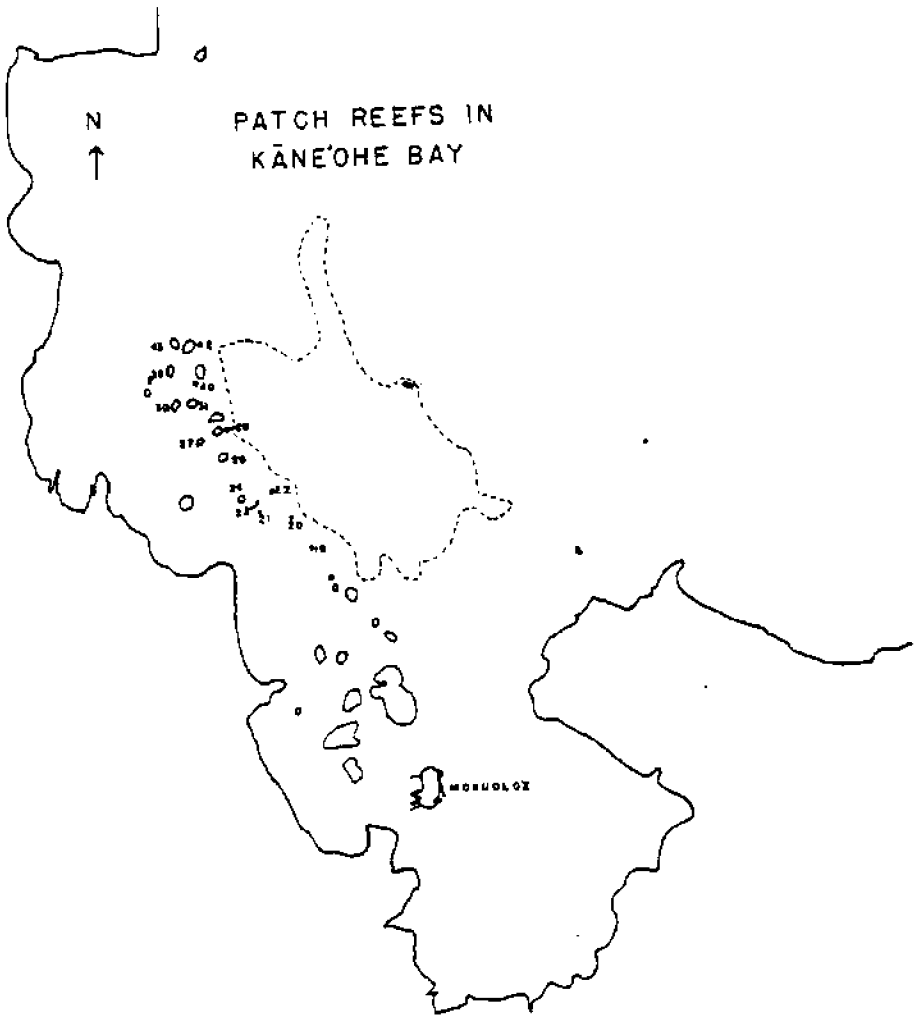

Fig. 1. Primary study site (#42) in Kaneohe Bay, Oahu, Hawaii.

from the impact of a selective corallivore, C. unimaculatus, which prefers M. verrucosa as a food source. The purpose of this investigation was to test the effects of the selective predator on the outcome of these interactions.

Table 1. Comparison of growth rates in Kaneohe Bay (change in radius in cm yr^{-1}) between the corals Montipora verrucosa and Porites compressa.

M. verrucosa	P. compressa	Reference
1.85	2.43	Polacheck (1978)
1.31	1.28	Maragos (1972)

Materials and Methods

Experiment 1

To test for differential growth and competitive interactions with and without predation, pairs of M. verrucosa and P. compressa were placed in contact inside and outside of predator exclusion cages. Small coral colonies (approx. 10 cm diam.) for these experiments were collected from Coconut Island reef. Coral colonies of each species were cut in half with a rock saw. During cutting the corals were cooled with sea water to minimize tissue damage. Corals heal quickly along such cut surfaces. Corals were stained with Alizarin Red S to permit measurement of linear growth (Lamberts, 1974). Each half colony of M. verrucosa was grafted along the cut surface with a half colony of P. compressa, thereby producing two genetically identical pairings. The two halves were held in contact with monofilament and tied to wire screens for placement on the reef. One pair of each of 12 matched sets was protected from chaetodontid grazing by 1.3 cm mesh chicken wire cages; the other pair was left unprotected. These screens were placed at the edge of patch reef #42 on 12 January, 1983, at approximately 2 m depth. Cages were brushed every week to prevent algal fouling. The corals were removed from the field after 160 days. Two were lost during the trial period, and one set of pairs was removed from the data analysis because the competitors became separated. For each remaining set, the percentage of the colony surface which had died was estimated, and growth was calculated by cutting a minimum of ten branches and measuring skeletal growth in the axial plane beyond the Alizarin Red S stain.

Experiment 2

A second series of experimental pairs was prepared by gluing the cut corals to concrete bricks with underwater epoxy (Sea Goin' brand) putty, with cut surfaces flush to the brick face and branch tips in contact. Again, one set of competitors was protected from chaetodontid grazing by chicken wire cages, and the other set was left unprotected. This series of 12 pairs was placed in a similar position on patch reef #42 on 29 March 1983, and removed after 130 days. Cages were brushed at least once per week to prevent algal fouling. Colony mortality was estimated and vertical growth was measured by cutting a sample of ten branches. Observations of direct killing of opposing branches and overgrowth were also made.

Experiment 3

Another chaetodontid, Chaetodon trifasciatus, feeds on M. verrucosa in laboratory situations (Reese, 1977). C. trifasciatus occurs in low numbers on patch reef #42 (pers. obs.). In an attempt to separate out the effects of this chae-

todontid on competition between corals from that of C. unimaculatus, the third series of five experimental sets, prepared identically to the second series, was placed at approximately two m depth off the fringing reef at Coconut Island, an area lacking C. unimaculatus but with approximately the same density of C. trifasciatus as patch reef #42. This series was put out on 17 June 1983 and removed after 100 days. Colony mortality and growth were measured as previously described. Light levels inside and outside of cages were measured with a Li-Cor Model 188B Integrating Quantum Radiometer and an underwater quantum sensor.

Results

Experiment 1

Several of the sets did not survive the experimental period, coming apart from each other or coming loose from the screen. Damage from the contact of the cut surface with another coral seemed to affect both species, although M. verrucosa consistently had a wider margin of dead tissue at the interface. On the basis of a t-test for paired comparisons, there was no difference in the growth rates for P. compressa in the two treatments (t=0.512, df=16), but the caged M. verrucosa grew significantly taller than the uncaged (t=4.657, df=16, P<0.001, Table 2).

Experiment 2

There appeared to be less mortality following the cutting procedure than in Exp. 1: in fact some colonies were growing over the epoxy and out onto the brick surface. Three sets of corals were eliminated from the analysis: M. verrucosa on the uncaged brick of set #2 came unglued and was lost, corals in pair #11 came partially unglued, and set #12 was overturned during a period of heavy surge activity and was destroyed. Measurements of vertical growth (Table 3) were analysed as a randomized blocks ANOVA, with replication from ten branches measured per coral. P. compressa shows no significant difference between treatments, however there are some differences among individuals. The analysis of the data from M. verrucosa indicated a significant interaction component - i.e., all pairs were not responding in a consistent manner. Part of this may be related to the substrate on which the bricks were placed. Sets #5, #6, and #10 were placed on the tongue of M. verrucosa which approaches the edge of the reef. The two sets with the poorest growth rates, #8 and #3, were located at the opposite end of the test area, on P. compressa substrate. The data were reanalysed as a paired t-test comparing mean growth in uncaged and caged pairs. Growth was significantly greater in caged corals (t=4.867, df=16, p<0.001, Table 3).

Where branches of the two competitors came in contact there was a zone of dead tissue, usually on both species with algae covering the exposed corallum. Where branches did not come into contact, no dead zones occurred. Judging from predictions of dominance of M. verrucosa based on results of immunological work, in which M. verrucosa consistantly killed P. compressa tissue that was in contact with it, there should have been more dead surface on P. compressa than on M. verrucosa. For caged pairs, M. verrucosa was the dominant coral, killing P. compressa tissue as far as 1.5 cm from the contact zone. In contrast, in uncaged pairs #3, #8 and #10, P. compressa had killed M. verrucosa tissue, as much as 1 cm from the contact zone.

Experiment 3

There were no significant differences between treatments or among individuals for P. compressa. M. verrucosa showed significant effects both between caged and uncaged individuals, with higher vertical growth in the caged treatment (Table 4). Caging resulted in a decrease of approximately 26% in Photosynthetically Active Radiation (Table 5).

Discussion

A number of factors could produce a difference in the vertical growth rates of M. verrucosa inside and outside of predator exclusion cages on patch reef #42, including various cage artifacts (lower light, lower water motion) and the exclusion of other corallivores. It is clear that exposure to grazing by fishes has a detrimental effect on the growth of M. verrucosa. The surface of the severely grazed test colonies of M. verrucosa from patch reef #42 resembles the gnawed surface of colonies left for several days in aquaria containing C.

Table 2. Comparison of mean vertical growth (cm/160 days) in the coral Montipora verrucosa and Porites compressa in the caged and uncaged treatments in experiment 1.

Pair	M. verrucosa		P. compressa	
No.	caged	uncaged	caged	uncaged
2	0.92	0.00	0.92	0.99
3	0.47	0.00	0.98	1.16
5	0.99	0.30	1.12	0.86
6	1.03	0.52	1.11	0.80
8	1.11	0.53	0.94	0.89
9	1.50	0.40	0.91	1.11
10	1.54	0.45	1.14	1.00
11	0.94	0.00	1.18	1.08
12	1.17	0.48	1.06	1.02
mean	1.074	0.298	1.029	1.001
S.D.	0.321	0.233	0.092	0.133

Table 3. Comparison of mean vertical growth (cm/130 days) in the coral Montipora verrucosa and Porites compressa in the caged and uncaged treatments in experiment 2.

Pair	M. verrucosa		P. compressa	
No.	caged	uncaged	caged	uncaged
1	1.36	0.54	1.13	1.06
3	1.11	0.09	0.76	0.98
4	1.28	0.82	0.96	0.99
5	1.18	0.67	1.05	1.02
6	0.93	0.91	1.02	1.00
7	1.74	0.97	1.05	0.99
8	1.21	0.00	1.08	0.98
9	1.21	0.54	1.14	1.06
10	1.43	0.84	0.96	0.99
mean	1.27	0.60	1.02	1.01
S.D.	0.23	0.35	0.12	0.03

ANOVA

M. verrucosa

Source	df	MS	F	
Treatments	1	19.39057	475.6	P<.001
Individuals	7	1.36156	33.4	P<.001
Interaction	7	0.47313	11.605	P<.001
Error	144	0.04077		

P. compressa

Source	df	MS	F	
Treatment	1	0.02405	1.109	n.s.
Individuals	10	0.10248	4.726	P<.001
Interaction	10	0.04524	2.087	0.025<P<0.05
Error	198	0.02168		

Table 4. Comparison of mean vertical growth (cm/100 days) in the coral Montipora verrucosa and Porites compressa in the caged and uncaged treatments in experiment 3.

Pair	M. verrucosa		P. compressa	
No.	caged	uncaged	caged	uncaged
1	0.88	0.62	0.95	0.86
2	1.18	0.65	0.91	0.88
3	1.37	0.88	0.94	0.94
4	1.29	0.86	0.97	0.99
5	1.26	0.90	0.96	0.96
mean	1.20	0.78	0.95	0.93
S.D.	0.19	0.14	0.02	0.05

ANOVA

M. verrucosa

Source	df	MS	F	
Treatment	1	4.28490	134.570	P<0.001
Individuals	4	0.48385	15.189	P<0.001
Interaction	4	0.05765	1.810	n.s.
Error	90	0.00318		

P. compressa

Source	df	MS	F	
Treatment	1	0.01000	0.076	n.s.
Individuals	4	0.02585	0.197	n.s.
Interaction	4	0.00925	0.070	n.s.
Error	90	0.13141		

Table 5. Mean number quanta (integrated over 10 seconds, 4 readings/block) for caged and uncaged treatments at Coconut Island (std. dev.).

Pair No.	Caged	Uncaged
1	393 (8.0)	493 (8.7)
3	444 (6.2)	583 (15.6)
5	490 (6.5)	758 (10.1)

Table 6. Comparison of growth rates (cm X 10^{-3} d^{-1}) for both corals at the two study sites.

Site	M. verrucosa		P. compressa	
	caged	uncaged	caged	uncaged
Reef #42	9.71	3.92	7.82	7.74
Coconut Island	11.96	7.82	9.46	9.26

unimaculatus. C. trifasciatus has a less well developed jaw and tooth structure (Motta, 1980), which it uses to delicately remove coral polyps, and presumably its more delicate mouth is less able to remove skeletal material than C. unimaculatus. Other researchers (Motta, 1980; T. Hourigan, pers. comm.) indicate that C. trifasciatus takes single polyps or parts of polyps with each bite, a type of feeding behavior which would not produce severely gnawed skeletal surfaces.

There were distinct changes in the growth morphologies of M. verrucosa in the two treatments (Fig. 2). Uncaged specimens had thicker, stubbier branches, while the caged colonies had thinner, finer branches. This undoubtedly affects the measurement of growth, as thinner branches may show more vertical growth, but lateral expansion of the stubbier branches may represent as much mass increase as the thinner branches.

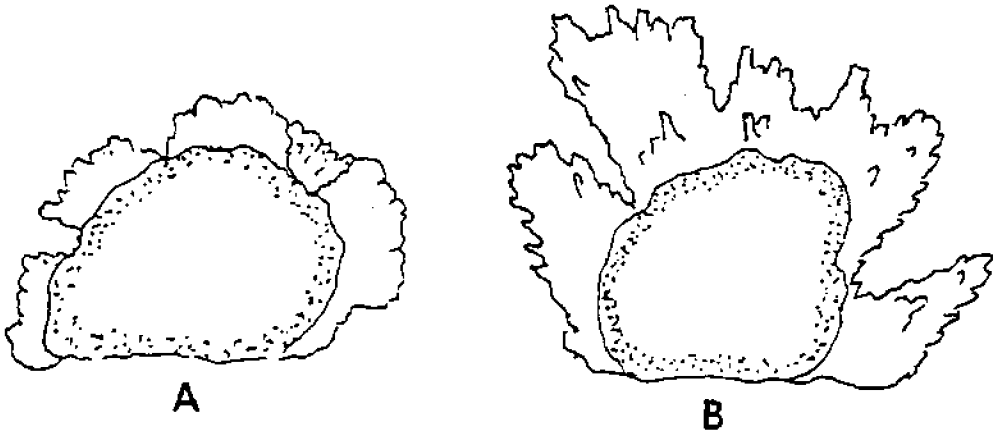

Fig. 2. Sawed cross sections of the coral Montipora verrucosa at the end of the growth experiment revealed original alizarin staining bands. Corals from the uncaged treatment (A) were exposed to fish grazing and developed a stunted growth form. Corals in the caged treatment (B) became finely branched.

The reduction of light levels within cages may have an effect on coral growth rates. Studies have shown that M. verrucosa grows faster in reduced light levels (Houck et al., 1977; Coles and Jokiel, 1978). However, the increase in growth rate is only statistically significant at extremes of temperature. Therefore, it seems unlikely that the additional decrease in light levels observed within the cages could significantly alter growth rates.

The effects of the cages on water motion are more difficult to assess. Even if the cages do not appreciably decrease the total volume of water passing by the corals, they could alter the pattern of flow, perhaps allowing the coral to construct thinner branches.

There is a between site difference in growth rates for both coral species (Table 6). Part of this difference may be due to the additional month of growth of the corals at Coconut Island under elevated summer temperatures, as temperature has been shown to increase growth rates (Maragos, 1972; Coles and Jokiel, 1978). Other physical parameters may differ between the two sites. However, it is readily apparent from these data that the between site differences represent an approximate 18% decrease in growth rates at patch reef #42 for all treatments excepting the uncaged M. verrucosa. In the presence of abundant C. unimaculatus, the selective corallivore, M. verrucosa suffered an additional decrease in growth rate of approximately 32%, presumably due to the effects of grazing by C. unimaculatus.

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Feeding biology of a Hawaiian sea star corallivore, Culcita novaeguineae Müller and Troschel

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Abstract

The Hawaiian sea star corallivore, Culcita novaeguineae, preferentially fed on pocilloporid corals (Pocillopora damicornis and P. meandrina) over the nonpocilloporid species examined (Porites compressa, Montipora verrucosa, and Fungia scutaria) in both laboratory experiments and in the field. The potential factors implicated in prey choice were the imperforate character of pocilloporid corals, percent digestable organic matter, the caloric density of the tissues, the potency of the cnidocysts, and the mucus producing capabilities of the corals. Factors that did not appear important in prey selectivity were colony form, the relative amount of coral tissue available, the total calories digested by the sea star, and the potential presence of toxic substances in the tissues of the coral. It was concluded that prey selection was the result of a number of interacting characteristics of the prey involving the suitability of the coral as a food source and the defense (cnidocyst and/or mucus discharge) of the coral. Field studies suggested that the sea star Culcita novaeguineae is not present in great enough abundance to exert a significant effect upon reef growth in Hawaiian waters. However, the possibility that C. novaeguineae may affect coral community structure by feeding preferentially on pocilloporid species remains.

Introduction

Endean (1971, 1976) and Goreau et al. (1972) noted that the 'pillow' or 'cushion sea star' Culcita novaeguineae Müller and Troschel commonly preys on reef-building corals. C. novaeguineae generally attacks small or encrusting coral colonies. Culcita novaeguineae, like the crown-of-thorns sea star Acanthaster planci (Linnaeus), feeds by everting its stomach over the coral and digesting the soft tissues in situ.

Culcita novaeguineae is present on coral reefs in the eastern Indian Ocean, and in the western and central Pacific Ocean (Clark, A. M., 1954; Clark, A. M., 1976; Yamaguchi, 1975, 1977; Marsh and Marshall, 1983). It occurs on outer reef slopes to 20 m depth, on reef flats, and on patch reefs in protected areas (Goreau et al., 1972; Grosenbaugh, 1981; present observations). C. novaeguineae is often more abundant on coral reefs than A. planci (Saipan, Mariana Islands, Goreau et al., 1972; Guam, Mariana Islands, Yamaguchi, 1975 and unpublished observations; and Oahu, Hawaiian Islands, present study). Preliminary information indicates that Culcita spp., like A. planci, preys selectively on corals and may be important in affecting coral community structure (Goreau et al, 1972; Thomassin, 1976).

Laboratory experiments were undertaken to examine the feeding preference of Culcita novaeguineae with respect to coral colony form, mucus production, cnidocyst defense, organic matter and caloric contents, and the possible presence of noxious substances. Some information is presented on the abundance of C. novaeguineae and its feeding behavior in the field.

Materials and Methods

Feeding Behavior

Specimens of Culcita novaeguineae were maintained in large (1.5 X 0.8 m) indoor tanks with continuously running seawater under indirect, natural light. During the feeding experiments, individual sea stars were confined to separate circular (40 cm diameter) screen enclosures placed in the large tanks. Twelve C. novaeguineae were collected off Kawaihoa Point (near Koko Head) and Waikiki Beach, Oahu, from 1 to 4 months before the study: one C. novaeguineae from Kaneohe Bay (Fig. 1) had been captive for about one year. These sea stars had been fed dead fish and clams. Twenty-two C. novaeguineae were also collected at Kawaihoa Point during the study and their feeding behavior observed immediately after confinement. No differences in feeding behavior (prey species selected and time to feeding) were apparent in long-term captive or recently collected animals. Since the beginning of this study (June, 1983), all laboratory C. novaeguineae were fed corals (Pocillopora damicornis) regularly, at least every other day.

Of the four principal corals offered as food, three form branching colonies - Pocillopora damicornis (Linnaeus), Montipora verrucosa (Lamarck), Porites compressa Dana, while one is solitary and plate-like - Fungia scutaria Lamarck. These corals were collected in Kaneohe Bay and held in large partially shaded, outdoor tanks supplied with running seawater. Pocillopora meandrina Dana, a branching coral, collected at Kahe Point, was offered as food in several instances.

Crustacean guards, present only in the pocilloporid species studied, were not removed from corals that were offered to Culcita novaeguineae. A shrimp and several species of crabs that are obligate symbionts on Pocillopora spp. characteristically defend their host corals from attacking sea stars by snapping and pinching, hence the term 'crustacean guards' (Glynn, 1983). The incidence of crustacean guards was low in Pocillopora damicornis collected at Coconut Island, Kaneohe Bay. In a sample of 45 colonies, only 4 (8.9%) contained Trapezia intermedia (Miers), a xanthid crab, and 1 (2.2%) contained Alpheus lottini Guerin, a pontoniine shrimp. Coral prey (8-12 cm, maximum diameter) were placed in contact with sea stars; when two coral species were offered, these were placed in contact with the sea stars at opposite sides. Corals were offered to individual C. novaeguineae at about 1700-1800 hours, and removed the following afternoon (after ca. 24 h). Food was always supplied in excess of the amount that could be eaten in a single feeding bout. The linear dimensions (length, width, height) of whole live colonies, and the portions eaten, were measured.

The organic matter content of corals was determined from the weight lost after ashing in a muffle furnace at 500 °C for 3 hours. Before ashing, the live corals (8-12 cm, maximum diameter) were rinsed gently with small amounts (10 ml total vol.) of distilled water and oven-dried at 60 °C to a constant weight. To determine the amount of $CaCO_3$ lost through decomposition, corals of each species were soaked repeatedly in 5% sodium hypochlorite, rinsed thoroughly, dried and then ashed. This correction amounted to 2-3% of the skeletal dry weight.

In another feeding experiment, corals offered to Culcita novaeguineae were first autoclaved at 121 °C, 15 psi, for 20 minutes. Microscopical examination of the tissue of autoclaved corals revealed discharged or ruptured cnidocysts.

Corals wrapped in a single layer of cotton cloth (flour-sack towels) were also offered as food. In another treatment, the cotton cloth was soaked for 15 minutes in a 0.2% solution of culinary meat tenderizer (active ingredient papain). Wrapped corals did not die during these experiments.

Caloric Measurements

The caloric values of coral tissues were determined with a Phillipson microbomb calorimeter (Phillipson, 1964). The tissues analyzed came from the peripheral portions of coral colonies, those normally eaten by Culcita novaeguineae: the outer branches (2-3 cm long) of ramose colonies and the margins (approx. 2 cm in from the edge) of the solitary Fungia scutaria. Corals were rinsed gently with small amounts of distilled water to remove salts before the tissues were removed using a jet of recirculated distilled water from a "Water Pik" for 5 min (Johannes and Wiebe, 1970). A total volume of 60 ml of coral tissue homogenate was obtained. The residual organic matter content of the washed skeleton was

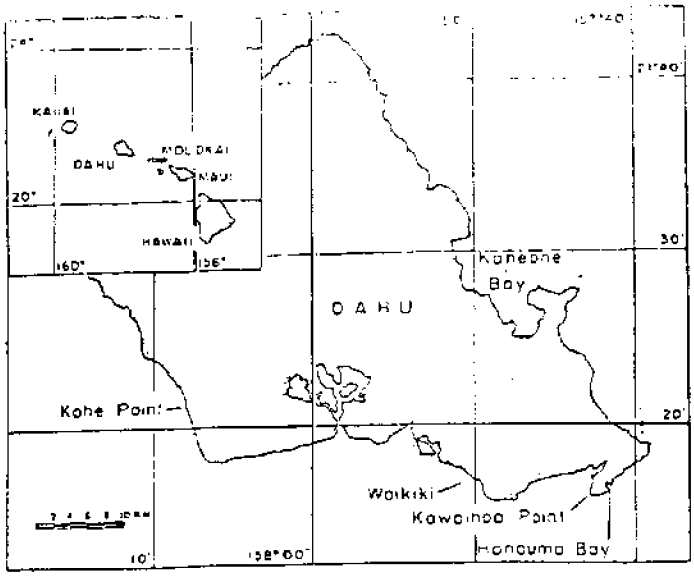

Fig. 1. Study sites on Oahu Island, Hawaiian Islands.

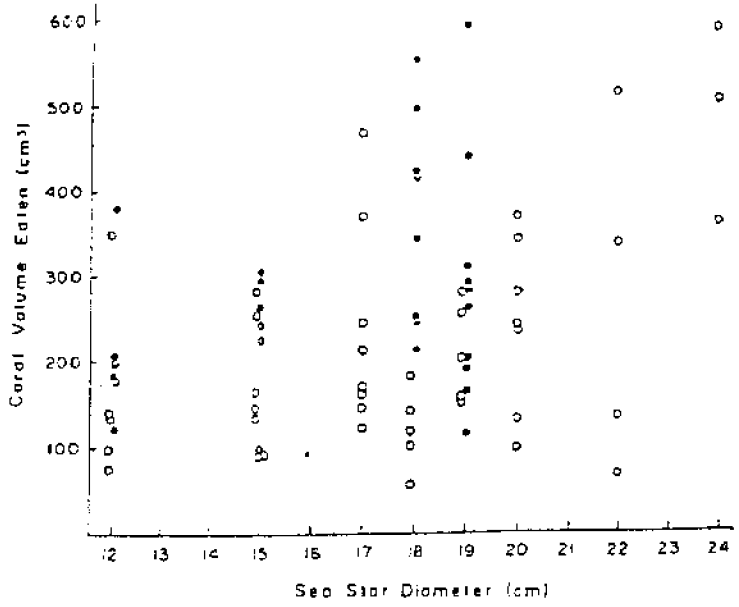

Fig. 2. Relationship between size of Culcita novaeguineae and amount of Pocillopora damicornis eaten. The symbols identify different individual seastars of similar size (n=13 individuals with 74 feeding observations).

determined by ashing (500 °C for 3 hrs). The tissue homogenate was frozen, lyophilized and stored in a vacuum desiccator. Some pelletized samples, ranging from 3-24 mg, were analyzed for caloric content, while others from the same coral were ashed to determine the ash-free organic matter content of the tissues. An endothermy correction was employed for all samples with ash contents exceeding 25% (Paine, 1966). At least three benzoic acid standards (6.318 cal/mg) were run prior to each set of samples.

Mucus Release

The amounts of mucus produced by corals were determined by precipitating mucus with cetylpyridinium chloride, CPC (Krupp, 1982, 1984), and then collecting, weighing and ashing the precipitate. Corals were inverted over glass beakers and filtered seawater (total volume = 50 ml) was gently dripped onto the corals for 10 minutes to stimulate mucus secretion and to extract it from the surface. Extraneous material was removed from the seawater-mucus suspension by centrifugation: CPC (1% solution) was added to the supernatant (3:1, v/v) and incubated overnight at 40 °C. The precipitate was centrifuged, washed with distilled water, and collected on pre-ashed (500 °C, 3 hrs) Whatman GF/C glass fiber filters. These samples were dried overnight at 60°C and then ashed (500 °C, 3 hrs) to determine the organic matter weight of the CPC-complexed mucus. Corrections were made for filter blanks. Mucus-CPC production was adjusted for colony volume, determined from linear measurements (length x width x height).

Cnidocysts

Cnidocyst (nematocysts and spirocysts) numbers and sizes were assessed in the outer branches and colony margins of corals preserved in formalin (5%) and then decalcified (2% acetic acid + 5% formalin). The outer margin (approx. 1 cm in from the edge) was sampled for cnidocysts in the solitary Fungia scutaria. Approximately 2 x 2 mm sections (1 mm thick) were cut from the decalcified tissues. The tissue block was blotted lightly with an absorbant towel and weighed. The weight of each block was adjusted to 6 mg by trimming the sides. Three different areas from a single colony of each species were analyzed with at least four replicates from each area. Tissues were finely macerated and examined microscopically: cnidocysts were counted at 100X and measured at 200X. Measurements were made of only the larger cnidocysts in each species, and therefore indicate maximum sizes. Weill's system (in Mariscal, 1974) was used for cnidocyst identifications.

The occurrence of potentially noxious substances in coral prey was tested by observing the growth rate of a marine diatom, Cylindrotheca fusiformis Reimann et Lewin, (isolated from Kaneohe Bay waters) in the presence of corals, and from the condition of freshwater mosquito fish Gambusia affinis (Baird and Girard) collected from ponds in Kaneohe Bay) exposed to freshly prepared coral slurries. Small, 0.1 gm wet weight, pieces of live coral were broken from peripheral, actively growing areas of coral colonies. These were washed vigorously (by hand shaking) in sterile sea water and then immersed in 0.1 ppt (by volume) sodium hypochlorite for 3 hours to sterilize tissue surfaces. The coral fragments were next rinsed in sterile sea water for 15 minutes and then introduced to 10 ml volumes of the algal cultures at initial cell concentrations of 1.67×10^4 per ml. The cultures were grown in "f" medium (Guillard and Ryther, 1962) made up with enriched seawater. Sixteen hours of light per day was supplied from 4 Vita-lite fluorescent bulbs (40 W each). Consult Jokiel and York (1982) for further details on the growth conditions. Cell counts were made with a hemacytometer, and exponential growth rates (RE) were calculated according to Stein (1975).

Coral tissue slurries were otained by blasting colonies with jets of distilled water from a "water pik." Two fractions were collected from each colony: (1) a highly viscous and colored portion filtered through plankton netting (225 um), and (2) a less viscous and clear portion filtered through plankton netting and a Whatman 3 filter with suction applied. Ten ml of each filtrate were added separately to 10 l (1 ppt by volume), of aerated water containing 10 fish. Adult male and female fish, ranging from 16 to 32 mm (SL) were tested. The condition of test and control fish was observed repeatedly over 48 hours.

Field Observations

The numbers of Culcita novaeguineae observed in the field were recorded on each dive. At Kawaihoa Point (Fig. 1), two divers estimated the area surveyed

to provide a quantitative measure of sea star abundance. Prey items were collected (bagged *in situ*) from feeding sea stars for laboratory study. Pocilloporid corals were separated from the substrate and bagged to assess the composition of their crustacean fauna. Crustacean guards were identified, measured and sexed in the laboratory.

Results

Laboratory Feeding Behavior

When offered a single prey species (no choice feeding), *Culcita novaeguineae* fed more frequently on *Pocillopora damicornis*, (21 colonies eaten out of 34 offerings = 62% feeding rate) than on the other coral species (Table 1). Acceptance of nonpocilloporid corals was low: four colonies of *Porites compressa* (11%) were eaten, only one colony of *Montipora verrucosa* (3%) and none of *Fungia scutaria* (0%). Several small (8 cm maximum diameter) colonies of *Pocillopora meandrina* were eaten by *C. novaeguineae* at about the same rate (9 colonies eaten out of 15 offerings = 60% feeding rate) that *P. damicornis* was eaten.

When offered two coral species simultaneously, *Culcita novaeguineae* always fed significantly ($p<0.0001$, Fisher exact test) more often on *Pocillopora damicornis* than on the other three coral species (Table 2). The frequency of sea stars feeding when offered two corals (81-86%) was higher than when offered a single coral (62%), although nonpocilloporid species were still largely ignored.

The amount of *Pocillopora damicornis* eaten by *Culcita novaeguineae* during a single feeding, as a function of sea star size, is shown in Fig. 2. These pooled data, for 13 individuals, represent feeding in no-choice and choice situations. The latter treatments had no effect on the amount (volume) of coral eaten. In general, larger sea stars tended to consume more coral tissue. However, the variability, both within and between individuals, was considerable: a weighted least squares analysis of the mean coral volume eaten by each sea star exhibited no significant trend with increasing sea star diameter ($F_{1,11}=2.23$, $0.10<p<0.25$). Thus it can only be said that sea stars ranging between 12 and 24 cm in diameter can consume an average of about 250 cm^3 of coral colony volume per feeding bout.

When *Culcita novaeguineae* did feed on nonpocilloporid corals, they ate smaller amounts of the other species than of *Pocillopora damicornis* ($p < 0.001$, Kruskal-Wallis test, Table 3). *A posteriori* testing indicates that significantly smaller amounts of *Porites compressa* and *Fungia scutaria* were eaten than *P. damicornis*. The amounts of *Montipora verrucosa* and *P. damicornis* eaten were statistically similar in spite of considerable differences in their median values.

Considering the amount of coral cover eaten, based on the areas of projected images of corals, the mean feeding rate of *Culcita novaeguineae* on *Pocillopora damicornis* was 27.8 cm^2/day (s.d. = 16.67, n = 77 feeding observations on 13 individuals). This assumes that 85% of the individuals in a *C. novaeguineae* population feed daily (Table 2). The feeding rate on all four corals was slightly less, namely 25.2 cm^2/day (s.d. = 16.53, 97 feeding observations on 13 individuals).

The median percent organic matter contents of the four coral species (Table 4) differed significantly ($0.05>p>0.02$, Kruskal-Wallis test). Percent organic matter contents were relatively low (1.60 - 2.52%) and similar in *Pocillopora damicornis*, *Fungia scutaria*, and *Montipora verrucosa*. *M. verrucosa* was also statistically similar to *Porites compressa* which showed the highest percent organic matter content of the four species (3.74%). In terms of colony volumes, *P. damicornis* and *M. verrucosa* with 1.52 and 5.01 mg dry weight organic matter per cm^3 respectively were statistically similar and relatively low; *F. scutaria* and *P. compressa* with 10.99 and 14.46 mg organic matter per cm^3 respectively contained the highest tissue levels (Table 5). The only significant trend between organic matter content and colony volume was found in *P. compressa*, which showed a negative correlation ($R = -0.800$, $p = 0.042$), indicating a relative decline in organic matter content with increasing colony volume.

There were significant differences ($0.01>p>0.001$, Kruskal-Wallis test) in the residual organic matter contents of corals on which *Culcita novaeguineae* had fed

Table 1. Incidence of feeding by Culcita novaeguineae when offered single coral prey.

Coral offered Species	Number	Number eaten	% sea stars feeding
Pocillopora damicornis	34	21	61.8
Porites compressa	36	4	11.1
Montipora verrucosa	30	1	3.3
Fungia scutaria	9	0	0

Table 2. Incidence of feeding by Culcita novaeguineae when offered pairs of coral prey.

Pairs offered Species	Number	# eaten	% species eaten	% sea stars feeding	Fisher exact probability
Pocillopora damicornis	28	20	71.4	85.7	0.000015
Montipora verrucosa		4	14.3		
Pocillopora damicornis	31	27	87.1	87.1	<<0.00001
Porites compressa		0	0		
Pocillopora damicornis	32	25	78.1	81.2	<<0.00001
Fungia scutaria		1	3.1		

Table 3. Volume (cm^3) per day eaten by Culcita novaeguineae.

	Pocillopora damicornis	Montipora verrucosa	Porites compressa	Fungia scutaria
Median	250	78	20	14
Range	96-419	38-146	8-120	12-17
Multiple Comparisons tests (=0.20)	_____	_____		
Number[1]	13	4	5	4

[1]These observations are from six sea stars that fed on P. damicornis and at least one of the other three coral species.

Table 4. Organic matter content (% dry wt.) of live coral prey.

	Pocillopora damicornis	Fungia scutaria	Montipora verrucosa	Porites compressa
Median	1.60	2.18	2.52	3.74
Range	1.38-2.08	1.48-2.99	2.46-3.18	3.46-5.02
Multiple comparisons test (=0.20)				
Median colony volume (l x w x h)	456	45	416	312
Number	3	5	3	3

Table 5. Organic matter content (% dry wt.) of live coral prey in relation to colony volume (mg dry wt./cm³). Statistical correlations (Kendall's and associated p) between organic matter content and colony volume are also shown for the respective species.

	Pocillopora damicornis	Montipora verrucosa	Fungia scutaria	Porites compressa
Median	1.52	5.01	10.99	14.46
Range	0.46-2.13	1.67-11.77	6.06-23.89	3.52-28.93
MCP[1]				
Median colony volume, cm (l x w x h)	66	31	12	10
(p), Rank correlation	0.524(0.068)	0.333(0.191)	-0.143(0.386)	-0.800(0.042)
Number	7	7	7	5

[1]Multiple comparisons procedure ($\chi^2 = 0.20$): median values are significantly different ($p<0.001$, Kruskal-Wallis test).

(Table 6). Live and eaten corals showed the same ranking by species, but multiple comparisons testing indicates slightly different groupings of species with similar values. Organic matter loss as a result of feeding (Table 7) was greatest in Pocillopora damicornis (69%), which was about two times that in the second ranked coral, Porites compressa (34%). P. damicornis had the lowest organic matter content, but this species also lost the greatest amount to feeding sea stars.

The organic matter content of corals after "water-picking" provides another indication of how firmly the tissues of the four species adhere to the skeleton (Table 8). These analyses were carried out during the caloric determinations to ascertain the efficacy of tissue removal by "water-picking." But they also provided a comparison of tissue removability by Culcita novaeguineae to tissue removability by purely physical means. Percent organic matter content after this physical treatment was similar to that observed in corals eaten by Culcita novaeguineae, and followed the same rank order (Tables 6 and 7). The median values of "water piked" corals were significantly different ($0.02>p>0.01$, Kruskal-Wallis test) and *a posteriori* testing indicates the same groupings in terms of median similarities. Statistical testing of median percent organic matter for the respective species in Tables 6 and 7 (e.g., the comparison of Pocillopora damicornis medians of 0.50% and 0.36%) indicates that all of these values were similar ($p>0.10$ in every case, two-tailed Mann-Whitney U tests).

Sea stars mounted corals wrapped in cloth and extended their stomachs. Greater proportions of the corals wrapped in cloth (Table 9) elicited feeding behavior by the sea stars compared with corals that were not wrapped (Table 1). The apparent increases in acceptability, however, are not statistically significant. Some digestive dissolution of the coral tissues occurred as whitened skeletal areas were left after feeding. Fungia scutaria wrapped with cotton cloth soaked first in a meat tenderizer elicited a significantly higher feeding rate than untreated Fungia scutaria. Five of 30 colonies so treated were eaten by Culcita novaeguineae, while no untreated colonies were eaten ($p=0.0285$, Fisher exact test).

Increased feeding by Culcita novaeguineae on all autoclaved corals (Table 10) were great and highly significant for Porites compressa, Montipora verrucosa and Fungia scutaria when compared with untreated prey, but non-significant in the case of Pocillopora damicornis.

Caloric Densities and Calories Consumed

Median tissue caloric values of the four coral species ranged from 5.12 cal mg^{-1} ash-free dry weight (AFDW) for Montipora verrucosa to 5.60 cal mg^{-1} AFDW for Pocillopora damicornis (Table 11), but showed no significant differences ($0.70>p>0.50$, Kruskal-Wallis test).

Caloric digestion per daily feeding bout by Culcita novaeguineae is shown in Table 12 for the four prey species. The caloric consumption of sea stars feeding on Porites compressa was significantly the greatest, due to the high tissue density per volume in this species (Table 5).

Mucus Release

Fungia scutaria was the most active mucus producer, releasing over thirty times the mucus released by Montipora verrucosa, the second highest producer (Kruskal-Wallis test, $p<0.005$, Table 13). Although multiple comparison testing indicates that mucus release was statistically similar in F. scutaria and M. verrucosa, all individual values were non-overlapping, suggesting that F. scutaria is probably the most active producer. The lack of statistical discrimination between mucus production in Fungia scutaria and Montipora verrucosa was probably a result of the great variability in mucus production by Fungia scutaria. M. verrucosa, Porites compressa and Pocillopora damicornis released relatively small and similar amounts of mucus.

Cnidocysts

Cnidocyst densities (median number per mg wet tissue weight) were significantly higher in Porites compressa (155) and Pocillopora damicornis (115) than in Montipora verrucosa (10) and Fungia scutaria (10) (Kruskal-Wallis test, $p<0.001$, Table 14). Median cnidocyst sizes (lengths) were significantly greater in M. verrucosa (112.3μm) and P. compressa (78.2 μm) than in P. damicornis (38.5 μm)

Table 6. Organic matter content (% dry wt.) of corals after feeding by Culcita novaeguineae.

	Pocillopora damicornis	Fungia scutaria	Montipora verrucosa	Porites compressa
Median	0.50	1.53	2.32	2.46
Range	0.16-0.64	1.33-2.27	2.16-2.45	1.84-3.13
Multiple Comparisons test (= 0.20)				
Median colony volume (l x w x h)	238	29	73	192
Number	9	3	3	5

Table 7. Percent organic matter loss ("utilization") in corals after feeding by Culcita novaeguineae.

	Pocillopora damicornis	Fungia scutaria	Montipora verrucosa	Porites compressa
Difference[1]	1.10	0.65	0.20	1.28
% difference[2]	68.75	29.82	7.94	34.22

[1]Calculated from median difference in organic matter content of live corals (Table 4) - organic matter content of corals after feeding by C. novaeguineae (Table 6).

[2]Overall percentage difference = Table 4 median percent value - Table 6 median percent value / Table 4 median percent value (100).

Table 8. Organic matter content of corals after "water piking".

	Pocillopora damicornis	Fungia scutaria	Montipora verrucosa	Porites compressa
Median	0.36	1.44	2.54	2.78
Range	0.22-0.46	0.77-1.98	0.55-3.29	1.37-3.37
Multiple comparisons procedure (= 0.20)				
Median colony volume, cm (l x w x h)	8	4	31	10
Number	4	4	7	4

Peripheral portions of colonies used.

Table 9. Incidence of feeding by Culcita novaeguineae when offered single coral wrapped in cotton cloth. Statistical testing is for the proportion of non-wrapped and wrapped corals eaten for each species.

Coral offered Species	Number	Number eaten	Percent eaten	Prey ratio non-wrapped:wrapped	Fisher exact probability
Pocillopora damicornis	27	18	66.7	0.93	0.19646
Porites compressa	30	5	16.7	0.66	0.22679
Montipora verrucosa	27	2	7.4	0.45	0.35988
Fungia scutaria	27	3	11.1	0	0.10552

Table 10. Incidence of feeding by Culcita novaeguineae when offered single autoclaved coral species. Statistical testing is for the proportion of live and autoclaved corals eaten for each species.

Coral offered Species	Number	Number eaten	% sea stars feeding	Prey ratio live:autoclaved	Fisher exact probability
Pocillopora damicornis	10	9	90.0	0.69	0.0807
Porites compressa	10	9	90.0	0.12	0.0000058
Montipora verrucosa	11	6	54.5	0.06	0.00062
Fungia scutaria	10	9	90.0	0	0.0000005

Table 11. Caloric densities of coral tissues (calories/mg ash free weight).

	Pocillopora damicornis	Porites compressa	Montipora verrucosa	Fungia scutaria
Median	5.60	5.42	5.12	5.25
Range	0.65-6.86	5.00-5.75	4.48-5.59	4.68-9.86
Number[1]	5	4	6	7

[1]One outlier was omitted, 4.17 cal/mg-AFDW determined for P. compressa.

Table 12. Calories assimilated per feeding bout by Culcita novaeguineae preying on four coral species.

	Fungia scutaria	Montipora verrucosa	Pocillopora damicornis	Porites compressa
Median[1]	1,656	1,986	2,128	10,190
Range	1,472-2,085	973-3,748	818-3,567	7,051-37,620
MCP[2]				
Number	4	4	13	5

[1]Organic matter consumed is product of coral volume eaten (Table 3) and median value of organic matter per cm³ for respective species (Table 5). For P. compressa, where the percent organic matter declined significantly with increasing colony volume, the organic matter consumed was determined from the least squares regression curve of these variables. The respective median caloric densities (Table 11) were used to convert ash-free organic matter to calories consumed.

[2]Multiple comparisons procedure (χ^2= 0.20): median values are significantly different (0.01>p>0.001, Kruskal-Wallis test).

Table 13. Mucus released by corals. Mucus-CPC precipitate (mg dry weight) /100 cm³ coral volume/10 minutes.

Fungia scutaria	Montipora verrucosa	Porites compressa	Pocillopora damicornis
1.59	0.08	0.02	0.01
2.93	0.13	0.02	0.01
6.58	0.18	0.03	0.02
6.61	0.26	0.15	0.04
10.62	0.32	0.21	0.05
Median 6.58	0.18	0.03	0.02
Multiple comparisons procedure(=0.20)			

Table 14. Cnidocyst densities (number per mg wet tissue weight) and sizes (m) in four coral species.

DENSITY

	Porites compressa	Pocillopora damicornis	Montipora verrucosa	Fungia scutaria
Median	155	115	10	10
Conf. lim.[1]	62-315	75-150	2-30	5-55
MCP[2]				
Number[3]	20	14	18	28

SIZE

	Montipora verrucosa	Porites compressa	Pocillopora damicornis	Fungia scutaria
Median	112.3	78.2	38.5	33.6
Conf. lim.[1]	106.4-115.8	73.5-81.1	31.8-41.8	30.1-40.6
MCP[2]				
Number[3]	13	18	18	17

[1]Confidence limits of median calculated as K = 0.5 (n+1) - [n] 1/2 of the range, where K is the number of units from each end of the distribution toward the median.

[2]MCP, multiple comparisons procedure ($\chi^2_{.1}$ = 0.20) for Kruskal-Wallis test.

[3]Total number of replicates from three areas of colony (density); number of cnidocysts measured (size).

and F. scutaria (33.6 µm) (Table 14). The largest and most abundant cnidocysts found in M. verrucosa were microbasic p-mastigophores; some small atrichous and holotrichous isorhizae were also present. P. compressa contained numerous, large holotrichous isorhizae. Only small microbasic p- and b-mastigophores and holotrichous isorhizae were found in P. damicornis and F. scutaria.

Bioassays

Growth rates of the marine diatom C. fusiformis in response to four coral species are presented in Table 15. Cell doublings were highest after four days; six cultures in four treatments showed negative growth after six days. The four day cell counts were used to test the effects of corals on diatom growth. Cell numbers were transformed to square root values to stabilize the unexplained variances. Results of the nested ANOVA computations are presented in Table 16. Comparable culture growth (with RE >1.34) was observed in each treatment (Table 15). Significant variance components were found among treatments and among replicates. Within replicate error was high with a variance component of 47.78%. Based on the highly significant differences among replicates and the high error rate within replicates, these results do not provide evidence for growth inhibition due to any of the four corals tested.

Neither group of the mosquito fish Gambusia affinis exposed for two days to crude coral tissue slurries or filtered coral extracts showed signs of altered swimming and feeding behavior or opercular ventilation activities.

Field Observations

Culcita novaeguineae was present at four sites on the open coast of Oahu: Hanauma Bay (outer south point), Kawaihoa Point, Waikiki, and Kahe Point (Fig. 1). The highest population density was at Kawaihoa Point, with 21 individuals ha^{-1}. Many sea stars at Kawaihoa Point were present in relatively turbulent water between 4-7 m depth. Under these conditions the sea stars were usually wedged between rock cracks and difficult to dislodge. While no C. novaeguineae were found in protected Kaneohe Bay, they have been observed on reefs in the bay (L. C. Zukeran, pers. comm.).

Of nine Culcita novaeguineae observed feeding in the field, six (67%) were eating corals and three (33%) were eating bryozoans, algae and sponges. Two C. novaeguineae were eating the latter three prey items as an aggregate; one C. novaeguineae was eating a bryozoan alone. The coral prey consisted of Pocillopora meandrina (4), Montipora verrucosa (1), and Porites lobata (1). All of these colonies were small, with a maximum diameter <10 cm. Although prey availability was not determined, it was obvious that P. lobata, primarily small colonies (<20 cm maximum diameter), predominated in this area. These limited observations suggest a preference for Pocillopora meandrina, in accordance with the laboratory results indicating a preference for pocilloporid corals.

Analysis of two groups of small colonies of Pocillopora meandrina indicated a higher incidence of crustacean guards in the larger (100%) compared with the smaller (47%) colonies (Table 17). The size of xanthid crab guards (Trapezia spp.) was also greater in larger (6.0 mm median carapace width) than smaller (3.4 mm) colonies. A shrimp guard, Alpheus lottini, occurred in 15% of the larger colonies, but was absent from the smaller colonies.

Discussion

Field studies in the western Pacific (Goreau et al., 1972; Endean, 1976) have indicated that small corals of low relief, species of Pocillopora and Acropora, Porites lichen and faviids, are the usual prey of Culcita novaeguineae. In some Pacific habitats, e.g., shallow reef flats on Guam, C. novaeguineae also preys heavily on plate-like and encrusting pavonid species (Wilkins, 1979; Glynn, unpublished observations). On reef flats in Madagascar, Thomassin (1976) observed Culcita schmideliana feeding on small colonies of Galaxea fascicularis (Linnaeus) and Goniopora stokesi Milne Edwards and Haime. Goreau et al. (1972) concluded that C. novaeguineae specialized on small corals, regardless of colony form (i.e., massive or branching), because the sea star lacks prehensile arms and cannot climb large or high corals. Glynn (unpublished) has observed in the field that small (juvenile) colonies of several large species are also avoided, suggesting the presence of some deterrent other than size.

Table 15. Growth rate response of *Cylindrotheca fusiformis* to coral fragments introduced into diatom cultures. Number of cells and exponential growth rate (RE) per day in seven treatments after two time intervals.

	after 4 days		after 6 days	
Treatment	no. cells	RE	no. cells	RE
Control 1[1]	6.80 X 10^4	1.30	1.61 X 10^5	0.62
Control 2	7.82 X 10^4	1.38	9.22 X 10^4	0.12
Control 3	1.25 X 10^4	0.72	1.58 X 10^5	1.83
Fungia 1[2]	2.26 X 10^5	1.77	2.99 X 10^4	1.86
Fungia 2	2.08 X 10^5	1.74	3.36 X 10^4	2.00
Fungia 3	1.68 X 10^5	1.66	8.48 X 10^4	-0.49
Fungia 4[3]	1.74 X 10^5	1.68	1.41 X 10^5	-0.15
Fungia 5	1.39 X 10^5	1.59	1.75 X 10^5	0.17
Fungia 6	2.24 X 10^5	1.76	2.72 X 10^4	1.80
Fungia 7[4]	1.43 X 10^5	1.60	9.10 X 10^4	-0.33
Fungia 8	1.62 X 10^5	1.65	3.19 X 10^4	2.15
Fungia 9	2.00 X 10^5	1.72	7.40 X 10^4	-0.72
Porites 1[4]	3.10 X 10^4	1.05	2.02 X 10^4	3.01
Porites 2	2.20 X 10^4	0.93	1.92 X 10^4	3.22
Porites 3	1.38 X 10^5	1.59	2.51 X 10^4	2.09
Montipora 1[4]	7.42 X 10^4	1.37	1.27 X 10^5	0.39
Montipora 2	6.35 X 10^4	1.31	1.26 X 10^5	0.49
Montipora 3	2.00 X 10^4	0.90	5.95 X 10^4	0.79
Pocillopora 1[4]	9.52 X 10^4	1.46	4.65 X 10^4	-0.52
Pocillopora 2	1.65 X 10^4	0.83	8.82 X 10^4	1.21
Pocillopora 3	8.85 X 10^4	1.43	6.98 X 10^4	-0.17

[1]Diatom in culture medium.
[2]Fresh coral fragments washed vigorously in sterile seawater then introduced into culture.
[3]Coral fragments autoclaved (121° C, 15 psi, 20 min.) then introduced into culture.
[4]Coral fragments treated with 0.1 ppt sodium hypochlorite then introduced into culture.
[5]$RE = \log 2X2 - \log 2X1 / t2 - t1$

Table 16. Anova table for diatom bioassay.

Source of variation	df	SS	MS	Fs	components (%)
Among treatments	6	710.1	118.35	5.818[1]	33.66
Among replicates	14	284.9	20.35	8.772[2]	18.57
Within replicates	399	924.3	2.32		47.78
	419	1,919.3			

[1] $p<0.005$ $F_{0.005\ \langle 6,14\rangle} = 5.26$

[2] $p<<0.0005$ $F_{0.0005\ \langle 14,399\rangle} = 2.84$

Table 17. Incidence and size relations of crustacean guards in small and relatively large colonies of Pocillopora meandrina.

	Small colonies[1]	Large colonies[1]
Colony size range (cm^3)	5-52	99-400
number	17	13
Percent colonies with crustacean guards	47.1	100.0
Size of Trapezia spp. (mm)[2]		
median[3]	3.4	6.0
0.95 conf. lim.	2.9-4.5	3.0-7.0
number[c]	15	21
Percent colonies with Alpheus lottini	0	15.4

[1] Collected at Kahe Point, 7-10 meters: small colonies on 15 June 1983, large colonies during 1976 (1976 data set courtesy S. L. Coles).

[2] Carapace width of Trapezia intermedia, the dominant crustacean species. One individual each of Trapezia wardi and Trapezia ferruginea was found in the larger colonies.

[3] Median values are significantly different ($p<0.05$, Mann-Whitney U test).

Laboratory feeding results were similar to field observations and showed that Culcita novaeguineae had a strong preference for Pocillopora damicornis. One of the three coral species avoided by C. novaeguineae, Montipora verrucosa, is nearly identical to P. damicornis in colony form and branch thickness. This indicates that colony habit per se is probably not critical in prey choice.

Compared with the other coral prey, Culcita novaeguineae ate the largest colony volume and removed the highest percentage of tissues from Pocillopora damicornis. The tissues of Pocillopora are not intricately connected and deeply penetrating, but form a superficial layer over the corallus. Montipora verrucosa, Porites compressa and Fungia scutaria (the latter in the highest septa cycles) are "perforate" corals with ramifying vertical and lateral connections between corallites (Wells, 1956). It may be difficult for C. novaeguineae to digest anything but surface tissues. Thus the deep tissues in perforate corals largely escape digestion. 'Water-piking' mimicked digestion and further suggested that tissue availability and removability at the surface of the coral are important in determining how much coral tissue may be ingested.

While the caloric density of coral tissues did not vary significantly among the species studied, there was greater variability among colonies within species for Pocillopora damicornis and Fungia scutaria than for Porites compressa and Montipora verrucosa. This variability may be due to differences in the reproductive states of the corals at the time of collection. Prior to the release of gametes or brooded planulae, the tissues of the coral may be of higher caloric density. Planulae from Pocillopora damicornis are rich in calories (7.5 cal mg^{-1} AFDW), while the caloric density of the adult tissues after release of the planulae (5.0 cal mg^{-1} AFDW) are substantially lower (Richmond, 1982). Our values, which were intermediate to these extremes, probably reflect the collection of adult colonies at different times in their reproductive cycle. Colonies possessing many well-developed planulae would exhibit higher caloric densities than colonies that have just released their planulae. Thus, P. damicornis may represent an energy-rich food source just before planula release.

Of further consideration, is the timing of reproduction. Corals such as Pocillopora damicornis that release brooded planulae throughout the year with a lunar periodicity (Richmond and Jokiel, 1984) would represent a year-round source of energy-rich tissues to corallivores. On the other hand, corals that are reproductive during only part of the year, such as Porites compressa, Montipora verrucosa and Fungia scutaria (Heyward, pers. obs.; Krupp, 1983), could not be relied upon to yield energy-rich tissues throughout most of the year. The colonies of Porites compressa and Montipora verrucosa used in the present study were collected after they had completed their reproductive seasons. This observation would explain the low ranges of caloric values obtained for these two species. Fungia scutaria spawns on a lunar cycle during the summer months (Krupp, 1983). Thus, some specimens of F. scutaria used in this study probably contained gametes, while others did not.

However, of the four species examined, Pocillopora damicornis also had the lowest percent organic matter and the lowest organic matter density per colony volume. C. novaeguineae did not digest tissues so readily from P. compressa (34% removal) as from P. damicornis (69%), but the high density of tissues in P. compressa made this species the most profitable in terms of caloric yield per feeding bout, assuming that the assimilation of coral tissues is proportional to the digestion of coral tissues regardless of the species of coral prey. Thus caloric yield does not appear to be an important factor in prey choice.

The cnidom has a defensive function in corals. Cnidocysts cause arm rearing, tube foot retraction, and stomach withdrawal in Acanthaster planci (Brauer et al, 1970; Barnes et al, 1970; Moore and Huxley, 1976). Ormond et al. (1976) claimed that a strong cnidocyst defense, in such corals as Fungia spp. and Millepora spp., was probably the reason why these corals were generally avoided by A. planci.

The wrapping in cloth or autoclaving of coral prey, to reduce or nullify cnidocyst action, generally increased the acceptability of corals avoided by Culcita novaeguineae. This could indicate that heat-labile cnidocysts were nullified, but that heat-stable attractants (settlement-inducing activity) were not altered (Brauer et al., 1970; Collins, 1974). Two physical attributes of cnidocysts examined in this study, density in tissues and size, did not show a consistent relationship with the feeding preferences of Culcita novaeguineae. For

example, cnidocysts in nonpreferred Fungia scutaria were small and few in number. This suggests that the toxic properties of the cnidom and/or coral tissue toxicity (Mariscal, 1974; Moore and Huxley, 1976) may be more important than cnidocyst size and number in acting as deterrents. The bioassays investigating the presence of potentially toxic substances from coral tissues did not reveal any obvious repellent effects. However, extrapolation of these bioassay results to any effects of coral tissue/cnidocyst toxins on true corallivores may not be valid.

Fungia scutaria and Montipora verrucosa, the two least preferred species, released the greatest amounts of mucus. Mucus could enhance the protection of these corals (1) by providing a matrix or carrier for cnidocyst exposure to foreign bodies, e.g., an encroaching corallivore, (2) by serving as a carrier for cytotoxic molecules (in F. scutaria, Hildemann et al., 1977), and (3) by forming an insoluble barrier to digestive enzymes (Edwards, 1978). Culcita novaeguineae digested few calories from F. scutaria and M. verrucosa. Few calories were digested from Pocillopora damicornis as well, a coral that released relatively small amounts of mucus.

In terms of optimal prey choice, the preference of Culcita novaeguineae for Pocillopora damicornis could be based on a combination of factors: high abundance and predictability, high digestibility (superficial location of tissues and low mucus release), and absence of potent cnidocysts. Porites compressa is also abundant and calorically the most rewarding coral, but possesses numerous, large cnidocysts. Some of the costs in feeding on pocilloporid corals are increased handling time (mounting and stomach extrusion) and injuries caused by crustacean guards protecting their coral host (Glynn, 1976, 1983). Feeding studies in Guam (Glynn, unpublished observations) have demonstrated that C. novaeguineae eats significantly ($p<0.01$, Mann-Whitney U-test) larger amounts of Pocillopora stripped of crustacean guards (median colony volume eaten = 616 cm^3, $n=9$) than P. damicornis with guards (median colony volume eaten = 216 cm^3, $n=9$). The lower incidence and smaller size of crustacean guards in small compared with large colonies may be one of the reasons why C. novaeguineae feeds preferentially on small colonies.

Culcita novaeguineae does feed occasionally on "nonpreferred" corals and other kinds of organisms, as noted by Potts (1982) in Acanthaster planci. This could be due in part to the adaptability of the sea star's feeding behavior vis-a-vis local prey availability (Ormond et al., 1976). Comprehensive studies on temperate sea stars off Washington state (USA), have demonstrated that several undesirable prey are frequently consumed if they are abundant and always available (Paine, 1969; Menge, 1972).

To the extent that laboratory and field feeding rates can be compared, it is possible to contrast Culcita novaeguineae with Acanthaster planci in terms of coral cover killed. Laboratory feeding showed that C. novaeguineae can eat 1.0 $m^2\ y^{-1}$ (projected image) of Pocillopora damicornis or 0.9 $m^2\ y^{-1}$ of mixed coral prey (the four species examined here). These mean rates represent only one-fifth the feeding rates reported for A. planci, namely from 5.3 $m^2\ y^{-1}$ (Dana and Wolfson, 1970) to 5.8 $m^2\ y^{-1}$ (caged field animals; Pearson and Endean, 1969). On the basis of a study in Panama, demonstrating that positive reef growth was possible at A. planci densities of 65 individ. ha^{-1} (Glynn, 1973), it is doubtful that the highest C. novaeguineae abundances thus far reported, around 25 individ. m^{-2}, could have a serious impact on reef growth.

The non-random feeding by Culcita novaeguineae could have an effect on coral community structure. The selective predation by C. novaeguineae on Pocillopora spp. may be a factor in limiting the abundance of these corals, thus contributing to the predominance of Porites spp. in certain Hawaiian coral assemblages. Acanthaster planci also avoided Porites (Porites compressa) and fed selectively on Montipora verrucosa at Molokai Island, Hawaii (Branham et al., 1971). The simultaneous feeding of C. novaeguineae and A. planci, observed at Kawaihoa Point, could together accelerate predation and reduce local species richness.

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Aggressive interactions of the solitary coral, Fungia scutaria (Lamarck)

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Abstract

The solitary free-living coral, Fungia scutaria, caused unilateral tissue damage to colonial corals in over 93% of 277 natural contacts in Hawaii. Macroalgae overgrew and smothered F. scutaria in all 52 natural cases observed. 41% of a population of F. scutaria occurred in contact with other species of live coral or macroalga, with no significant difference between reefs. The remainder of the population occurred in the midst of monospecific aggregations or singly on reef flats. Large F. scutaria induced local tissue necrosis on corals in over 80% of field experimental contacts, while smaller individuals moved away and caused significantly less damage. Control patches of colonies lacking F. scutaria exhibited no localized damage. In over 150 cumulative field observations, F. scutaria did not cause necrosis on corals at interskeletal distances of greater than 15 millimeters. The mechanism of interspecific aggression appears to involve nocturnal expansion of the polyp and deposition of nematocyst laden mucus onto adjacent corals. Within two days, the victim's tissue under this mucus becomes necrotic and sloughs off, exposing bare skeleton. This area remains dead for the duration of contact. The aggressive dominance and aggregative nature of F. scutaria appear to retard overgrowth by other species and prevent settlement of coral fragments or larvae within aggregations. These defensive mechanisms of solitary corals may facilitate maintainance of living space by solitary corals and slow monopolization of the substrate by colonial species on coral reefs.

Introduction

Competition for space has been established as an important limiting factor for sessile invertebrates on temperate rocky shores (Connell, 1961; Dayton, 1971; Quinn, 1982), coral reefs (Glynn, 1976; Buss and Jackson, 1979), and marine fouling communities (Buss, 1982). Colonial organisms may exert a competitive advantage over solitary species due to their capacity for asexual reproduction and indeterminate growth, and they dominate and substrate in both cryptic and exposed reef habitats (Jackson, 1977). However, solitary forms do occur at low densities on reefs (Lang, 1971) and have developed an array of defense mechanisms to prevent overgrowth. They may use allelopathy (Jackson and Buss, 1975), direct aggression (Lang, 1971; Sheppard, 1979), or an escape in size (Wells, 1966). In addition, some solitary organisms form large aggregations. Among these are some clonal sea anemones (Carlgren, 1949; Rand, 1954), bivalves (Paine, 1976), and sabellid worms (Wilson, 1968). The feeding activities of aggregations may prevent settlement of larvae of other species and inhibit overgrowth by adjacent plants and animals (Jackson, 1977).

On Hawaiian reefs, the solitary free-living coral Fungia scutaria exhibits several of these characteristics. All members of this genus thus far studied aggressively damage neighboring corals (Hildemann et al., 1975, 1977; Sheppard, 1979) and cluster in aggregations on the reef (Abe, 1939; Wells, 1966). Aside from evidence from laboratory induced contacts and occasional field observations, little in known of the aggressive response of F. scutaria. In particular, no published work exists concerning the natural frequency of interspecific contact, mechanism of damage, or constancy of outcome in the field. I present here evidence concerning the occurrence, outcome, and duration of natural and experimentally induced contacts, and discuss effects on community structure. I also describe a mechanism of interspecific damage employed by F. scutaria which is unique among scleractinian corals.

Materials and Methods

Field observations and experiments were conducted during the summer of 1983 in Kaneohe Bay, Oahu, Hawaii. This bay supports numerous patch reefs and is protected from oceanic swells by a wide barrier reef across the entrance. Laboratory observations were made at the Hawaii Institute of Marine Biology, on Coconut Island in Kaneohe Bay.

To determine the frequence of natural contacts between Fungia scutaria and other corals or macroalgae, observations were made in shallow water at three patch reefs (sites 1, 2, and 3 in Fig. 1). Each F. scutaria, hereafter referred to simply as Fungia, was recorded as in contact or not in contact with other species of live coral or macroalga. The tissues of Fungia expand nocturnally to a distance of up to 15 mm from the skeletal surface (Wells, 1966; person observation). Other species were considered to contact Fungia if they occurred within this distance.

Outcomes of contact were assessed at five additional sites (sites 4 to 8, Fig. 1). Effects of contact were rated as damage to (1) Fungia, (2) other species, (3) both, or (4) neither. Local damage to corals was clearly visible as a zone of necrotic tissue or exposed skeleton along the region of interspecific contact (after Wellington, 1980).

In order to examine the interaction in great detail, including effects of proximity and size of Fungia, an experiment was initiated at a patch reef adjacent to Coconut Island (site 6 in Fig. 1). The windward edge of this reef supports a large population of Fungia and has been described by Jokiel et al. (1983). Three of the most common corals in Kaneohe Bay were used: Porites compressa, Montipora verrucosa, and Pocillopora damicornis (Polacheck, 1978). Thirty Fungia in three size classes (mean maximum skeletal width ± standard deviation: small = 56 ±13 mm, medium =99±13 mm, and large = 175±13 mm) were moved into tissue contact with live, naturally occurring coral colonies. Small healthy areas on each colony were marked to serve as controls and did not receive translocated Fungia. Observations of each experimental pair were made weekly for a period of one month.

Laboratory observations on the mechanism of damage were made by placing Fungia adjacent to live coral colonies in outdoor aquaria supplied with continuously flowing sea water. Forty interacting pairs were observed both nocturnally and diurnally for several months. Behavioral interactions are reported as a composite of these observations. Samples of mucus were obtained from Fungia by drawing small amounts into pipettes held above the surface of expanded individuals. Care was taken not to touch or otherwise disturb the tissues of Fungia during collection. Mucus was then examined by phase contrast light microscope at 400 power magnification. Nematocyst types therein were classified according to Mariscal (1974), and their relative abundances estimated.

Results

Natural Contacts

Of 485 Fungia observed in the field, 40.7 ±1.9% (mean ± standard deviation) occurred in contact with other species of live coral or macroalga. The proportion of the population in interspecific contact was remarkably constant, with no significant difference between reefs (chi square = 0.3176, $p > 0.80$). In particular, 31.5 ±2.9% of the population contacted the common colonial coral species of Porites compressa, Montipora verrucosa, Pocillopora damicornis, Cyphastrea ocellina, or Pavona varians. The remaining 9.2 ±4.0% contacted the green bubble alga, Dictyosphaeria cavernosa, or crustose coralline algae. Those Fungia not touching other species occurred in the midst of monospecific aggregations or singly on sandy reef flats.

In natural contacts with colonial corals, Fungia caused unilateral tissue damage in over 93% of the cases (Fig. 2). The polyps of other species often appeared expanded and healthy except in the immediate vicinity of Fungia. The tips of coral branches adjacent to Fungia usually bore encrusting algae or a layer of mucus. In one case a spreading plate form of Montipora verrucosa surrounded a Fungia on three sides, with the outer edge of the plate damaged only where facing Fungia. Small fragments of colonial corals which had fallen into the midst of aggregations were completely dead if less than two centimeters in diameter.

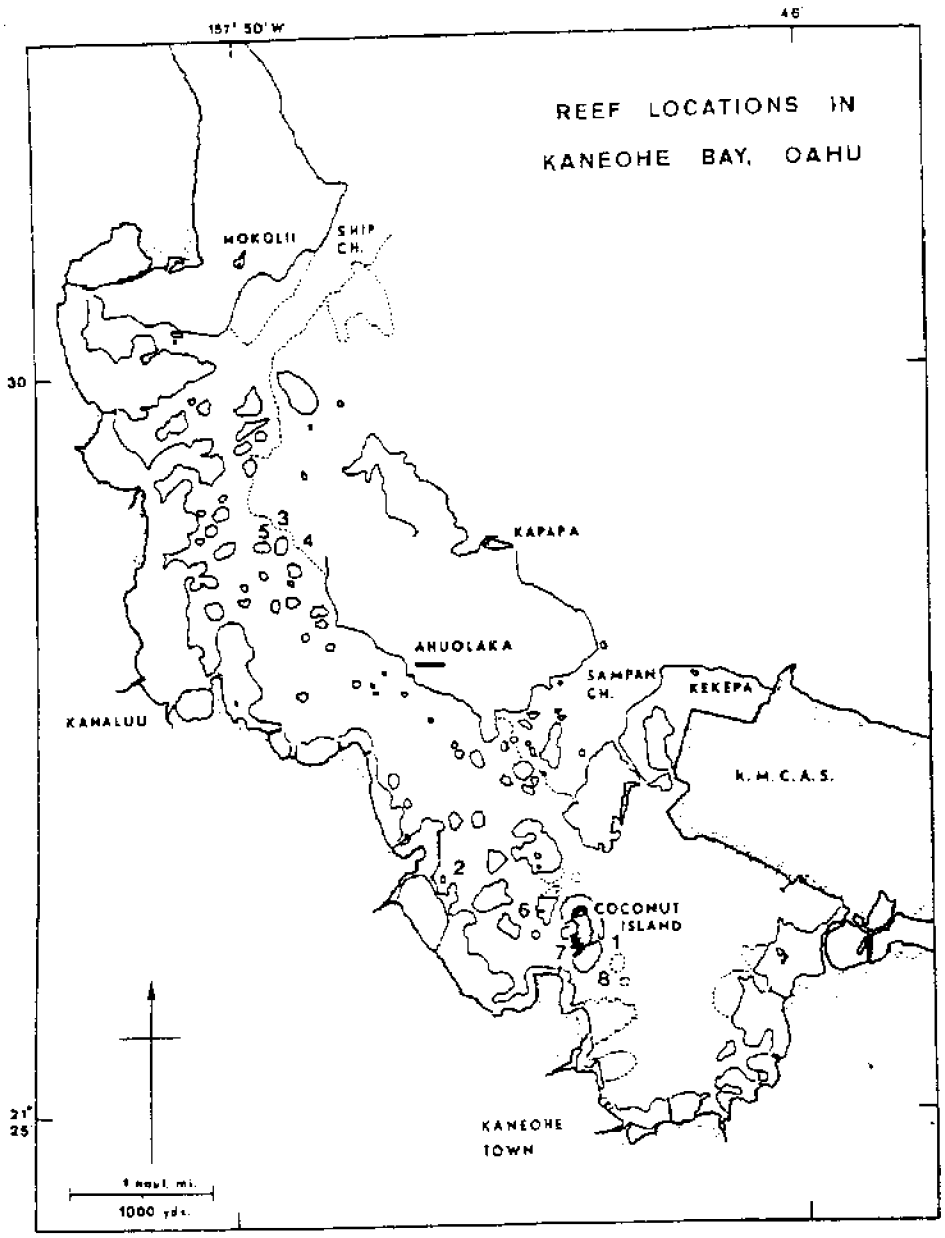

Fig. 1. Reef locations for assessment of aggressive interactions by Fungia scutaria in Kaneohe Bay, Oahu, Hawaii. Numerals one through eight indicate study sites. K.M.C.A.S. is the Kaneohe Marine Corps Air Station; dotted line represents reef areas below 10 feet; solid reef lines represent reefs at or near surface. Adapted from U.S.C. & G.S. Chart 4134 and aerial photographs.

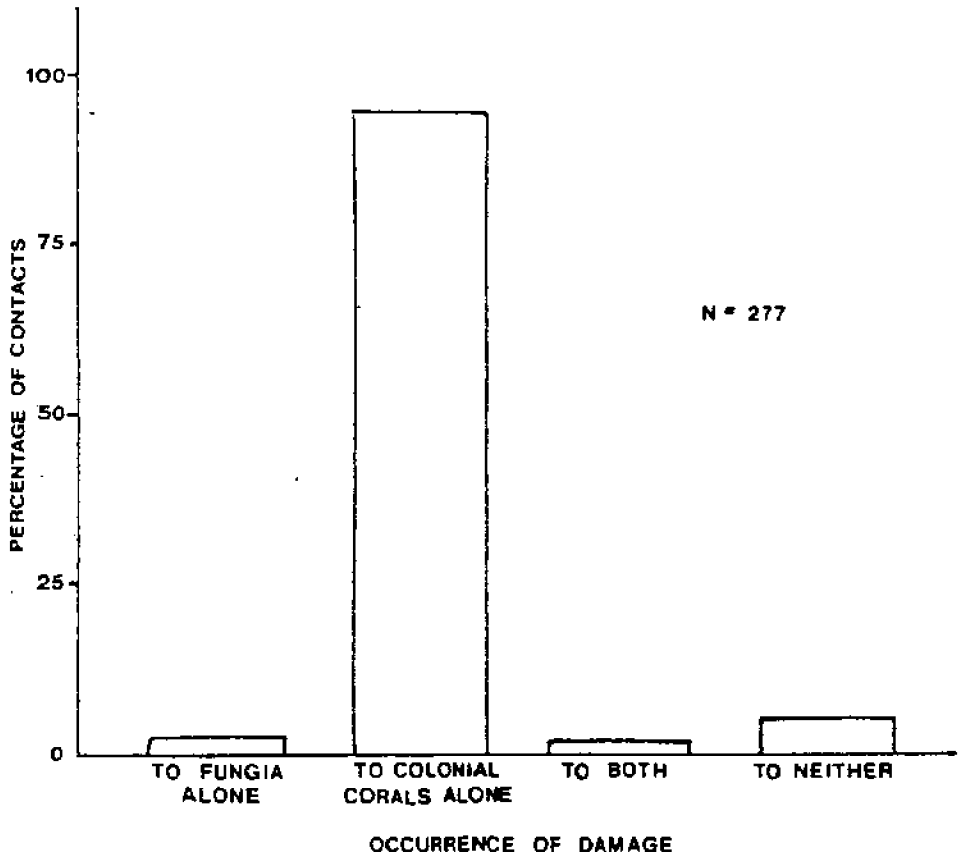

Fig. 2. Occurrence of tissue damage in natural contacts between Fungia scutaria and colonial corals on patch reefs in Kaneohe Bay, Oahu, Hawaii.

Macroalgae showed no deleterious effects of contact with Fungia. They appeared instead to overgrow and smother any corals encountered. In all 52 cases observed, the tissues of Fungia were dead or decaying where overgrown by macroalgae.

Experimental Contacts

Occurrence of damage on colonial corals varied greatly with size and proximity of Fungia. Large and medium Fungia induced damage in adjacent corals in over 70% of experimental field contacts (Fig. 3). During the course of the experiment, smaller Fungia moved away from their colonies and subsequently caused significantly less damage than did larger individuals (chi square = 9.723, $p < 0.01$) (Fig. 3). Mortality to colonial corals decreased dramatically with distance from Fungia and ceased completely at greater than 15 millimeters in interskeletal distance (Fig. 4). No deleterious effects of colonial corals were observed on relocated Fungia.

Mechanism of Damage

In the laboratory Fungia expanded its soft tissues to a distance of 5 to 15 millimeters from the calcareous skeleton nocturnally. Portions of colonial corals situated within this radius were covered by the tissues of Fungia for ten to twelve hours nightly. Upon contraction of Fungia in the morning, a layer of mucus was observed on adjacent corals. During the first day following contact, polyps under this layer were still intact. Within two days, microorganisms had invaded the mucus, and coral tissue underneath began to decay. By four days, the mucus had sloughed off and exposed bare skeleton. After two to three weeks a layer of encrusting algae had colonized this area and remained on the coral for the duration of contact with Fungia. Corals were capable of complete regeneration of tissues within three weeks after separation from Fungia.

The copious mucus secreted by Fungia contained microbasic p-mastigophores and holotrichous isorhizas. Spirocysts were also present but rare. Mucus collected from Fungia which had been disturbed by exposing them to air contained at least eight times the number of nematocysts as that from undisturbed individuals. In either case nematocysts were only a minor component of the mucus by volume.

Discussion

Solitary corals appear to unilaterally damage scleractinian coral colonies in almost all interactions thus far examined. Lang (1971) discovered that two solitary species of Scolymia extrude mesenterial filaments to digest most other scleractinian corals in a hierarchy on Jamaican reefs. Fungia species in the Indian Ocean cause damage to all six colonial corals they were observed to contact (Sheppard, 1979). Hildemann et al. (1975, 1977) found that Fungia fungites at Enewetak Atoll and F. scutaria in Hawaii induce tissue necrosis in collectively fifteen species of colonial corals in the laboratory. Evidence presented here suggests that Fungia is also consistently dominant over other corals in the field. Heavy algal encrustation on contacted corals and the apparent diversion of colony growth around Fungia also indicate that natural contacts may persist over long periods of time. When Fungia is overgrown, it is by organisms which might be expected to resist the nematocysts or toxins produced by coelenterates. The macroalgae observed to smother Fungia in this study were covered with hard outer layers of either calcium carbonate or cellulose. Algae are also known to resist damage by corals in other systems (Potts, 1977).

This shows for the first time that a substantial proportion, over forty percent of individuals in a population of Fungia, occur in contact with competing species of sessile organisms. Many of the remainder are in the midst of monospecific aggregations which may further protect them from encroachment. Several free-living corals are known to occur in aggregations (Abe, 1939; Wells, 1966; Hubbard, 1972), and do not appear to suffer deleterious effects from intraspecific contact, even when piled several layers deep (Goreau and Yonge, 1968; personal observation). However, in some corals the effects of intraspecific competition are quite subtle and would not have been detected here (Rinkevich and Loya, 1983). An even greater proportion of Fungia population may experience interspecific contact than reported here. Wave action (Jokiel and Cowdin, 1976) and the activities of mobile invertebrates (Goreau and Yonge, 1968) may frequently push unattached individuals against nearby coral colonies.

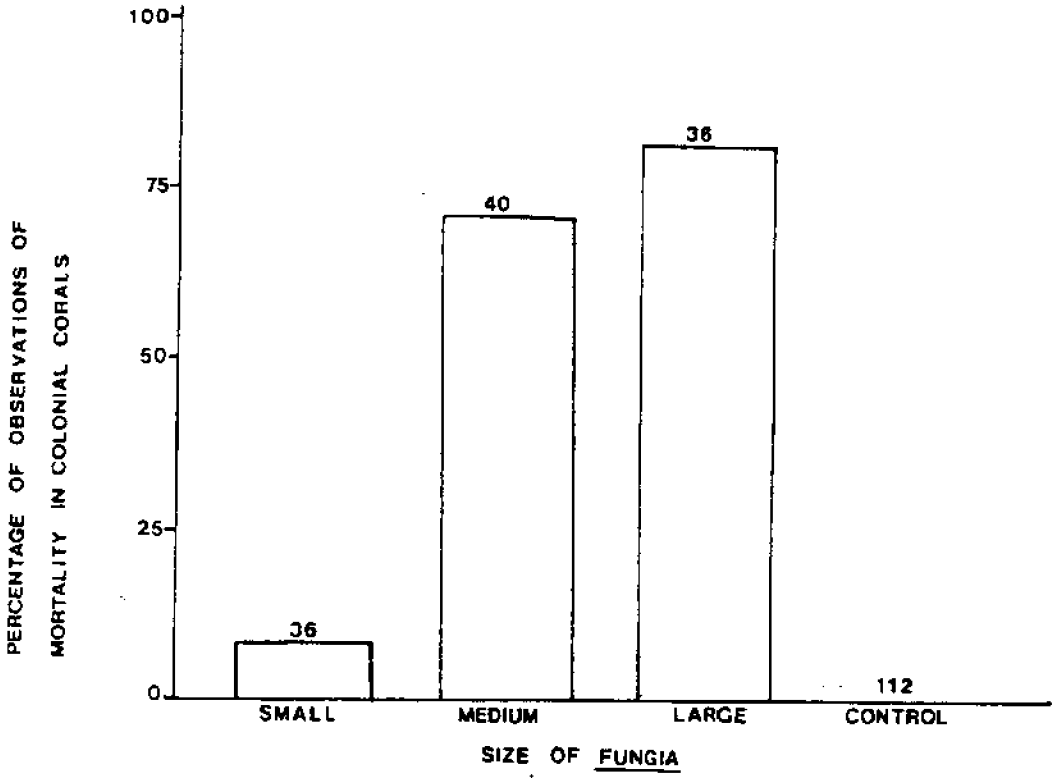

Fig. 3. Effect of size of Fungia scutaria in experimental field contacts with colonial corals in Kaneohe Bay, Oahu, Hawaii. Bars represent cumulative percentage of observations of corals in which local mortality was induced by a relocated Fungia. Pooled over the four sampling periods. Sample sizes are shown in parentheses.

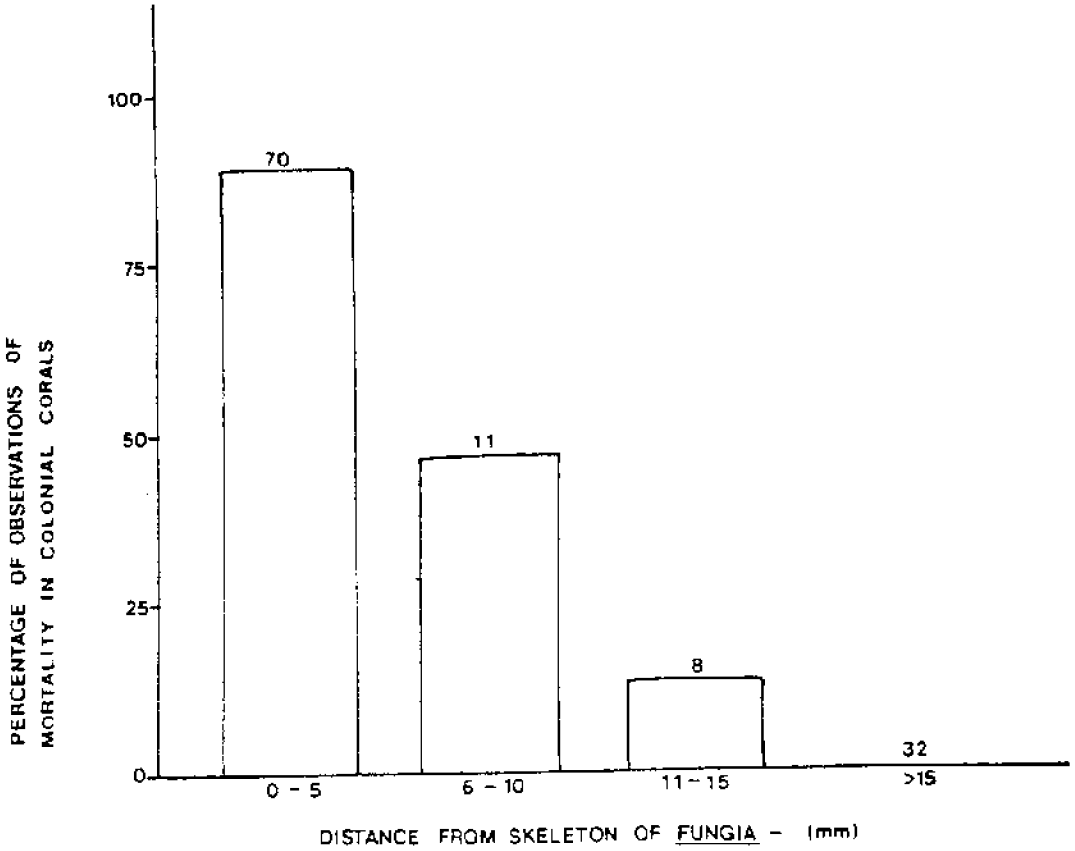

Fig. 4. Effect of proximity of Fungia scutaria in experimental field contacts with colonial corals in Kaneohe Bay, Oahu, Hawaii. Bars represent cumulative percentage of observations in which local mortality was induced by a relocated Fungia. Pooled over the four sampling periods. Sample sizes are shown in parentheses.

Fungia is able to move away from interspecific contact, although smaller individuals do so most frequently (personal observation). Some solitary corals exhibit great locomotory powers and can right themselves or resist burial (Hubbard, 1972). However, in comparison with more "acrobatic" species, Fungia is regarded as a "lazy" coral and is probably moved primarily by water motion (Jokiel and Cowdin, 1976). The higher movement rates of the smaller corals in this study may result in part from their increased susceptibility to dislodgement by wave action.

The relatively large polyp size of solitary corals may be another competitive adaption. Solitary species consistenly have larger polyps than do colonial corals, some reaching twenty-two centimeters in diameter (Abe, 1940; Well, 1966; Lang, 1971; Sheppard, 1981). This large individual size may in part compensate for their inability to produce the indeterminate branches of replicated units which occur in colonial species. Solitary corals are also more resistant to abrasion or burial by sediment than are many colonial corals (Hubbard and Pocock, 1972; Jokiel and Cowdin, 1976). They may thus be better able to survive physical disturbances such as hurricanes (Connell, 1978) or episodes of sedimentation (Hubbard and Pocock, 1972) which periodically decimate populations of colonial corals. Taken together, these characteristics of solitary corals may allow their persistence in a habitat dominated by colonial species.

The mechanism of interspecific damage employed by Fungia scutaria is unique among scleractinian corals thus far studied. Hildemann et al. (1977) suggested that the mucus of Fungia is responsible for damage to other corals. Another possibility is that Fungia releases toxic chemicals into the seawater, although this seems unlikely in that obvious damage is limited to corals within reach of nocturnally expanded tissues (Fig. 4). Alcyonarian soft corals which do exude toxins can damage corals up to ten centimeters distant (Sammarco et al, 1983). Evidence presented here suggests that nematocysts or toxins in the mucus or on the polyp surface of Fungia cause necrosis in adjacent corals. Nematocysts are secreted naturally into the copious mucus produced by this species (Coles and Strathmann, 1973, personal observation), and are known to be particularly toxic to starfish predators (Glynn and Krupp, in press). Spirocysts are common in the tentacular cnidom of Fungia, but are almost entirely lacking in mucus secretions (personal observation). This suggests that Fungia selectively releases certain types of nematocysts over others. The increased number of nematocysts secreted when individuals are disturbed by exposure to air also indicates an ability to control the volume of nematocysts in the mucus. Fungia scutaria is the only coral with nematocysts in its mucus, of at least six species examined by Coles and Strathmann (1973). This species-specific presence of nematocysts further suggests that they serve some specific function. Coral mucus is known to play a role in sediment rejection (Hubbard and Pocock, 1972), food capture (Lewis and Price, 1976), and supply of organic nutrients to fish and crabs (Johannes, 1967; Knudsen, 1967). In corals such as Fungia which secrete large quantities, mucus may also be specialized for use in competitive interactions.

Summary

(1) Over forty percent of a population of the free-living solitary coral, Fungia scutaria, occur in contact with colonial corals or macroalgae in Hawaii.

(2) Fungia causes unilateral tissue necrosis on all other species of coral in natural contacts.

(3) Macroalgae overgrow and smother Fungia.

(4) In experimental field contacts, large Fungia induce damage on other corals. Smaller individuals move away from coral colonies and cause significantly less damage.

(5) Fungia induces local mortality only on corals closer than fifteen millimeters in interskeletal distance.

(6) The mechanism of interspecific damage involves nocturnal expansion of Fungia and secretion of a nematocyst-laden layer of mucus onto adjacent corals. Necrosis occurs within three days and remains for the duration of contact.

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Cleaning behavior comparison of two shrimp species (Stenopus hispidus and Lysmata grabhami)

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Abstract

This comparative behavioral study was initiated to determine the variance in specialization of fish cleaning behavior between Stenopus hispidus, the Banded Shrimp, and Lysmata grabhami, the Red-backed Cleaner Shrimp, two of seven shrimp recognized as cleaners. Shrimp were tested with three host species: Chaetodon auriga, the Yellow Butterfly Fish; Chaetodon miliaris, the Millet Seed Butterfly Fish; and Zebrasoma flavescens, the Yellow Surgeon Fish. Fifty-four hours were spent in observation, equally divided between the two shrimp species. Lysmata grabhami needed less prompting (posing of host), spent more time cleaning, and did a more thorough job than did Stenopus hispidus. Neither species of shrimp "displayed" to attract fish for cleaning as some other shrimp species recognized as cleaners are reported to do. The shrimp spent only a tiny fraction of their time cleaning. The fish cleaning behavior by shrimp is a small but important part of the cleaner shrimps' time budget, and the two shrimp species studied differed markedly in method and amount of fish cleaning behavior. Host posing influenced initiation of cleaning in these shrimp, but why the shrimp bother to clean at all is still a mystery because they are not dependent on cleaning for food.

Introduction

Biotic interactions among species are a major determining force in reef community structure, notwithstanding the stochastic physical processes mentioned by Baines et al., (1974) and Dollar (1982). One of the most unique relationships on coral reefs is the cleaning behavior between cleaner shrimp or cleaner fishes and a large number of fish species (Levinton, 1982). "Cleaning symbiosis is defined as the removal and subsequent ingestion of ectoparasites, diseased and injured tissue, and unwanted food particles by the cleaning organism" (Feder, 1966). Cleaning of fish by shrimp has been noted by several authors (Limbaugh, 1961; Limbaugh et al., 1961; Feder, 1966; Higa, 1967; Johnson, 1971; Mahnken, 1972; Sargent and Wagenbach, 1975; Losey, 1978) and some preliminary studies on the actual cleaning behavior have been done (Limbaugh et al., 1961; Stolen, 1964; Sargent and Wagenbach, 1975).

While much has been written on the symbiotic cleaning of fish by fish, very little has been written on the cleaning of fish by shrimp. There are at least 45 species of fish that are recognized as cleaners, but so far only seven species of shrimp have been recognized as cleaners, including three genera which are placed in three families and superfamilies, and in two distinct sections of the decapod suborder Natantia (Limbaugh et al., 1961). The literature shows 26 Periclimenes spp., three of which are known to be cleaners, four Stenopus spp., two of which are known to be cleaners, and 22 Lysmata spp., two of which are recognized as cleaners (Deman, 1928; Holthuis, 1947, 1949, 1951; Limbaugh et al., 1961, and Sargent and Wagenbach, 1975) (Table 1). Of these seven cleaners, only two, Stenopus hispidus and Lysmata grabhami, are found in Hawaiian waters (Higa, 1967).

Although cleaning behavior is a unifying characteristic of these shrimp, they differ considerably in behavior, morphology, and habitat utilization, even within a genus (Limbaugh et al., 1961). These differences make it necessary to consider each species separately in order to accurately assess their cleaning behavior. Questions have been raised with respect to the ecological importance of cleaning (Limbaugh, 1961; Hobson, 1969; Losey, 1972) and the origin of cleaning behavior (Losey, 1974; Fricke, 1975). The origin of cleaning behavior by shrimp is puzzling because they are extremely vulnerable to predation while they are cleaning, making the "development" of cleaning behavior apparently improbable from an evolutionary standpoint. This origin question has not been adequately

Table 1. Species of shrimp in the genera Periclimenes, Lysmata, and Stenopodidae. Those species known to be cleaners are designated with an asterisk.

Phylum: Arthropoda
Class: Crustacea
Order: Decapoda
Suborder: Natantia

Family: Palaemonidae

1. Periclimenes americanus (Kingsley) 1878
2. *P. anthophilus Holthuis 1964
3. P. bowmani Chace 1972
4. P. brevicarpalis (Schenkel)
5. P. crinoidalis Chace 1972
6. P. finlayi Chace 1972
7. P. harringtoni Lebour 1949
8. P. impar Kemp 1922
9. P. infasrinis (Rathbun)
10. P. insignis Costa 1844
11. P. iridescens Lebour 1949
12. P. longicaudatus (Stimpson) 1860
13. P. lucasi Chace
14. P. magnus Holthuis 1951
15. P. meyeri Chace 1969
16. P. paivai Chace 1969
17. P. pandionis Holthuis 1951
18. P. pauper Holthuis 1951
19. *P. pedersoni Chace 1958
20. P. perryae Chace 1942
21. P. petitthouarsii
22. P. petitthouarsii var. spinifera DeMan 1902
23. P. rathbunae Schmitt 1924
24. P. tenellus (Smith) 1882
25. P. veleronis
26. *P. yucatanicus (Ives) 1891

Family: Hippolytidae

1. Lysmata amboinensis
2. L. anchisteus Chace 1972
3. *L. californica Stimpson 1866
4. L. dentata Kemp 1914
5. L. durbanensis Stebbing
6. L. ensirostris Kemp 1914
7. L. ensirostris var. punctata Kemp
8. *L. grabhami Gordon 1935
9. L. hastatoides (Balss)
10. L. intermedia (Kingsley) 1878
11. L. kukenthali DeMan
12. L. moorei (Rathbun) 1901
13. L. multiscissa Nobili
14. L. porteri Rathbun
15. L. prima (Borradaile) 1915
16. L. rathbunae Chace 1970
17. L. rhizophorae
18. L. trisetacea (Heller)
19. L. tuggelae (Stebbing)
20. L. unicornis Holthuis 1952
21. L. vittata Stimpson 1860
22. L. wurdemanni (Gibbes) 1850

Family: Stenopodidae

1. *Stenopodidae hispidus (Oliver) 1811
2. *S. scutellatus Rankin 1898
3. S. spinosus Risso 1826
4. S. tenuirostris DeMan

* Known to be cleaners

(Chace, 1972: Colin, 1978; DeMan, 1928: Feder, 1966; Holthuis, 1946; 1947; 1949; 1950; 1951; 1964; Limbaugh, 1961; Mahnken, 1972; Sargent and Wagenbach, 1975)

addressed, and the central purpose of this study is to begin developing a phylogenetic hierarchy for the array of cleaning behaviors observed in shrimp. Through laboratory observation and computerized event recording, this study describes, quantifies, and compares the fish cleaning behavior of the Banded Shrimp, Stenopus hispidus and the Red-backed Cleaner Shrimp, Lysmata grabhami.

Material

Shrimp

Stenopus hispidus is the largest of the known cleaner shrimps, reaching 7.5 cm in length (Limbaugh et al., 1961). The conspicuous white antennae are longer than its white spiny body, that is banded with red. At the base of the leg where it attaches to the body, a blue color can be seen, and the third chelated pereipods are greatly enlarged. It pairs when juvenile, apparently for life (Johnson, 1967), inhabiting quiet, shallow water (2-4 m) in rocky or coralline areas. They can often be found in association with the morey eel, Gymnothorax spp. and are considered to be more active at night (Limbaugh, 1961; Feder, 1966; Johnson, 1967, 1977).

Lysmata grabhami is characterized by a longitudinal red stripe on which a narrower brilliant white stripe is centered, and a pair of white third maxillipeds. The remainder of the body is a dull ochre color. Unlike S. hispidus its third chelated pereipods are not enlarged. The antennae are longer than the body, the body usually being 5 cm or less in length (Limbaugh et al., 1961). Its habitat is similar to that of S. hispidus. There are several reports of shallow water (2-4 m) sightings (Limbaugh et al., 1961; Riga, 1967; Jokiel, personal communication) but Randall (1958) records sighting L. grabhami at 21 m in the Society Islands and Frank Stanton (personal communication) remarked that L. grabhami inhabits deep water (>15 m) in Hawaii.

Fish

Three species of fish were used in this study, Chaetodon auriga, C. miliaris and Zebrasoma flavescens. C. auriga, the Yellow Butterfly Fish, is the largest species of its family, reaching 15 cm in length. The individuals used in this study were 13 cm in length. It is most easily identified by a filament of the soft dorsal fin and the black spot below it (Tinker, 1978). C. miliaris, the Millet Seed Butterfly Fish, is smaller, reaching up to 13 cm in length. The individuals used in this study were 9 cm long. C. miliaris is a rather small, flat species with a bright yellow body marked by many small round dark spots arranged in vertical rows (Tinker, 1978), and also has a black eye stripe. Zebrasoma flavescens, the Yellow Surgeon Fish, may reach 20 cm in length, but those used in this study were only 10 cm in length. Z. flavescens is a radiant yellow with a slightly bleached longitudinal line just above the caudal peduncle.

Observation Equipment

Three, 500-liter saltwater tanks were set up indoors at the Hawaii Institute of Marine Biology with unfiltered seawater at a flow rate of 12 liters per minute, and airstones. Large tanks (relative to the size of the fish and shrimp) were used so no forced shrimp-fish interactions would occur. One "refuge" was made for each tank consisting of nine (arranged three by three) 10 cm lengths of 5 cm PVC pipe. Large black plastic blinds were set up one meter from the front of the tanks. Animals were fed every other day with a small piece of fish. A low intensity fluorescent desk lamp was used for the artificial light observations and was covered with a sheet of red acetate to develop the low light viewing conditions listed as Red Light observations in the results. Plankton samples were collected using a light at night in conjunction with a pump to deliver collected plankton to a bucket. An integrating Quantum Radiometer/Photometer, model LI-188B, was used to record the daily light change in the lab, and outside the lab to compare the difference in the light levels. A computerized 16 channel event recorder was used for the behavioral observations. The Hawaii Institute of Marine Biology Behavior Events Acquisition/Analysis System was used to analyze the recorded data.

Methods

Collection

The first three individuals of Stenopus hispidus were purchased at a pet store. All other individuals were collected in Kaneohe Bay, Oahu. Most of the individuals were collected on the concrete channel markers in the bay and around Coconut Island. Adults and juveniles were identified with the criterion for the age distinction being <3 cm considered a juvenile and >6 cm an adult. No intermediate sizes were collected. Limbaugh et al., (1961) sets the upper limit of the adult size around 7.5 cm, so the larger individuals used in this study can certainly be considered adults.

Lysmata grabhami were purchased from a pet store, and since all were about 4 cm in length, they were considered adults by the Limbaugh et al. (1961) criterion which lists the upper size of adults as being around 5 cm. The host fish were captured in Kaneohe Bay and held in large fish-pens on a floating dock prior to use in this study.

Observations

The shrimp and fish were allowed 24 h in the tanks before any observations were taken so their movements would not be an artifact of a new environment. Two individuals of each fish species were placed in the observation tanks together because single fish showed atypical behavior patterns. Nine individuals of each species of shrimp were observed for six, one-half hour sessions lasting from 0600 through 2130. An observation was defined as one, 30-min recording session. STE001, (S. hispidus number one) and STE002 were observed alone during the event recording sessions, STE003 was placed with STE002 and they formed a pair. STE004 and STE005 were caught as a pair and observations were made on them as such. STE006 was a single juvenile, STE007 was a female with eggs and STE008 and STE009 were paired juveniles, observed as such. LYS001 (L. grabhami number one), LYS002, and LYS003 were observed together. LYS003, LYS004, LYS005, and LYS006 were observed together, and LYS007, LYS008, LYS009, and LYS010 were observed together. The two shrimp species were not observed together because S. hispidus was aggressive toward L. grabhami, and distorted the observation session. Observations were also made under low light conditions (red light) and artificial light conditions. Prior to the observations, approximately six hours were spent in observing the shrimp's behavior and assigning behavioral acts to the 16 channels of the event recorder. To minimize observer bias, none of the collected data were considered for possible patterns or analysed until all the observations were completed. Fifteen keys were assigned to events and one key was assigned as an error flag so that mistakes in keying could be corrected. A total of 27 hours for each shrimp species was spent in observation, divided evenly among three fish hosts.

Action pattern definitions

The following action patterns were assigned to the 16 event recorder keys:

1. Orient to Host: Antennae and/or body moved so they are pointed in the hosts' direction.

2. Antenna Tap on Host: One or more antennae tapped on host.

3. Approach Host: Walk toward host when within one host length, and/or raise body off bottom of substratum toward a stationary host.

4. Board Host: Leave substratum and cling to host.

5. Clean Host Ventral: Pick at the hosts' ventral surface and fins (using the eye-tail line as the boundary definition) with chelae, ingesting collected material.

6. Clean Host Dorsal: Pick at the hosts' dorsal surface and fins (using the eye-tail line as the boundary definition) with chelae, ingesting collected material.

7. Clean Antennae: Draw antenna through pereipods and maxillipeds.

8. Shrimp-Shrimp Agonistic Interaction: Chase and/or flee.

9. Host Approach: Slow (about 2 cm sec^{-1}) swimming toward shrimp, within a host length or less and/or orienting toward shrimp.

10. Post Pose: Head down or up at 30 degree angle from horizontal, and/or 25% roll from vertical with rapid dorsal (and sometimes caudal) fin flutter.

11. Host Swim: Host swimming (>2 cm second^{-1}) around tank, without reference to the shrimp, and not orienting to or approaching shrimp.

12. Host Swim Away: Movement to be free of the cleaning shrimp and subsequent movement to another part of the tank.

13. Shrimp Movement: Walking, or swimming without reference to the host.

14. Shrimp-Shrimp Nonagonistic Interaction. Mutual antennae tap and/or sharing the same refuge tube or sitting in an open part of the tank together.

15. Chelae Spread: Spread third pereipods and opening the chelae.

Results

Sample Size

According to Fagen and Young (1978), if the repertoire is very small (20 types of acts or less), a reasonably complete catalogue can be obtained. Where R = repertoire size, a sample of 10R squared is sufficiently large to provide the necessary data for analysis, while 5R squared is borderline. In the case of this study, R = 11 for the shrimp, so 10R squared = 1,210. The total number of bouts for the 11 behaviors of S. hispidus was 6,884 and for L. grabhami 12,529, indicating the sample size of this study was certainly adequate for the repertoire size. A point not incorporated in this simple formula is the duration of the behavior, but this consideration would only increase the already adequate credibility of the sample size.

Observations

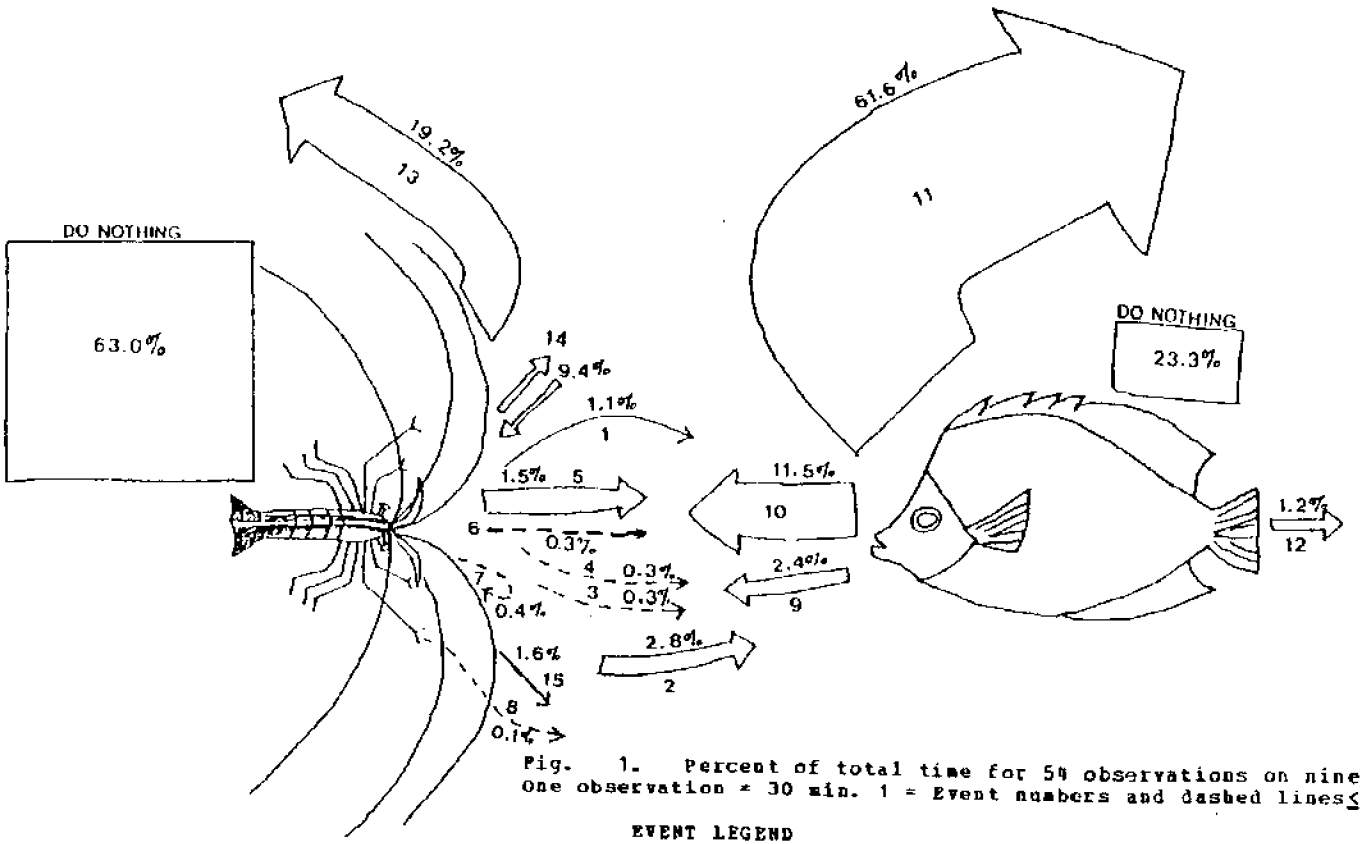
The shrimp and host fish seemed to ignore each other for large portions of time (events 11 and 13 in Tables 2 and 3). Figs. 1 and 2 give an "ethogram" representation of the time budgets for the shrimp and host fish. Note event 10 in relation to events 5 and 6. Table 4 gives a more detailed description of this behavioral interaction. Lysmata grabhami needs less prompting (posing by host), spends more time cleaning, and does a more thorough job than does Stenopus hispidus. Comparing Tables 5 and 6 one finds more information on this cleaning behavior discrepancy. Host pose and shrimp clean ventral (surface of the fish) differ greatly between the two shrimp species. It seems the host must pose more diligently to be cleaned by S. hispidus.

In addition to the data displayed in the figures and tables, the following may assist in the interpretation of the results. LYS001 died after the first 30 minute observation, so 10 individuals were needed to keep the number equal to S. hispidus. The data on LYS001 were not used and the data on LYS002 through LYS010 were treated as though it were LYS001 through LYS009 to better mesh with the S. hispidus data on the ANOVA statistical analysis.

Soliciting behavior

The day before LYS001 died it was shifting laterally without moving its feet for hours at a time. This has been considered a display (Limbaugh et al., 1961; Feder, 1966) but the following day this individual was found dead in the same area of the tank. LYS002 started this same behavior after the sixth observation was completed. After rocking incessantly hour after hour, it was found dead in the same area of the tank the following day. These observations and the fact that this author never saw a "display" to attract a fish by either of the two species studied causes one to question the interpretation of this behavior as soliciting behavior, at least in S. hispidus and L. grabhami. In the case of these shrimp, it seems the host initiates the cleaning behavior by posing. In Table 3, "Approach Host", event (3) shows no value for either shrimp species and Figs. 1 and 2 show <0.5% of the total time budget for this behavior.

In cases where the shrimp did not clean when the host posed for a minute or more, the other host individual would make "cleaning" passes at the poser. Losey (1971, 1972, 1974) stated that tropical cleaner fish such as Labroides spp. pursue a number of their hosts, and much cleaning is performed without so-



Pig. 1. Percent of total time for 54 observations on nine Stenopus hispidus. One observation = 30 min. 1 = Event numbers and dashed lines≤1%).

EVENT LEGEND

(1) Orient to Host
(2) Antenna Tap On Host
(3) Approach Host
(4) Board Host
(5) Clean Host Ventral
(6) Clean Host Dorsal
(7) Clean Antennae
(8) Shrimp-Shrimp Agonistic Interaction
(9) Host Approach
(10) Host Pose
(11) Host Swim Without Reference to Shrimp
(12) Host Swim Away
(13) Shrimp Movement Without Reference to Fish
(14) Shrimp-Shrimp Nonagonistic Interaction
(15) Chelae Spread

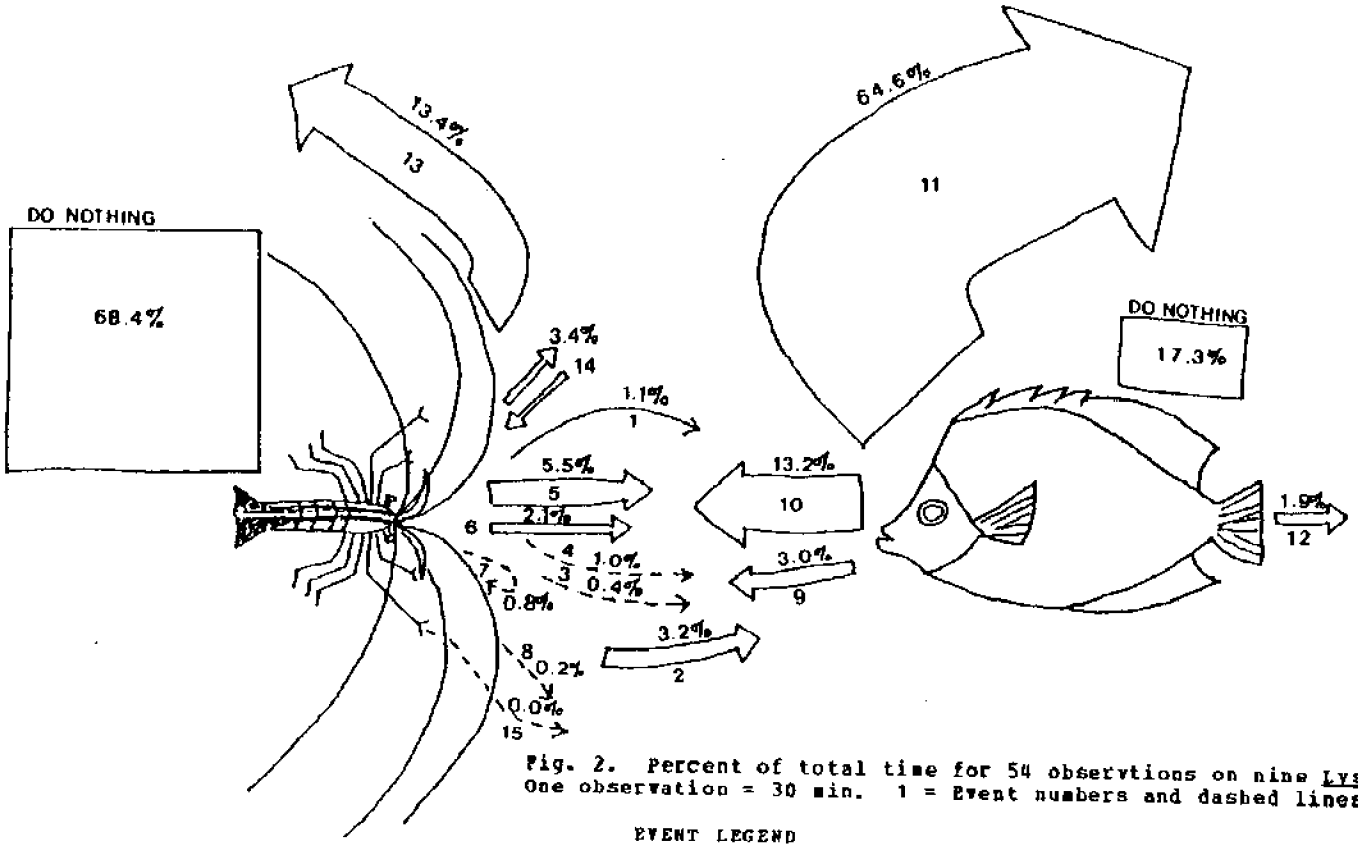


Fig. 2. Percent of total time for 54 observtions on nine Lysmata grabhami. One observation = 30 min. 1 = Event numbers and dashed lines ≤1%.

EVENT LEGEND

(1) Orient to Host
(2) Antenna Tap on Host
(3) Approach Host
(4) Board Host
(5) Clean Host Ventral
(6) Clean Host Dorsal
(7) Clean Antenna
(8) Shrimp-Shrimp Agonistic Interaction
(9) Host Approach
(10) Host Pose
(11) Host Swim Without Reference to Shrimp
(12) Host Swim Away
(13) Shrimp Movement Without Reference to Fish
(14) Shrimp-Shrimp Nonagonistic Interaction
(15) Chelae Spread

Table 2. Time budget data for shrimps Stenopus hispidus and Lysmata grabhami.

Sum of 6 observations per individual shrimp.

One observation = 30 minutes. Totals shown in seconds.

	EVENTS														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
STE001	81	369	119	0	183	4	36	0	315	949	5313	124	2409	0	165
STE002	84	648	6	5	83	5	10	0	317	2876	2909	114	1320	0	344
STE003	37	282	39	135	471	186	111	120	138	2576	5783	81	4827	2906	145
STE004	85	558	0	54	143	19	72	0	340	995	7311	178	5313	1123	237
STE005	78	642	0	15	166	13	23	9	178	1488	6971	126	546	1408	118
STE006	44	40	0	7	82	27	27	8	88	791	6698	69	412	2296	49
STE007	100	53	0	0	0	0	11	0	173	78	9194	61	73	0	21
STE008	306	105	99	37	235	38	68	0	422	975	7660	215	1988	745	190
STE009	216	57	26	9	62	0	63	8	326	406	8067	156	1730	693	243
LYS002	188	420	54	74	201	49	95	0	460	513	4328	232	1046	160	0
LYS003	135	374	1	25	341	63	100	0	292	882	7156	115	582	22	0
LYS004	90	147	26	56	209	45	132	13	210	380	8173	111	3187	499	0
LYS005	26	133	4	116	1127	509	74	0	86	2336	6869	96	1413	131	0
LYS006	111	432	5	166	862	150	157	0	306	2215	6322	271	551	1463	0
LYS007	128	592	4	142	756	302	115	0	390	2408	5887	244	610	741	0
LYS008	161	315	109	134	412	146	40	126	433	955	7904	278	3339	269	0
LYS009	79	279	37	97	456	214	22	49	248	1063	9275	202	1738	3	0
LYS010	144	440	136	163	1023	505	44	31	502	2097	6893	257	1048	23	0

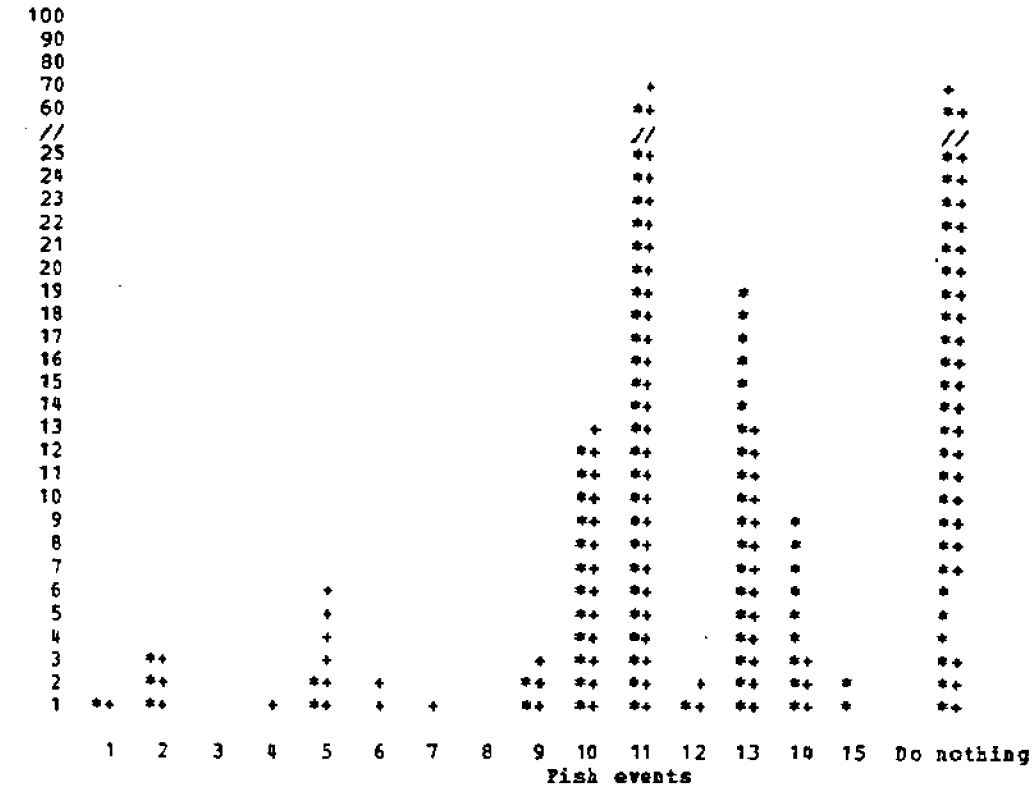
EVENT LEGEND

(1) Orient to host
(2) Antenna tap on host
(3) Approach host
(4) Board host
(5) Clean host ventral
(6) Clean host dorsal
(7) Clean antenna
(8) Shrimp-shrimp agonistic interaction
(9) Host approach
(10) Host pose
(11) Host swim without reference to shrimp
(12) Host swim away
(13) Shrimp movement without reference to fish
(14) Shrimp-shrimp non-agonistic interaction
(15) Chelae spread

HOSTS

Chaetodon miliaris	Chaetodon auriga	Zebrasoma flavescens
STE001, STE002, STE003	STE004, STE005, STE006	STE007, STE008, STE009
LYS002, LYS003, LYS004	LYS005, LYS006, LYS007	LYS008, LYS009, LYS010

Table 3. Comparison of time budgets of Stenopus hispidus = * and Lysmata grabhami = +.



Event Legend - Ordinate values are percent of total observed time.

(1) Orient to host
(2) Antenna tap on host
(3) Approach host
(4) Board host
(5) Clean host ventral
(6) Clean host dorsal
(7) Clean antenna
(8) Shrimp-shrimp agonistic interaction
(9) Host approach
(10) Host pose
(11) Host swim without reference to shrimp
(12) Host swim away
(13) Shrimp movement without reference to fish
(14) Shrimp-shrimp non-agonistic interaction
(15) Chelae spread

Table 4. Host post to shrimp clean ratios. Host post to shrimp clean ratio = P/C. Clean in P/C ratio includes dorsal and ventral cleaning. Clean ventral to dorsal ratio = V/D. N = number of observations. 54 observations per shrimp species (9 individuals observed 6 times each). One observation = 30 minutes.

Individuals n=6	P/C	V/D	Individuals n=6	P/C	V/D
STE001	5.1	45.8	LYS002	2.1	4.1
STE002	32.7	16.6	LYS003	2.5	4.7
STE003	3.9	2.5	LYS004	1.5	4.6
STE004	8.4	5.0	LYS005	1.4	1.9
STE005	8.3	12.8	LYS006	2.2	5.7
STE006	7.3	3.0	LYS007	2.3	2.5
STE007	0.0	0.0	LYS008	1.7	2.8
STE008	3.2	6.2	LYS009	1.6	2.1
STE009	6.5	0.0	LYS010	1.4	2.0
TOTAL-All hosts n=54					
Stenopus hispidus	6.5	4.9	Lysmata grabhami	1.7	2.6
HOSTS n=18, n=6 for each individual					
Chaetodon miliaris	6.9	3.8	C. miliaris	2.0	4.8
C. auriga	7.2	6.5	C. auriga	1.8	2.6
Zebrasoma flavescens	4.4	7.8	Z. flavescens	1.5	2.2

Table 5. ANOVA table for Event 5 - Clean ventral.
108 observations: 6/individual shrimp, 18/host, 54/shrimp species.
One observation = 30 minutes.

Source of variation	df	SS	MS	Fs
Among three hosts	2	39.958	19,979	3.736ns
Between two shrimp species	3	223,897	74,632	12.427***
Among nine individuals	12	72,070	6,006	1.024ns
Among six observations	90	528,089	5,868	
TOTAL	107	864,014		

$F_{.05<3,2>} = 19.2$

$F_{.05<3,12>} = 3.49$

$F_{.01<3,12>} = 5.95$

$F_{.001<3,12>} = 10.8$

$F_{0.5<12,90>} = 1.88$

Expressed as a percentage:

13.5 (hosts)
34.0 (species within hosts)
0.2 (individuals within species)
52.3 (observatons within individuals)

(Rohlf and Sokal, 1981 for F statistic)

Table 6. ANOVA table for Event 10 - host pose
108 observations: 6/individual shrimp, 18/host, 54/shrimp species.
One observtion = 30 minutes.

Source of variation	df	SS	MS	Fs
Among three hosts	2	303,400	151,700	2.567ns
Between two shrimp species	3	1,168,148	389,383	7.435**
Among nine individuals	12	626,430	52,369	1.500ns
Among six observations	90	3,141,699	34,908	
TOTAL	107	5,241,677		

$F_{.05\langle 3,2\rangle} = 19.2$ $F_{.05\langle 3,12\rangle} = 3.49$ $F_{0.5\langle 12,90\rangle} = 1.88$

$F_{.01\langle 3,12\rangle} = 5.95$

$F_{.001\langle 3,12\rangle} = 10.8$

Expressed as a percentage:
10 (hosts)
30 (species within hosts)
5 (individuals within species)
55 (observations within individuals)

(Rohlf and Sokal, 1981 for F.statistic)

licitation. I never found this to be the case with the two species of tropical cleaner shrimp.

Predation

There were several molts by each species (4 S. hispidus and 3 L. grabhami.) and the fish were never observed to attack or harrass the molters, although the pre- and post-molt shrimp were not as interested in "cleaning" the fish as the non-molters. In one instance, two Chaetodon auriga were kept with a L. grabhami overnight in a 20 liter bucket, and during the course of the night, the shrimp molted but was unharmed. The antennae of some of the other L. grabhami were clipped short but it is not known whether the other shrimp or the hosts were responsible for this.

More than one shrimp was occasionally seen cleaning a host and on one occasion, S. hispidus climbed over a posing fish to clean a fish. Often when the host was being "cleaned" the colors and patterns would change on the host, becoming darker, more intense and sometimes new colors and patterns were displayed.

The ectoparasites placed in the tanks seemed to have more effect on the shrimp than on the fish. Shrimp were seen darting backwards waving their chelae at the tiny specks (copepods) in the tank immediately after introduction of the parasites. The fish appeared to be unchanged in their posing behavior.

The data from Table 7 were collected to determine if water temperature or light levels had a noticeable effect on the behavior of the shrimp or the fish. The water temperature was extremely constant in the tanks and varied little from the bay temperature, therefore it was excluded as a possible factor affecting the behavior relative to what was observed in the field. Observations were made in red light (which was virtual darkness according to the meter) and in artificial light, to determine a difference in reaction to ambient light levels but no correlation was found.

Discussion

Stenopus hispidus and Lysmata grabhami exhibited clearcut differences in the quality and quantity of their cleaning behavior, however, these shrimp displayed much inactivity relative to the fish. This was not due to diurnal-nocturnal differences between shrimp and host, for even in the low light conditions (red light) and in crepuscular observations, the relative behavior patterns showed little change over that observed during the day. Figs. 1 and 2 show little difference in the overall host's reaction to the two species in terms of posing (event 10), approaching (9), and swimming without reference to the shrimp (11). Likewise the sum of all observations for the shrimp showed little difference in inactivity, antennae tap (2), orienting to host (1), approaching host (3), and agonistic behavior (8). There were however, real differences among individual shrimp and a great deal of variance between each observation. This was probably due to a synergistic effect of shrimp and fish. This synergism may explain the significant F statistics in Tables 8 and 9. Table 3 (Events 9-12) shows a good deal of stationarity in the way the three host species related to the two shrimp species. One of the major differences seen in Table 2 is chelae spread (15). Lysmata grabhami never displayed this behavior during any of the observations.

The two Butterfly fish (Chaetodon spp.) posed longer than the Surgeon fish (Zebrasoma). This might be because Zebrasoma flavescens seemed less interested in being cleaned and the shrimp cleaned it more readily when it finally did pose. Z. flavescens is more aggressive than the Butterfly fish and S. hispidus was more timid about boarding Z. flavescens than was L. grabhami. Because of this, S. hispidus cleaned the ventral surface of Z. flavescens for most of the bouts from the substratum of the tank, probably adding to the low value for dorsal cleaning (Figs. 1 and 2).

Fish were quite persistent in their posing, but they posed less for shrimp individuals that cleaned less. STE007 (gravid female) did not clean at all, and the host only posed a total of 78 seconds (Table 2). Could the host have "learned" that the shrimp was not interested in cleaning? The lack of cleaning by STE009 in ventral/dorsal (V/D) ratios shows that no dorsal cleaning took place and only 62 seconds of ventral cleaning was observed (Table 2). The host posed a little less than half (Table 6) of the time it spent posing for STE008.

Table 7a. Water temperature during experiments.

n=3	Buoy #20 Kaneohe Bay (2m depth)	Observation Tanks	Coconut Island Lagoon (2m depth)
Mean	25.6°C	26.0°C	28.0°C
S.E.	0.173	0.000	0.000

Table 7b. Irradiance during experiment.
Readings in μEm-2 s-1.
Each reading was taken as a 10 second integration. n=3.
The sensor was taped 15 cm from the bottom of the tank on the outside facing up.

TIME Sunrise 0530	Mean	S.E.	V=%
0600	0.02	0.018	92.8
0800	0.44	0.327	80.9
1000	1.81	1.229	73.6
1200	6.66	1.539	25.0
1400	3.81	0.609	17.3
1600	0.61	0.063	11.3
1800	0.23	0.034	16.4
2000	0.00	-----	----
artificial light	1.49	0.006	0.436
red light	0.00	-----	---
daylight 1200 h	2,553.33	393.107	16.674

Sunset 1930 12,13,14 June 1983 Kaneohe, Oahu

Table 8. ANOVA table for Event 11 - host swim.
108 observations: 6/individual shrim, 18/host, 54/shrimp species.
One observation = 30 minutes.

Source of variation	df	SS	MS	Fs
Among three hosts	2	3,294,425	1,647,212	4.900ns
Between two shrimp species	3	1,008,564	336,188	1.374ns
Among nine individuals	12	2,936,488	244,707	2.786**
Among six observations	90	7,904,066	87,822	
TOTAL	107	15,143,543		

F = 9.55 .05<2,3>

F = 3.49 .05<3,12>

F = 1.88 .05<12,90>

F = 2.420 .01<12,90>

F = 3.165 .001<12,90>

Expressed as a percentage:
23 (hosts)
3 (species within hosts)
18 (individuals within species)
56 (observations within individuals)

(Rohlf and Sokal, 1981 for F statistic)

Table 9. ANOVA table for Event 13 - shrimp move.
108 observations: 6/individual shrimp, 18/host, 54/shrimp species.
One observation = 30 minutes.

Source of variation	df	SS	MS	Fs
Among three hosts	2	310,570	155,285	1.974ns
Between two shrimp species	3	919,732	306,577	1.417ns
Among nine individuals	12	5,213,592	434,466	13.3167***
Among six observations	90	4,782,985	32,628	
TOTAL	107	11,226,879		

$F_{.05<3,2>} = 19.2$ $F_{.05<12,3>} = 8.74$ $F_{.05<12,9>} = 2.42$

$F_{.01<12,90>} = 2.420$

$F_{.001<12,90>} = 3.165$

Expressed as a percentage:

4 (hosts)
6 (species within hosts)
61 (individuals within species)
29 (observations within individuals)

(Rohlf and Sokal, 1981 for F statistic)

There must be some cues the fish are keying on, that causes them to make a more persistent effort for greater probability of reward.

It may be that "cleaning behavior" has been ill defined because the fish seem to seek tactile stimulation from the shrimp, not relief from parasitic infestation. Losey (1971) and Sargent and Wagenbach (1975) hold similar opinions. During the course of this study, I noticed some of the hosts (mostly Chaetodon auriga) hovering in the bubble stream from the air stone, probably for the tactile sensation.

Not only does the idea of tactile sensation for hosts cause questions about "cleaning behavior" but so does the deviant aspect of the cleaning process. Cleaning behavior is certainly not altruistic and may in some cases be parasitic because not only do the shrimp remove parasites and diseased tissue, but also apparently healthy fin and scale tissue. The hosts were often seen to jump, twitch, or dart forcefully away from the shrimp, when the shrimp ripped at the healthy tissue.

Extrinsic factors for the shrimp studied included water temperature and light levels. A possible reason for the variance of the light levels over the three days could be cloud cover which was almost always heaviest in the mornings. The main reason for taking readings in the wet lab and in the field (daylight 1200 hours) was to show that indeed, the wet lab represented a very low light situation, possibly similar to the crespuscular periods in the reef community. The reading of 2,553 micro Einsteins per second is many orders of magnitude greater than any of the other readings taken in the wet lab.

The intrinsic factors (physiology, injury, relative previous experience affecting the relationship of the host to the shrimp, and the shrimp to the host) could not be monitored and were not previously known. These factors play a significant role in the behavioral interactions, and Losey (1979) found learning changed the host's reactions. Shrimp may also modify their behaviors as a result of experience. Notwithstanding intrinsic and pre-observation factors, the following conclusions precipitate from the data:

(1) Fish cleaning behavior is a small but important part of the cleaner shrimps time budget.

(2) The two shrimp species studied differ markedly in method and amount of fish cleaning behavior.

(3) Host posing influences initiation of cleaning in these shrimp, but why the shrimp bother to clean at all is still a mystery because they are not dependent on cleaning for food.

Acknowledgements

I would like to thank Dr. George S. Losey, Jr. for making his Behavioral Analysis System available, and for his advice and assistance during this study, Frank Stanton for his help, and comments, and Paul Jokiel, for his help and enthusiasm in the early period of this study.

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A blue pigmented bacterium symbiotic with Terpios granulosa, a coral reef sponge

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Abstract

Symbiosis between a blue-pigmented bacterial symbiont and its marine sponge host, Terpios granulosa Bergquist, was examined. Sensitivity to ultraviolet and full spectrum solar radiation of different intensities indicated a requirement for a cryptic habitat as occurs on Hawaiian coral reefs. Exposure to 50% ambient ultraviolet radiation resulted in mortality of bacterium and, ultimately, sponge cells. Separation and isolation of the bacterium was achieved using sponge and echinoderm blastula dissociation protocols. The gram negative, extracellular symbiotic bacterium possessed multicellular trichomes containing bi-refractile inclusions of blue pigment and unique terminal cells as revealed by light microscopy, SEM, and TEM. Thylakoid structures and chlorophyll were absent. Similarities with Cyanobacteria include hormogonia type of reproduction and septal centripetal annular ingrowth from the cytoplasmic membrane. The blue pigment was soluble in aqueous solutions but not in organic solvents. Symbiotic bacteria and sponge cells were resistant to high dosages of common antimicrobial agents.

Introduction

Symbioses found on coral reefs can enhance the growth capabilities of organisms in oligotrophic tropical waters. The best documented coral reef symbiosis is between scleractinian corals and dinoflagellate zooxanthellae. Muscatine and Porter (1977) discuss the adaptive significance of this mutualistic symbiosis that allow corals to efficiently exploit a habitat with low nutrient availability. Other symbioses between marine organisms and algae have been reported for the Protozoa, Porifera, Coelenterate, Mollusca and Platyhelminthes (see review by Taylor, 1973). Symbiotic relationships between Cyanobacteria (blue green algae) and tropical marine sponges are common and believed to be an important component in coral reef productivity and ecology (Wilkinson, 1981). Investigations of cyanobacterial associations with tropical marine sponges have been conducted by Sara (1971), Vacelet (1970, 1975), Vacelet and Donadey (1977), and Wilkinson (1978c, 1980a, b, 1981, 1983). Coccoid Cyanobacteria are the most frequently reported sponge symbionts (Wilkinson, 1980a). Relatively few studies have been conducted on non-photosynthetic marine bacteria naturally associated with marine sponges. Reports by Betrand and Vacelet (1971) and Vacelet (1975) postulate that large specific bacterial populations found in the mesophyl regions of sponges are symbiotic. Vacelet (1970, 1975) suggests three modes of bacterial symbioses found with sponges: 1) small populations of non-specific bacteria of a composition similar to those in ambient water, 2) large specific populations that inhabit the mesophyl region different from those in ambient water, and 3) small specific bacteria located intracellularly.

Few workers have examined the ecological significance of the possible function of bacteria in sponges. Composition and relative proportions of bacterial strains located in Porifera are reported (Bertrand and Vacelet, 1971; Imhoff and Trüper, 1976; Madri et al., 1971; Reiswig, 1975; and Wilkinson, 1978a, 1978b, 1978c), but most authors do not elaborate on possible roles. Wilkinson (1978 a-c) surveyed microbial associations in some coral reef sponges and suggests that the primary function of cyanobacterial symbionts is product translocation from bacteria to sponge. The roles of heterotrophic bacterial symbionts are uncertain. Wilkinson (1978b) and Imhoff and Trüper (1976) report facultative anaerobic bacteria in sponges. Heterotrophic bacteria, found in marine sponges are capable of metabolizing many sponge substances (Wilkinson, 1978b), including sponge collagen (Wilkinson et al., 1979). These bacteria may be important in removing and recycling sponge metabolites during dormant stages of reduced water circulation, a condition reported by Reiswig (1975). Some bacteria produce mucoidal substances in culture that could contribute to structural rigidity in sponge skeletons (Wilkinson, 1978b).

Castro (1979) describes an extracellular symbiotic relationship between the marine sponge Hymenaphiastra cyanocrypta de Laubenfels, and a filamentous, multicellular, apochlorotic bacterium. The bacterium contains a water soluble carotono-protein biochrome in characteristic blue-pigmented vacuoles. Ultrastructural examination confirms a prokaryotic cellular structure with no evidence of thylakoids. Tests for the presence of lipids, sulfur, and chlorophylls are reported negative. Castro (1979) suggests a close affinity to the flexibacter group with morphological similarities most clearly resembling Leucothrix mucor.

Castro (1979) reports a Hawaiian sponge, Terpios granulosa Bergquist, to also contain a blue bacterial symbiont of the same type as the bacteria described in Hymenaphiastra cyanocrypta. Bergquist (1967) makes no mention of any associated symbiotic bacteria in the original species description, only that a dark blue coloration was retained after preservation in alcohol.

The primary objective of this study was to determine the nature of the symbiosis between Terpios granulosa and the bacterium. Cellular organization of the symbiont and relationship to the host were studied using light microscopy, scanning electron microscopy and transmission electron microscopy. Techniques to separate, isolate, and culture the bacterium in vitro, necessary to proceed with bacteriological classification, and interpret the nature of this symbiosis were tested. Procedures to eliminate the bacterium from the sponge using antimicrobial substances were attempted, to elucidate the nature of the bacterium-sponge relationship. Two series of solar radiation experiments were conducted to test radiation sensitivity of the symbiotic bacteria and host sponge.

Materials and Methods

This study was conducted between May 1983 and August 1983 at the Hawaii Institute of Marine Biology, on Coconut Island in Kaneohe Bay, Oahu, Hawaii. All specimens were collected by SCUBA and snorkeling from the reef rubble zone and the fringe area of patch reefs in Kaneohe Bay. Habitat description, associated organisms, and other ecological information were noted.

Sponge samples containing the bacterial symbiont were prepared for viewing with light microscopy, scanning electron microscopy (SEM) and transmission electron microscopy (TEM). Isolated bacterial cells were viewed with fluorescence microscopy using an HBO 50W super-pressure mercury vapor lamp with a BG-38 heat filter and LP-520 barrier filter, and phase microscopy stained with methylene blue and Gram stain. Sponge specimens containing the bacterial symbiont were fixed for SEM using the Parducz method as described by Johnston and Hildemann (1982) for Calyspongia diffusa. Tissue was stored in 70% ethanol until cryofracture and critical point drying could be completed. Ethanol cryofracturing was done to reveal subsurface architecture (Humphreys et al., 1974). Specimens were critical point dried, coated with gold-palladium, and viewed with an AMR 1000A scanning electron microscope.

TEM prepared specimens were fixed in 2% glutaraldehyde buffered in 0.22 u membrane filtered seawater (FSW) for one hour (960 mOsm tonicity) and post-fixed in 2% osmium tetroxide buffered in FSW, for two hours. All procedures were carried out at 25 °C. Dehydration followed in a graded ethanol series, and specimens were stored in 70% ethanol until embedding in Spurrs brand resin could be completed. Ultrathin sections were obtained with glass and diamond knives. Sections were stained with 2% uranyl acetate and 1% lead citrate and were viewed with an RCA EMU-3G transmission electron microscope.

The technique developed for isolating the symbiont combined two cellular dissociation techniques. Small pieces of sponge with the bacterial symbiont (1 cm^3) were removed from the calcareous substrate and washed in three 20 ml changes of calcium-magnesium free artificial seawater at pH 8 (CMFSW), a sponge dissociation solution (Humphreys, 1963). Specimens were allowed to remain ten minutes in each wash. The specimens were transferred to 20 ml of Kane's solution (1 M glycine, 0.01 M Tris, and 0.002 M EDTA pH 8) and echinoderm blastula dissociation solution (Kane, 1973). Following two ten minute washings in this solution specimens were then transferred to fresh Kane's solution and the sponge tissue was squeezed gently with the forceps until most of the blue color (the bacterium) was released from the sponge matrix. The blue solution was decanted from the remaining spicule debris.

More refined separation was achieved using density gradient gravity fractionation. A 250 ml separatory funnel was layered with a two percent stepwise density gradient of Kane's solution and Ficoll brand 400 ranging from 2% to 8%. The solution containing the bacterium was layered on top of the gradient and alloved to settle for three to five hours. The fraction containing the bacterium was centrifuged; the bacterial pellet was resuspended in Kane's solution and used in culture experiments.

Attempts were made to culture the bacterium on 2% agar filtered seawater (FSW) media supplemented with different nutrients: doubly enriched F-2 nutrients (Guillard and Byther, 1962); doubly enriched F-2 diluted to 75% volume salt concentration; 4% autoclaved Terpios granulosa extract; 4% autoclaved Chondrosia chucalla extract; 2% glucose; 2% peptone and a control with no added nutrients. The extraction from C. chucalla, a sponge occupying the same habitat as T. granulosa, was used to test for host specificity. To avoid precipitating nutrients in FSW, solid agar and individual nutrients were added to one fifth volume of the total FSW volume and autoclaved. This solution was aseptically added to the remaining FSW volume.

Each petri plate was aseptically inocolated with 6.73 x 10^5 cells per ml (determined with a Speirs-Levy Eosinophil counting chamber) using spread plate techniques on a sterile 0.45µm membrane filter on the agar surface. The cultures were incubated in the dark in an environmental chamber and maintained at a temperature range of 25.6 - 27.7 °C. Five replicates of each medium were inoculated. Cultures were scored every 48 hours for growth and viability. After 14 days, final results were evaluated.

Bacterial pigment was extracted from one gram of sponge tissue by maceration with a tissue grinder and ultrasonification. Solubility of the pigment in aqueous solutions of FSW, distilled water, Kane's and phosphate buffer; and the organic solvents ethanol, methanol, isopropyl, acetone, benzene, phenol, and hexamine was tested and determined by colorimetric analysis.

Two series of solar radiation experiments were conducted to test the effects of full spectrum solar radiation and ultraviolet radiaton on the relative fitness of the sponge and the bacterial symbiont, and to elucidate the cryptic requirement of the sponge. The first series of experiments used full spectral solar radiation at 100%, 50% and 0% illumination. The second experimental series used 100% and 50% illumination, with and without ultraviolet exclusion filters. Specimens attached to coral rubble were positioned downward and unexposed to light, as they naturally occur, to act as controls to test for significant tank effects. Relative fitness of the sponge-bacteria complex was established by correlating bacterial density with pigment intensity and sponge tissue degradation. Bacterial densities were determined by light microscope counts of methylene blue stained trichomes.

For the first experiment, two adjacent tanks fully illuminated with sunlight were utilized for the 100% and 50% illumination treatments. The 0% illumination treatment tank was maintained in a darkroom with a tight fitting black plastic lid. Fifty percent solar radiation was achieved by placing a neutral-density black mesh screen (Lumite Chicopee brand black mesh fabric) over the tank (50.77% light transmittance was determined with a LiCor brand Instrument LI-185 quantameter). Due to the spectral exclusion properties of water, the actual solar radiation levels impinging on the specimens were 68.7% for 100% intensity, and 39.6% for 50% intensity (G. Scelfo, personal communication). All tanks were supplied with constant running seawater from Kaneohe Bay. The 0% illumination treatment was maintained at ambient seawater temperature and did not experience the temperature variation due to solar heating apparent in the 100% and 50% illumination tanks (26.2 - 27.8 °C). Each treatment contained five experimental units (sponges exposed in an upward postion) and five controls (sponges unexposed in a downward position).

All specimens were collected in the vicinity of Coconut Island, and randomly assigned to tanks and subsequent treatments. They were allowed to acclimate 24 h before applying treatments. The aquaria were fully aerated from a central position to insure adequate levels of dissolved oxygen, thorough mixing, and to provide water motion to decrease sediment accumulation. Aluminum mesh racks lined the bottom of each tank to elevate specimens 12.5 cm above the tank floor. Specimens were placed in random positions in the central area of the tank to minimize shading effects of the tank sides. The racks helped to minimize sediment accumulation on the control sponges. Sediments accumulated on the experi-

mental units were removed with a large syringe every twelve hours. The duration of the experiment was ten days. The sponge and symbiont complexes were monitored daily and scored for relative fitness at the end of the experiment. The treatment completely devoid of solar radiation exposure was monitored using a dark red light. Differences of relative fitness between the three levels of illumination were analyzed using the chi-square test of association (Sokal and Rohlf, 1969).

Ultraviolet-radiation exclusion experiments on the sponge bacterial symbiosis complex were conducted in conjunction with photoadaptation experiments on Montipora verrucosa, a Scleractinian coral. Two adjacent fully enclosed tanks were set up under conditions similar to those of the solar radiation experiments with the following modifications. One half of each tank allowed transmittance of 100% illumination and the other 50% illumination. The neutral-density mesh was held in position with monofilament line and anchored to the bottom of the tank so that the top and exposed side was completely encased with the filter. Each side contained its own water inflow source and circular airstone. One tank was covered by a fluorohalocarbon lid (Allied Chemical Corp. Aclar Brand) that allowed full spectral solar radiation transmittance (Paul Jokiel, personal communication). The other tank was covered with a UV-stabilized polycarbonate lid (Rohm and Haas Tuffak Brand), opaque to UV (Jokiel and York, 1982). Due to the spectral exclusion properties of water, the actual solar radiation levels impinging on the specimens were 61.5% for 100% intensity, and 38.5% for 50% intensity (G. Scelfo, personal communication). The aluminum racks in these tanks were supported by cinder blocks. Each treatment contained two experimental units in an exposed position and two controls in an unexposed position. The temperature ranges were 26.8 - 28.4 °C. Final results were evaluated after 12 d. Differences between treatments with and without ultraviolet filters were determined by relative fitness states using probabilities derived from Fisher's Exact Test (Zar, 1974).

The bacterium-sponge assemblage was tested for its resistance and sensitivity to several common antimicrobial agents in two series of experiments. In each case the substrate pavement to which the specimens were attached was broken with a geologists pick into small pieces (approximately 9 cm^2) so the specimens would fit easily into 50 ml beakers. The specimens were acclimated for a period of 24 hr in a running sea water aquaria prior to inoculation. The antimicrobial mixtures indicated in Table 1 were prepared by adding the anti-microbial agent to FSW and filtering the solutions through a 0.22 µm membrane filter. The lowest concentration of each antimicrobial agent was the amount recommended for standard culture media (50 µg/ml Merthiolate, D. Krupp, personal communication; 50 µg/ml Gentamycin, manufacturer's recommended dosage; Streptomycin/Penicillin G mixture, M. Hadfield personal communication). Specimens were randomly assigned to 30 ml antimicrobial solution in a 50 ml glass beaker. The beakers were covered with cellophane wrap secured with rubber bands. All beakers were incubated in the dark in an environmental chamber at 25.6 - 27.7 °C for twenty four hours. Data were collected accessing the relative fitness of the sponge and bacterium as before.

Results

Terpios granulosa was always found with the filamentous blue bacterium symbiont and cryptically encrusting calcareous substrates. The sponge-symbiont complex was never found in a viable state when directly exposed to light. Specimens occasionally found upright, presumably exposed by wave action, were deteriorating. Terpios granulosa was commonly found encrusting the crustose coralline algae Sporolithon erythraeum (Rothpletz) Kylin, overgrowing Bryozoa, and encrusting the denuded bases of the Scleractinian corals, Porites compressa and Pocillapora damicornis. The encrusting black sponge Chondrosia chucalla was commonly found proximal to Terpios granulosa. The sponge and bacterium were most common in the reef rubble zone, areas of high wave activity, less than one meter deep.

Light microscopy revealed the bacterium was extracellular in relationship to the sponge cells. The blue pigmented bacteria were multicellular trichomes, uniform in width (one micron). The trichome length averaged 3.1 - 12.4 µm, and individual cell lengths averaged 1.5 µm ± 0.25 (S.E.). Light micrographs revealed the filaments possessing outer membranes containing each individual cell unit, and a thickened periplasmic space. The cytoplasm of individual cells was less dense than the periplasmic space and was bound by a discrete membrane.

Table 1. Sensitivity of sponge-bacterial assemblages to antimicrobial agents measuring a change in relative fitness state. (3) indicates no change in relative fitness state from beginning of experiment. (2) indicates some bleaching of blue sponge with approximately 15-45% bacterial loss. (1) indicates strong bleaching of blue sponge at times resulting in yellow color, with up to approximately 85% bacterial loss. (0) indicates mortality of yellow sponge with more than 85% bacterial loss. The change in relative fitness was an average of scores from each experimental unit run in triplicate.

ANTIMICROBIAL AGENT	CONCENTRATION (g/ml)	EXPERIMENTAL NO.	CHANGE IN FITNESS
Control	---	1	3
	---	1	3
	---	1	3
	---	2	3
	---	2	2
	---	2	3
Merthiolate	50	1	0
	100	1	0
	200	1	0
Gentamycin	50	1	3
	100	1	3
	200	1	3
	400	2	1
	600	2	0
Penicillin G /Streptomycin	25/33	1	0
	53/60	1	0
	100/120	1	3
	200/240	2	3
	300/360	2	2
	450/560	2	2

Viewed with phase contrast, blue refractile vacuoles common in the cytoplasm, were the only distinguishable inclusions. The bacterium was Gram-negative. Methylene blue stained the refractile vacuoles blue, while the periplasmic spaces stained red. No fluorescent material was observed when viewed with mercury halide illumination.

SEM confirmed that the symbiont exists extracellular to the tissue of Terpios granulosa (Fig. 1 and 2). The organization of the spicule tracts was oliquely transverse from the substrate to the sponge surface resulting in terminal spicule tufts. Many loosely aligned tylostyles were dispersed between the tracts and an intermeshed spicule layer, arranged parallel to the surface, supported the epithelial pinacoderm. Individual bacterial filaments appeared longer when viewed with SEM (=15.0 um) as compared to light microscopy. This might be explained by fragmentation of the trichome during extraction for light microscopy. SEM observations revealed a characteristic terminal cell with a flattened conical shape. Annular invaginations occurred with a regular periodicity of 5-6 µm along the filaments (Fig. 2). This periodicity corresponded well with the average length of a single trichome as viewed with phase contrast microscopy, suggesting there was more than one individual trichome contained within the same sheath-like structure.

The bacterium was abundant in the skeletal matrix of the sponge. Bacterial filaments were most numerous in the mesohyl region of the sponge where they comprised 40-60% of the mesohyl volume. The trichomes appeared to be embedded in a fibrous collagen matrix loosely organized in a plane parallel to the surface. The pinacoderm, or epithelial layer, that lined the surface and aquiferous system had a very smooth texture, relatively free of symbiotic bacterium. No cellular relationships between specific sponge cell types and the symbiotic bacteria could be determined.

TEM micrographs confirmed the presence of the bacterium in the mesohyl embedded in a fibrous collagen matrix. No specific sponge-cell association with the symbiotic bacterium was observed. The bacterium had no thylakoid membrane structures and a typical Gram-negative envelope as defined by Forsberg et al. (1970) for a marine Pseudomonas. Micrographs confirmed the multicellular nature of the trichomes divided by regular septation with conically flattened terminal cells. Growth appeared to occur by cell elongation and septal formation as evidenced by centripetal annular growth inward from the peripherial walls (Fig. 3). No flagella, fimbriae, or unusual appendages, spores, akinetes, or other resistant bodies were observed.

Nuclear regions and vacuoles were electron transparent zones located in the cytoplasm within each cellular compartment. Membrane bound vacuoles found intracytoplasmically resembled sulfur or polyhydroxybutyric acid granules found in some sulfur oxidizing bacteria (Brock and Conti, 1969). The membrane system of this bacterium was more extensive than the typical Gram-negative bacterium. The terminal cell envelope had two electron dense membrane layers separated by an electron opaque region. This region, which may be artifactual, varied in width and shape and separated this bimembrane layer from the electron dense periplasmic space. The membrane structure of the terminal cell was not observed to extend around the periphery of the trichome. The remainder of the trichome was covered by an undulate cell wall. The cytoplasmic membrane was beneath the thick electron dense periplasmic space. A mesosome-like structure was observed in one filament attached to the septal wall. This structure was approximately 0.5 µm wide and contained two concentric membrane bound chambers. The inner chamber contained homogeneous electron-dense material while the outer chamber was filled with coccoid forms that encircled the inner chamber.

The CMFSW did not cause Terpios granulosa to dissociate, even after hand homogenization for separation and isolation of the bacterium. Kane's solution caused sponge cell dissociation and freeing of the symbiotic bacterium only after gentle homogenization with forceps. When Kane's solution was used with no prior rinsing in CMFSW the dissociation of sponge cells did not occur as readily, more forceful squeezing with forcep was required, and the number of bacteria released were fewer.

Other methods of tissue homogenization were tried, including disruption in a glass tissue grinder, but results were always inferior to the above technique. Of several different filtration and centrifugation schemes attempted, the gravity settling separation method gave the best resolution. The fractions removed

Fig. 1. SEM of densely packed filaments of the bacterial symbiont in the mesohyl region of the sponge. Membrane (Me) sheets of collagen form layers in mesohyl. Quadrilobate tyolstyle (t) head exposed. Magnification (x1800).

Fig. 2. Higher magnification SEM of the bacteria trichomes (b) embedded in fibrous collagen (Cl). Arrow indicates the periodic invaginations along the bacteria trichome. Flagellated cells (Fl) probably choanocytes are shown. Capped terminal cells are quite distinctive. Magnification (x 7650).

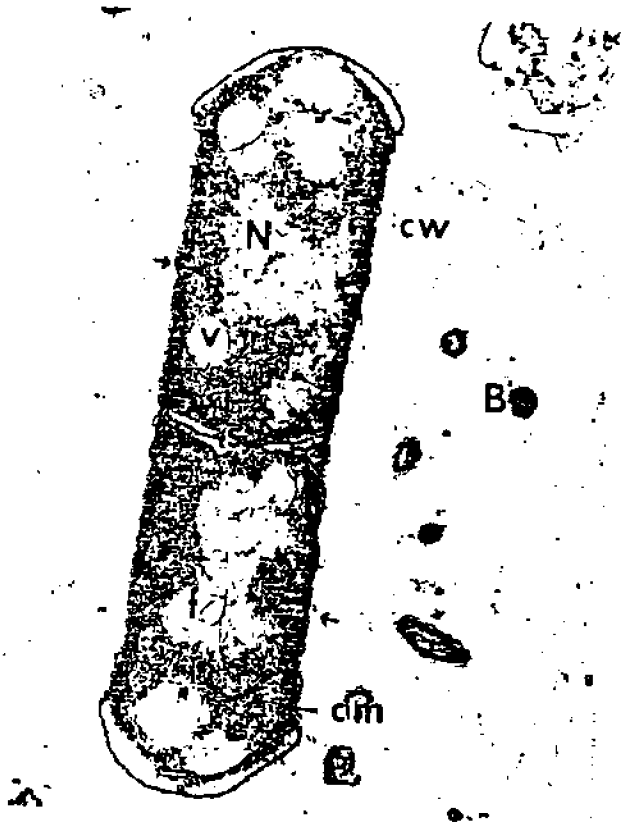

Fig. 3. Elongated cells in one trichome of the symbiotic bacterium. Septal invaginations (indicated by arrows) of inward growth from cross walls dividing each cell. V-vacuole, cw-cell wall, cm-cytoplasmic membrane, N-nuclear region, f-DNA strands, s-septal wall, B-small coccoid bacteria. Magnification (x 26,200).

after separation were not homogeneous. Flagellated cell aggregates, large single sponge cells and spicule debris were retrieved from the bottom of the 6% to 8% fraction. Symbiotic bacterial cells contaminated with smaller sponge cells and ruptured cellular debris were retrieved from the center of the 4% fraction.

The major problems encountered with this separation method were damage to the symbiotic bacterial membranes, failure to completely isolate the bacterium, and leaching of the blue pigment in the fresh water of Kane's solution. Osmotic shock to the bacterial cells induced swelling, morphological distortion and eventually cell wall rupture after four to six hours in Kane's solution. If the fraction containing the bacteria was washed, centrifuged, and the pellet resuspended in CaFS%, the sponge cells would reaggregate into masses of sponge cells, and the symbiotic bacteria would reassociate with the sponge cells.

No bacteria growth was observed in any of the culture media tested. All the cultures had viable symbiotic bacteria cells after being maintained in culture conditions for two weeks, with a minimal amount of other bacterial contaminants. Cells were determined viable by the presence of pigment vacuoles and intact membranes, as determined with methylene blue. The longer the cells were maintained in culture the greater the loss of pigment vacuoles in individual cells. Some cells remained viable for longer than five weeks in cell cultures.

The bacterial pigment was soluble in aqueous solutions and insoluble in common organic solvents. A blue supernatant resulted when ruptured bacterial cells were suspended in distilled water, FSW, Kane's solution and phosphate buffer. No colorimetric change was observed when the cells were suspended in ethanol, methanol, isopropyl, acetone, benzene, phenol, and hexamine.

In experiments testing the affects of solar radiation, the data suggested that different levels of solar radiation were related to the relative fitness or mortality of the bacteria and sponge. The results of the chi-square test for association between treatments showed that the relative fitness states were not independently associated with the three levels of illumination ($p<0.025$). Controls maintained the highest relative fitness state indicating no effects due to the containment in tanks between treatments.

Daily observations support these results. Specimens subjected to 100% illumination showed noticeable paling of color after three d of the experiment, with no sponge tissue deterioration. Eight days after the onset of the experiment, the sponge tissue was devoid of blue pigment with obvious deterioration. By 10 d most of the sponge-bacterial complex had completely deteriorated. Specimens subjected to 50% illumination remained in the highest fitness state up to 6 d, following which were noticeable signs of color loss. After 10 d most of these specimens were 40-60% of the original color intensity. The peripherial edges of the sponges showed signs of yellowing and some deterioration. Specimens subjected to 0% illumination showed no changes in their relative fitness state, all remained in the highest rank as did all of the unexposed controls in all three treatments. These results showed that high levels of solar radiation cause death in exposed assemblages of Terpios granulosa and the blue symbiont.

The results from the ultraviolet radiation experiments at different levels of illumination, allowed inferences to be drawn only about the effect of ultraviolet radiation on the relative fitness of the sponge bacteria complex. Too few experimental units were tested to determine the effects of different levels of illumination in these experiments. Using the Fishers Exact Test of association the results inferred that the specimens shielded from UV maintained a higher relative fitness than the specimens that were exposed to full spectrum radiation ($p<0.20$). The experimental units that were exposed to ultraviolet free radiation had no change in their relative fitness state. They maintained a dark cobalt blue color, with no tissue loss over a 12 day period. The specimens exposed to ultraviolet radiation experienced noticeable paling of color at six days and about 60% bleaching effect after 10 days. At the termination of the experiment, 12 days later a small amount of sponge tissue degradation was found.

All but two of the x controls maintained the highest level of fitness. These two controls were positioned in direct contact with the cinder blocks supporting the aluminum racks, and they suffered great tissue mortality at these points, but the surrounding tissue maintained a high fitness level. One control was in the tank with 50% illumination and ultraviolet radiation, the other effected control was in the tank with 100% illlumination and ultraviolet radiation excluded. Because the controls were in different tanks with very different treat-

ments, it was assumed that tissue mortality was caused by direct contact with the cinder blocks.

The bacterial-sponge symbiosis appeared to be resistant to all the anti-microbial agents tested with the exception of a high dose of Gentamycin 600 mg/l and all levels of merthiolate tested (see Table 1). In experimental series one these was no change in the relative fitness of the sponge and bacteria complex in all controls. Twelve hours after initiation of the experiment, the merthiolate treated specimens showed significant decline of their relative fitness states, and ultimately resulted in death of the yellowed sponge. Merthiolate also killed sponge epifauna and infauna (mostly polychaetes and amphipods).

In the second antimicrobial experimental series (see Table 1) all but one of the controls remained in the highest fitness state. The control beaker with a decline in fitness state was fouled with a dead actiniara. In the treatment of 600 mg/l of Gentamycin there was a substantial decline in all of fitness states of the sponge-bacteria associations and all experimental units died. In all experimental units with high dosages of antimicrobial agents there were the remains of dead polychaetes, amphipods, and other infauna and epifauna organisms commonly located in sponges.

Discussion

Terpios granulosa was found growing in crypic habitats rarely exposed to sedimentation and light. T. granulosa encrusted the bottom side of coral rubble and the top layer of coral pavement covered by rubble, in high energy environments where continuous water movement minimized sedimentation. These habitats were sites of low sediment accumulation. T. granulosa was commonly overgrowing other encrusting organisms. Another sponge often found as a cryptic form, Chondrosia chucalla, and found contemporaneously with Terpios granulosa, is not sensitive to ultraviolet radiation (Jokiel, 1980). Jokiel (1980) speculates that C. chucalla, having no spicules, is often limited to cryptic habitats by fish predation. The results of this study suggested that T. granulosa was sensitive to ultraviolet solar radiation resulting in moribundity and mortality. It was hypothesized by Jokiel (1980), that the cryptic nature of T. granulosa was a strategy to avoid light.

Jokiel (1980) found many reef epifauna to be sensitive to ultraviolet radiation, the most sensitive being cryptofauna. Many marine photosynthetic algal symbionts directly exposed to UV have pigments able to fluoresce ultraviolet radiation and thus shield the host organism from the deleterious effect of UV (Jokiel and York, 1982). A similar study by Wilkinson and Vacelet (1979) tested the responses of sponges with and without cyanobacterial symbionts to full spectral radiation. The results found light stimulated growth in the sponges with cyanobacterial symbionts and inhibited growth in sponges without cyanobacterial symbionts.

It was initially presumed that the bacterial symbiont in Terpios granulosa was a Cyanobacterium, as it had morphological similarities to the Cyanobacteria. Exclusive of Castro's (1979) study all filamentous prokaryotes that were reported to be symbiotic with marine sponges had been Cyanobacteria (Berthold et al., 1982; Vacelet, 1981; and Wilkinson, 1980). Evidence from this study suggested that this symbiotic bacterium was not a Cyanobacterium. The blue pigmented bacterium was not capable of photosynthesis: it contained no chlorophyll, thylakoid or other photosynthetic membranes, and was inhibited by solar radiation, specifically in the ultraviolet range. There are few trichome multicellular prokaryotes of this large size that are not Cyanobacteria. The similarities to the Cyanobacteria group are attributes also found in the family Beggiatoaceae, a group that are often called the apochlorotic Cyanobacteria (Wiessner, 1981). The presence of periodic invaginations of the sheath in scanning electron micrographs and separate filaments within a common sheath in transmission electron micrographs suggest hormogonia type fragmentation, a common mode of reproduction in the Cyanobacteria (Rippka et al., 1981). The formation of new cells elongating existing trichomes also was cyanobacteria-like: centripetal annular ingrowth of the septa from the cytoplasmic membrane (Rippka et al., 1979). The presence of the terminal capped cell was quite unique, a characteristic that can not be found in any other known taxon.

It has been hypothesized that the blue bacterium and its sponge host, Terpios granulosa, have developed a symbiotic relationship based on their close cellular association of the second type of bacterial symbiosis described by Vacelet and

Donadey (1977), i.e., monospecific, extracellular, and comprising a high density in the sponge mesohyl with a much lower density in the well irrigated aquiferous system and pinacoderm. The translocation of algal products in known for coral-zooxanthellae symbioses (Muscatine and Porter, 1977) and for sponge-cyanobacterial symbioses (Wilkinson, 1983). Since culture attempts of the symbiotic bacterium were unsuccessful, the functional aspects of this symbiosis could not be elucidated.

A possible benefit to the sponge in this relationship was increased strength and structural support contributed by the bacterium. The collagen fibers that bound the bacterial trichomes together could provide a structural scaffolding in an area that naturally has little skeletal rigidity. In T. granulosa, spicules were less abundant and more loosely organized in the mesohyl than in the pinacoderm. High numbers of symbiotic bacteria in the mesohyl may function to improve the strength and provide structural support for this low encrusting sponge. Wilkinson et al. (1981) first speculated on this role when they observed that cultured bacteria extracted from sponges produced mucoid colonies and that in vivo bacterial symbionts possessed a thickened capsule layer. Also, recycling and degradation of collagen by bacteria may aid in rearrangement of sponge skeletal infrastructure (Wilkinson et al., 1981).

Castro (1979) presumed that bacterial symbionts in Hyrtiamphiastra cyanocrypta and Terpios granulosa were similar, but this study revealed differences. Castro does not mention the presence of a characteristic terminal cell, a distinguishing feature of the T. granulosa symbiont. In H. cyanocrypta, the bacterium lacks the large intercytoplasmic space, the density of the intracellular components are strongly contrasting, and the nuclear region is the most electron dense region with the frequent appearance of low density inclusions. Some of these differences may be attributed to artifacts from different fixation procedures. The ultrastructure of the bacterium in this study most closely resembled that found in the study of Beggiatoa by Morita and Stave (1963), but did not resemble the ultrastructure of Beggiatoa described by Maier and Murray (1965). One must be cautioned that the usefulness of an ultrastructural study in prokaryotes is restricted by the simplicity of such organisms. Some unique and unusual cytological characteristics of the bacterial symbiont could not be related to any known prokaryote.

The separation and isolation protocols developed must be improved to acquire better recovery of bacteria from sponge cells and siliceous spicule debris. Adequate separation must be accomplished with a medium that prevents the sponge cells from reassociating in a very short period. This suspension could be separated by density differences in isopycnic ultracentrifugation. If no reaggregation occurred and the centrifuging medium was isotonic with the bacterial cells, adequate recovery with minimal damage could be possible.

The symbiosis between the extracellular bacterium and the sponge, Terpios granulosa appeared to be an obligate relationship. Death of the bacterium was observed to be followed by the death of the sponge. The sponge was never found without the bacterium, and attempts to axenically culture the bacterium were unsuccessful. Further culture studies are necessary to determine the metabolic requirement of the symbiont. The highest bacteria density was in the mesohyl of the sponge, and in much lower density in the well irrigated aquiferous system and epithelial pinacoderm. The symbiotic assemblage was highly sensitive to UV, and resistant to common antimicrobial agents except merthiolate and high dosages of Gentamycin. The bacteria exist as multicellular trichomes with blue pigment granules. Ultrastructure investigations reveal a conically capped terminal cell, a Gram-negative cell wall, and the absence of thylakoid structure. The bacterium most closely resembled the apochloratic cyanobacteria.

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A preliminary report on the histology of allograft rejection in the marine sponge Callyspongia diffusa.

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Abstract

During allograft rejection, the marine sponge Callyspongia diffusa reveals a sequence of pathological changes that are initiated by a cell mediated recognition of non-self. Following this recognition, the response proceeds to a cellular infiltration into the graft interface which produces tissue separation from cell death and tissue disintegration. This study presents a histological analysis of the tissue bridge stage of this response and, in agreement with earlier work using scanning electron microscopy, it shows that the mesohyl cells infiltrate into the graft interface, altering the local microanatomy of the responding cells.

Introduction

The kinetics of the immune system of the marine sponge, Callyspongia diffusa have been worked out in detail by Hildemann and his colleagues (Hildemann, et al., 1979a, 1980; Bigger et al., 1981, 1982; Johnston, et al., 1981). As assayed by tissue rejection, this animal fulfills the basic criteria that defines an immune system (Hildemann, et al., 1979b). Callyspongia can recognize non-self, become sensitized to a specific genotype of grafted tissue, react cytotoxically to the foreign graft, and respond at an accelerated rate upon second challenge (Bigger, et al., 1982). These investigations, conducted on the whole animal in the past, are now progressing to a cellular dissection of the immune system. Johnston and Hildemann (1982, 1983) described the normal architecture of the animal and noted that Callyspongia passes through a sequence of pathological changes during the rejection process. Briefly, the response begins with (1) a recognition of non-self, presumably by the exopinacoderm or a wandering surface cell, proceeds to (2) an infiltration of mesohyl cells forming a hyperplastic graft interface with tissue bridges, and culminates with (3) a necrotic reaction at the interface and a sloughing of the dead cells separating the grafted animals.

No major histological attempts have been made to observe the pathological changes found in Callyspongia rejections due to the sectioning problem presented by the skeleton of the animal. But by freezing paraffin embedded blocks of Callyspongia tissue, histological sections can be obtained without damage to the knife, the block or the section from the sponge spicules. The microanatomical changes observed during an allograft rejection using this method correlates well with changes previously documented by macroscopic observation (Hildemann, et al., 1979a, 1980) and by scanning electron microscopy (Johnston and Hildemann, 1982, 1983). In this preliminary study, the tissue bridge stage of the rejection was chosen for study. A more detailed analysis encompassing the entire process will be presented elsewhere.

Materials and Methods

Specimens of Callyspongia diffusa were collected from around Coconut Island (located in Kaneohe Bay, Oahu, Hawaii) and held in the running sea water system at the Hawaii Institute of Marine Biology. Small sized pieces (4 cm x 1 cm) were cut from the animals using dissecting scissors. Within 24 h, a new outer cell layer (exopinacoderm) had formed over the cut sites, and all of the small sponge pieces were filter feeding and appeared healthy. The sponges were tied together in autografts (self grafts) and allografts (grafts between different individuals of the same species). The two pieces were secured together by wrapping with 6 lb monofilament fishing line or ordinary sewing thread. When additional support for the graft was required, a small plastic splint was placed next to the sponges before being secured with line. Duplicate grafts were tied, and all were returned to the sea water tables.

Allografts in the tissue bridge stage were placed in Bouin's fixative over night and then washed several times with sea water followed by tap water. The specimens were dehydrated in ethanol, cleared in xylene and embedded in paraplast.

The hard silicious spicules of the sponges made it impossible to use conventional parrafin sectioning techniques. The sections were shredded and the knife soon became unusable. It was found that this problem could be avoided by freezing the blocks, hardening them to approach the hardness of the spicules, and then sectioning them in a cryostat. O.C.T. compound (Miles Laboratories) was used to freeze the blocks to cryostat stubs at -30°C, and then the sections were cut at 9 μ and placed on acetone cleaned, bovine serum albumin coated slides. Upon thawing, the sections were stretched on a "bubble" of water at 40°C, after which the water was wicked off and the sections were allowed to dry on the slide warmer, thus securing them to the slide. The slides were routinely deparaffinized and stained with hematoxylin and eosin. Stained slides were observed and photographed with a camera equipped Olympus microscope.

Results

The normal architecture of Callyspongia is rather open; most of the internal volume of the animal is actually sea water being pumped through the aquiferous canal system. Upon closer examination, one can discern a specific organization of endopinacoderm lined canals, choanocyte chambers, and small regions of mesohyl cells (Fig. 1). The animal is entirely contained within its exopinacoderm or outer epithelium which is perforated with holes or ostia. These function as the incurrent openings for water to enter the aquiferous system. Below this outer covering are the subdermal spaces which lead into the incurrent canals. These endopinacoderm lined canals eventually direct the water flow to the convexly curved outer sides of the choanocyte chambers. These chambers are constructed from a single layered sphere of choanocyte cells, each with a microvillar collar and single flagellum located on the inside of the chamber. Leading from the choanocytes is the excurrent canal which joins others and ends in the oscula or large excurrent pore. In addition to the choanocytes and pinacoderm, the other sponge cell types are located in the mesohyl. These cells are isolated from direct contact with the sea water in the aquiferous system by the choanocytes and the pinacoderm. The mesohyl contains cells of various morphologies and functions, none of which have been characterized for Callyspongia. In addition, the animal contains bundles of silicious spicules covered with spongin. Note that this and all other sponges have their cells organized into tissues; there are no organs or organ systems.

Organizational rearrangements of normal sponge tissue does not occur in an autograft. Oscula and some excurrent canals are rerouted if they are blocked in the grafting process, otherwise, the aquiferous and skeletal systems join and the grafted sponges appear as a single sponge. Fusion is complete in one or two days.

On the other hand, the tissue bridge stage of the allograft response is very different (Fig. 2). As has been noted by changes in gross (Hildemann, et al., 1979a, 1980) and ultrastructure anatomy (Johnston and Hildemann, 1982, 1983), histology reveals extensive alterations of the tissues at and near the graft interface, the most striking of which is a massive infiltration of mesohyl cells. This infiltration forms a hyperplastic region adjacent to the graft interface from which arise the tissue bridges that contact the allogenic tissue. During this infiltration process, the hyperplastic cells obliterate the aquiferous canals and squeeze the choanocyte chambers out of the vicinity of the graft zone. Most of the hyperplastic cells are basophilic by hematoxylin and eosin stain, but a few are acidophilic suggesting that the effector cell population is not homogeneous.

Discussion

In the limited literature addressing the microanatomical changes occurring in a poriferan graft rejection, two different rejection phenomena stand out. The first involves the physical walling off of non-self tissue by the depostion of a collagenous barrier. For example, Ephydatia fluviatilis responds immediately to allogeneic tissue in this manner. The exopinacoderm lays down a collagenous barrier much like that secreted by the basopinacoderm in securing the animal to the substrate (Van de Vyver and de Vos, 1979). Veronia longissima secretes a cuticular barrier against allogeneic tissue in addition to any other animate or

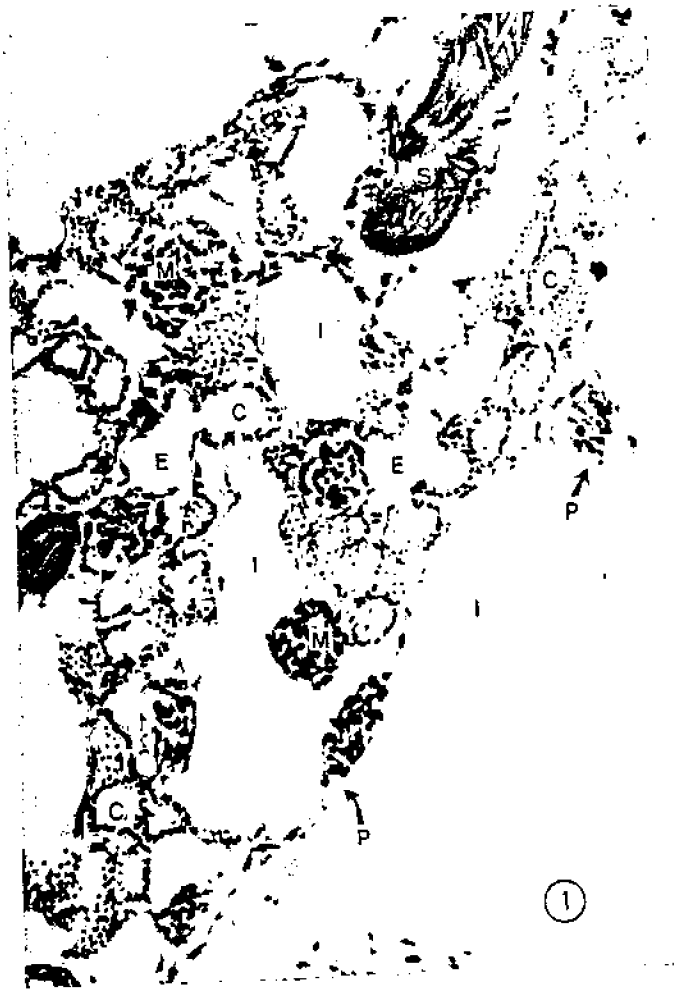

Fig. 1. Normal sponge anatomy showing the incurrent (I) and excurrent (E) canals lined by pinacoderm (P), the chanocyte chambers (C), the mesohyl (M) and the skeleton (S).

Fig. 2. Sponge tissue near the allograft interface [delineated by lines]. Note the tissue bridge (B), the hyperplastic areas (H), the squeezed choanocyte chambers (SC), and the normal sponge tissue in the vicinity of the excurrent canal (E).

inanimate object it contacts (Kaye and Ortiz, 1981). Axinella verrucosa deposits its collagen at the graft interface in differing amounts the more severe response producing an irregular collagenous barrier (Buscema and Van de Vyver, 1983).

The other type of allograft rejection documented in sponges does not invove the formation of a barrier. In this case there is direct and continued surface contact, which initiates a cellular infiltration into the graft zone, and leads to a cytotoxic phase that results in tissue necrosis, disintegration and separation. In addition to Callyspongia diffusa (Johnson and Hildemann, 1982, 1983), this form of rejection has been noted in Hymeniacidon perleve (Evans, et al., 1980), Toxadocia violacea (Bigger et al., 1983), Xestospongia exigua (Hildemann and Linthicum, 1981), and Axinella polypoides (Van de Vyver, 1980). The cells involved in the infiltration phase have been poorly characterized. For H. perleve it has been called an archeocyte (Evans et al., 1980) and in Callyspongia it has been called a medium sized mesohyl cell (Johnston and Hildemann, 1983).

The two dimensional view of the Callyspongia response presented here correlates well with the previously documented three dimensional view (Johnston and Hildemann, 1982, 1983). In this species the mesohyl cells infiltrate into the graft zone and alter the local anatomy by obliterating the aquiferous canals, squeezing out the choanocyte chambers and forming hyperplastic regions and tissue bridges. This overall response falls into the second category outlined above, and proceeds from cellular contact at the interface to cellular infiltration to tissue necrosis and sloughing which results in the separation of the parabionts.

In addition to the interest of comparative immunologists in various immune systems, the grafting response that an organism will show to non-self tissues has assisted population ecologists in unraveling the genetic structure of reef sponges (Jokiel et al., 1982; Neigel and Avise, 1983; Kaye and Ortiz, 1981) and corals (Jokiel et al., 1983; Hunter and Kehoe, this volume). When two organisms come into contact naturally or are parabiosed under controlled conditions, the grafting outcome will reveal the orientations of genetically identical animals within a given population. This is based on the assumption born in vertebrate immunology that graft acceptance is only possible between genetically identical organisms (Medawar, 1957). This assumption has been recently challenged with the suggestion that graft acceptance does not demonstrate clonal identity in reef organisms since substantial information on larval settling patterns, asexual reproduction, complexity of the histocompatibility locus, and chimera formation is unavailable (Curtis et al., 1982). Future work on the cellular mechanisms of recognition and rejection plus a better understanding of the mechanisms for species distribution will allow answers to this basic question.

The presence of the self identifying molecules or histocompatibility markers found on the surfaces of each cell within an animal underlies some of the questions pertaining to immune system origins and to population structure. The combined interests of immunologists and ecologists regarding these questions will result in the study of graft rejection for reef animals and will initiate a bridge between the two disciplines.

Acknowledgements

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The microfauna associated with three species of coral and their accessability to a reef community

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Abstract

Emergent microfauna were collected from a fringing reef adjacent to Coconut Island, Hawaii, from May 24 to August 1, 1983. Four substrates (sand, Pocillopora damicornis, Porites compressa, and Montipora verrucosa) were sampled from three zones (the lower, mid-, and upper reef flat, the reef crest and the reef front), using demersal traps (.25 m^2, 0.25 mm mesh) identical to the traps described by Birkeland and Smalley (1981). This study was conducted to determine if emergent microfauna are associated with a given coral species or reef zone.

Most microfauna showed no significant association with a coral species. Bursts of fish, crab, and shrimp larvae occurred in substantial numbers. These bursts were often sporadic 'one shot' occurrences. However, several species did show significant association with a given coral species. Large coral planulae of P. damicornis, associated with the adult, were collected in surprisingly great numbers throughout the study. Tunicate larvae showed an association with M. verrucosa, tanaids were most abundant over P. damicornis, and Acrocalanus inermis were most abundant over P. compressa. Most microfauna showed no significant zonal preference. A. inermis a 'holoplanktonic' calanoid, and Leptochelia dubia, an 'epibenthic' tanaid species, were ubiquitous throughout the reef. However, many holoplanktonic animals (cyclopoids, medusae, Oikopleura diocia and tunicate larvae) were most abundant on the reef front. Several epibenthic animals (cumaceans, amphipods) were most abundant on the reef flat.

Introduction

Coral associated microfauna have often been overlooked. These microfauna consist of holoplankton that swarm near the substrate, larval forms of coral-associated macrofauna (as well as coral larvae), and epibenthic species. The role of these organisms in coral reef energetics and ecology is just beginning to be understood, because methodologies are now available to examine these assemblages. The composition and abundance of microfauna have been examined with respect to zonation, substrate, diurnal patterns, and techniques (Odum and Odum, 1955; Gerber and Marshall, 1974; Glynn, 1973; Hobson and Chess, 1976, 1978; Porter and Porter, 1977; Alldredge and King 1977, 1980; Sale and Dybdahl, 1978; Hamner and Carleton, 1979; Birkeland and Smalley, 1981).

Several workers have investigated the composition and abundance of microfauna associated with individual coral species. Humes and Ho (1967, 1968) described cyclopoid copepods associated with coral species. Porter and Porter (1977) examined demersal plankton from mixed coral substrates. Alldredge and King (1977) examined zooplankton that emerged from only eight corals representing different species. However, most recent studies deal with the macrofauna rather than the microfaunal assemblages found associated with coral species (Knudsen, 1967; Garth 1974; Patton, 1974; Abele, 1976; Castro, 1976; Coles, 1980; Kropp and Birkeland, 1981). This study was undertaken in order to determine if emergent microfaunal assemblages are associated with three coral species on the windward reef adjacent to Kaneohe Bay, Hawaii.

Materials and Methods

Microfauna were taken from a fringing reef adjacent to Coconut Island (21° 26' 00'' N, 157° 47' 25" W) from May 24 to August 1, 1983. The fringing reef was sampled randomly at three different areas: 1) the lower, mid- (adjacent to a channel), and the upper reef flat, 2) the reef crest, and 3) the reef front.

Four different types of substrate were examined: sand, Pocillopora damicornis coral heads, Porites compressa coral heads and Montipora verrucosa coral heads. Replicate samples were collected over similar substrates both within days and between days.

The four demersal traps (.25 m², 0.25 mm mesh) were identical to the traps described by Birkeland and Smalley (1981). The opening of the inner cone was closed with a rubber stopper when transporting the trap. The traps were brought down sideways and placed over sand or solitary coral heads. All obstructing material was removed around the selected substrate. The traps were secured to the bottom by wire or "bungie cord" (elastic cord) on each corner of the trap. Sandbags and extra weights (coral rubble, bricks, rocks, lead weights) were placed completely around the trap upon the trap's skirts. The traps were collected 24 h after they were set. The contents of the trap were washed into the cod end by flushing the inverted trap, pulling it out of the water three times with the stopper still within the inner aperture. The contents were immediately placed in 5% formalin seawater (sand grains acted as a natural buffer). Total samples were counted with all individuals identified to major taxonomic group. The traps were rinsed with a high pressure freshwater hose between sampling.

Statistical Analysis

The Wilcoxon's matched pair signed rank test (Rohlf and Sokal, 1969) was used to test the null hypothesis that the three coral species were similar in the composition and abundance of all groups of zooplankton collected. Since only four demersal traps were used to take replicate samples of a coral species, only two coral species were sampled on any given date. All comparisons made between M. verrucosa and P. damicornis were made from samples collected on the same date. One comparison between M. verrucosa and P. compressa and three comparisons between P. compressa and P. damicornis were made from samples collected within two days of sampling the two coral species compared.

The Wilcoxon's matched paired signed rank test was also used to test the null hypothesis that the three reef zones from which all coral samples were taken were similar in the composition and abundance of all groups of zooplankton collected. The three reef zones were categorized as follows:

1) Reef front - deep (4-6 m) low light, turbid.
2) Reef crest - shallow (1 m), some wave action, hard substrate with 85-100% coral coverage.
3) Reef flat - shallow (0-1 m) exposed on spring tide, low water motion; sandy substrate with 10-50% coral coverage.

Since P. damicornis was not found on the reef front, and only four samples of P. damicornis were collected on the reef crest, the Wilcoxon's matched pair signed rank test was not used. If the standard deviation from the mean abundance of a given group of zooplankton did not overlap, the reef crest and reef flat were considered significantly different for P. damicornis.

Results

Table 1 represents the total mean number of zooplankton collected from each coral species. Tables 2-4 represent the total mean number of zooplankton collected from each reef zone for each coral species. Results from the Wilcoxon's matched pair signed rank tests are also shown. Since most groups of zooplankton showed no significant differences between coral species or within reef zones for each coral species, the groups of zooplankton will be categorized only with the coral species from which they were significantly ($p<.01$) more abundant and then categorized with the coral species from which they were found to have significant differences in abundances within the reef zones.

The following significant differences were found between the coral species:

P. damicornis:

more coral planulae than P. compressa ($p<<.001$) and M. verrucosa ($p<<.001$),

more L. dubia than P. compressa ($p<.01$) and M. verrucosa ($p<<.001$),

a greater total number of zooplankton than M. verrucosa ($p<.01$), and

Table 1. The total mean number (±SD) of each group or species of zooplankton collected from each substrate. Signifi ant Ts values for the probability that a match pair of coral species are shown as follows: +++ = p<.001, ++ = p<.005, + = p<.01.

Taxon	Sand n=6	Montipora verrucosa (Mv) n=23	Porites compressa (Pc) n=22	Pocillopora damicornis (Pd) n=17	Wilcoxin's matched pairs signed ranks test probabilities Mv/Pc	Pd/Mv	Pd/Pc
Coral plannlae		2.83 (6.34)	77.95 (222.33)	116.88 (215.73)		+++/	+++/
S. enflata	1.0 (2.0)	3.61 (9.20)	2.18 (5.22)	0.12 (0.33)		/++	
Polychaetes	1.5 (1.0)	3.04 (2.84)	3.32 (5.39)	2.59 (2.35)			
Bivalves	0.6 (1.6)	3.91 (10.77)	3.45 (6.97)	0.41 (0.87)		/++	
Gastropods	0.2 (0.4)	0.17 (0.65)	1.45 (5.12)	0.35 (0.78)			
A. inermis	11.6 (9.8)	48.40 (60.32)	53.77 (55.40)	14.47 (36.42)	/++	/+	
Cyclopoids	5.5 (5.3)	7.87 (8.12)	14.73 (17.52)	6.0 (5.02)			
Harpacticoids	6.8 (4.5)	18.30 (19.47)	15.41 (16.57)	26.24 (16.78)			+/
Mysids	0.2 (0.4)	0.56 (2.11)	0.18 (0.59)	0.35 (1.22)			
Cumaceans	3.2 (2.1)	3.36 (6.10)	2.41 (3.00)	7.18 (8.50)			+++/
L. dubia	22.8 (28.7)	10.96 (14.39)	15.38 (21.80)	35.76 (26.75)		+/	+++/
Amphipods	5.0 (4.0)	5.11 (11.16)	6.95 (10.55)	7.18 (3.88)			
Shrimp larvae	0.3 (0.5)	1.87 (3.62)	3.73 (8.83)	1.35 (2.21)			
Crab larvae	0.2 (0.4)	0.56 (1.31)	5.68 (25.32)	0.59 (1.12)			
Tunicate larvae		1.74 (4.93)	0.14 (0.47)	0.18 (0.73)	+++/	/++	
O. diocia	0.3 (0.8)	3.96 (9.80)	1.73 (2.55)	0.18 (0.39)		/+	/+
Fish larvae		13.39 (63.57)	0.23 (0.68)	0.06 (0.24)			
TOTAL	60.2 (32.4)	133.83 (144.56)	216.68 (247.78)	255.08 (247.86)		+/	

Table 2. The total mean number (±SD) of each group or species of zooplankton collected from each zone for P. dasicornis.

Taxon	Reef Zones: Reef Crest (CR) n=4	Reef Flat (FL) n=12
Medusae	0.25 (0.5)	0.42 (1.44)
Coral planulae	37.50 (47.87)	153.08 (249.20)
S. enflata	0	0.17 (0.39)
Polychaetes	1.50 (1)	2.67 (2.50)
Bivalves	1.00 (1.4)	0.25 (0.62)
Gastropods	0.50 (0.58)	0.33 (0.88)
A. inermis	1.50 (1.0)	19.17 (43.0)
Oithona spp.	2.25 (0.5)	5.33 (6.0)
Harpacticoids	19.25 (12.10)	28.42 (15.17)
Cumaceans	0.50 (0.58)	7.92 (9.43)
L. dubia	6.25 (3.59) *	41.50 (25.05) *
Amphipods	6.25 (3.30)	7.67 (4.40)
Shrimp larvae	0.75 (0.95)	1.42 (2.61)
Crab larvae	1.00 (0.82)	0.5 (1.24)
Tunicate larvae	0	0
O. diocia	0	0.17 (0.39)
Fish larvae	0	0
TOTAL	41.00 (14.58)	297.83 (277.57)

Table 3. The total mean number (±SD) of each group or species of zooplankton collected from each zone for Montipora verrucosa. Significant Ts values for the Wilcoxin's matched pairs signed ranks test are indicated as follows: * = p < .015.

Taxon	Reef Zones: Reef Front (FR) n=6	Reef Crest (CR) n=6	Reef Flat (FL) n=10	Wilcoxin's Probability Test: FR/CR Mv/Pc	CR/FL Pd/Mv	FR/FL Pd/Pc
Medusae	1.83 (4.02)	0.33 (0.82)	0			
Coral planulae	6.00 (8.2)	0	1.00 (2.8)			
S. enflata	12.50 (15.45)	0	0.20 (0.63)	+/	+/	
Polychaetes	3.50 (2.16)	4.50 (3.83)	1.60 (2.01)			
Bivalves	13.83 (18.70)	0.17 (0.40)	0.80 (1.0)			+/
Gastropods	0.67 (1.21)	0	0			
A. inermis	111.67 (84.92)	45.17 (28.06)	17.20 (21.03)			+/
Oithona spp.	13.50 (10.88)	8.50 (7.94)	5.00 (6.15)			
Harpacticoids	6.00 (8.0)	12.83 (6.79)	30.50 (23.5)		+/	
Cumaceans	2.50 (2.9)	1.67 (2.73)	4.90 (8.5)			
L. dubia	16.17 (20.84)	7.17 (16.09)	11.70 (6.22)			
Amphipods	2.67 (2.73)	4.67 (4.84)	10.70 (16.54)			
Shrimp larvae	3.33 (5.82)	0.67 (1.210	0.90 (1.29)			
Crab larvae	0.67 (1.21)	1.00 (2.0)	4.30 (13.60)			
Tunicate larvae	4.17 (9.72)	0.50 (0.84)	0.90 (1.10)			
O. diocia	13.00 (16.77)	1.17 (2.40)	0.60 (10.7)			+/
Fish larvae	51.00 (124.43)	0.33 (0.82)	0.10 (0.32)			
TOTAL	311.50 (311.50)	88.83 (50.51)	90.20 (62.80)			

Table 4. Total mean number (±SD) of each group or species of zooplankton collected from each zone for P. compressa. Significant Ts values for the Wilcoxon's matched pairs signed ranks test are indicated as follows: + = p<.015.

Taxon	Reef Front (FR) n=7	Reef Crest (CR) n=8	Reef Flat (FL) n=7	Wilcoxin's Probability Test FR/CR	CR/FL	FR/FL
Medusae	0.71 (0.95)	0	0			
Coral planulae	5.57 (10.55)	190.25 (350.19)	0			
S. enflata	1.29 (1.60)	2.88 (6.56)	2.86 (6.34)			
Polychaetes	6.43 (8.88)	2.25 (1.98)	2.57 (2.22)			
Bivalves	3.28 (4.82)	5.75 (10.55)	1.28 (1.99)			
Gastropods	5.14 (8.61)	0.12 (0.35)	0.14 (0.38)			
A. inermis	96.57 (64.20)	20.25 (19.52)	56.14 (46.02)		/+	
Oithona spp.	20.43 (12.92)	9.12 (12.28)	17.14 (24.50)			
Harpacticoids	10.71 (7.18)	21.00 (24.88)	16.14 (11.08)			
Cumaceans	1.14 (1.46)	1.88 (3.09)	4.14 (3.44)			
L. dubia	20.57 (13.28)	20.38 (32.34)	5.43 (5.06)			+/
Amphipods	2.86 (1.95)	3.88 (2.85)	13.57 (16.66)			
Shrimp larvae	1.43 (2.51)	8.38 (13.74)	0.86 (0.90)			
Crab larvae	0	15.25 (41.93)	0.29 (0.49)			
Tunicate larvae	0.29 (0.76)	0.12 (0.35)	0			
O. dioica	4.28 (2.87)	1.00 (1.51)	0			
Fish larvae	0.57 (1.13)	0.12 (0.35)	0			
TOTAL	173.00 (92.59)	300.25 (393.45)	120.43 (72.0)			

more cumaceans ($p<<.001$), amphipods ($p<.005$) and harpacticoids ($p<.01$) than P. compressa.

P. compressa:

More A. inermis than M. verrucosa ($p<.005$) and P. damicornis ($p<.07$), more S. enflata ($p<.004$), bivalves ($p<.005$), and O. diocia ($p<.01$) than P. damicornis.

M. verrucosa:

More tunicates than P. compressa and P. damicornis ($p<<.001$) and more O. diocia than P. damicornis ($p<.01$).

The following significant differences were found within reef zones for each coral species:

P. damicornis:

More L. dubia from the reef flat than the reef crest (standard deviation from mean didn't overlap).

P. compressa:

More A. inermis and cyclopoids (Oithona spp.) from the reef front than the reef crest ($p<.015$), but
more A. inermis from the reef flat than the reef crest ($p<..015$),
more L. dubia on the reef front than the reef flat ($p<.015$).

M. verrucosa:

More S. enflata and bivalves from the reef front than the reef crest ($p<.015$) or reef flat ($p<.015$),
more O. diocia ($p<.015$) and A. inermis ($p<.015$) from the reef front than the reef flat,
more harpacticoids from the reef crest than the reef front ($p<.015$), and
more polychaetes (predominately Ceratonereis tentaculata Kinberg) from the reef crest than the reef flat ($p<.015$).

Discussion

In general, most of the microfaunal species showed no significant association with a given coral species. There was considerable variability throughout the study. Coral planulae of P. damicornis were the most significant resource available to the reef during this study. The size and abundance of P. damicornis planulae were much greater than most of the other groups of animals examined. P. damicornis is represented by two morphological variants with larval release near third quarter of the moon for the first variant and first quarter and full moon for the second variant. At maximum production, several thousand planula per head are released during each complete lunar cycle (Richmond and Jokiel, 1984). An interesting event also occurred, where seven hundred and fifty M. verrucosa planulae emerged from a P. compressa head. These planulae were several days old, suggesting that they may be actively seeking refuge within or under the P. compressa head. Thus, coral planulae in general may play a very significant role in reef energetics as they are not only released several

times throughout the month but can maintain themselves within the reef for several days afterwards.

Other bursts of zooplankton (i.e. fish, crab, and shrimp larvae) were also substantial, however these bursts were more sporadic and variable compared to the planula. Tunicate larvae showed a significant preference for M. verrucosa, which may be more conducive for settlement of colonies than P. damicornis or P. compressa - both noted for aggressive commensal crabs.

P. compressa had the greatest total numbers for most holoplanktonic forms, significantly more of the predominant calanoid, A. inermis. P. compressa is generally a large massive coral, containing more interspace and thus may provide a more protective environment than the other two coral species.

Most groups of animals showed some zonal preference with generally the more holoplanktonic forms (cyclopoids, medusae, O. diocia, bivalves, tunicates) at the reef front and more epibenthic forms (cumaceans, amphipods) at the reef flat. One would expect to find the less active swimmers - the "hoppers" and "skippers" in the shallow quiet back waters. Cumaceans and amphipods were abundant in the sand (Table 1), also more characteristic of reef flat areas. A. inermis and L. dubia, two predominant groups of zooplankton, were ubiquitous over the entire reef and also found in sand, especially L. dubia (Table 1).

Most of the groups examined showed similar zonal preferences compared to a demersal study in Australia (Alldredge and King, 1977). The one exception was the greater abundance of harpacticoids in the reef flat in this study as opposed to the reef front in Australia. Several taxa were represented in significant numbers only in Australia (ostracods, mysids) or only in Hawaii (tunicates, S. enflata, O. diocia and coral planula). This is probably the result of different sampling periods (January in Australia, May - July in Hawaii) and geographical and physical differences of reefs.

Conclusions

Coral planula were the most significant energy source available to the reef during this study. Other taxon were either smaller in size or less abundant with greater variability in their availability to the reef. Only coral planula and tunicate larvae were significantly species specific. Other taxa were generally variable in abundance between coral species but found on all coral species as well as in the sand. Several differences in abundance of animals between coral species were caused by zonal difference rather than the coral itself, with holoplanktonic forms generally at the reef face and epibenthic forms at the back reef.

One cannot overemphasize the tremendous variability inherent to the reef community and the importance of each entity of it, especially the coral species themselves.

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Appendix

Table 1. Microfauna collected from *Pocillopora damicornis* substrate.

Month	June												July				
Day	03	03	05	05	25	25	29	29	30	30	12	12	15	15	17	24	24
Taxon																	
Coral planulae	32	42	2		105	375	850	80	77	279			100	50			
S. enflata			1				†										
Polychaetes			1	1	7	5	4	1		1	1	3	2	2	6	2	
Bivalves	2			1									3	1			
Gastropods	3	1											1			1	
A. inermis	16	5	10	1	16	18		6		4	154		1	3	4	1	1
Oithona spp.	3	5	2	4	8		20	3	14	3	1	1	3	2	4	2	2
Harpacticoids	26	26	16	8	21	41	8	34	50	47	47	17	15	33	55	10	19
Mysids			5													1	
Cumaceans	10	4		4	4	4	3	8	13	1	35	2	1		5	1	
L. dubia	85	31	32	10	76	28	39	64	71	50	56	20	8	7	21	1	9
Amphipods	9	3	4	1	11	15	7	13	7	3	9	9	8	10	6	3	4
Shrimp larvae		2	2	3	9						1		1	1	2		2
Crab larvae		4			2								1		1	2	
Tunicate larvae				3													
O. dioica		1	1						1								
Fish larvae											1						
Miscellaneous			1										1				
TOTAL	186	124	77	36	259	486	932	209	233	383	305	52	197	109	213	24	37

Appendix

Table 2. Microfauna collected from *Porites compressa* substrate.

	May				June										July						
	28	28	01	01	06	06	15	15	23	25	25	30	30	08	08	15	15	17	19	19	22	22
TAXON																						
Coral planulae																						
S. enflata								7								745	770			1	28	10
	17		1				3					1	3	1	19		2		1			4
Polychaetes	6	3		3	1	2		5	1	2	1	2	1	3		5	1	6	3	1	26	1
Bivalves			2			2	5	2				1				16	28		1		6	13
Gastropods								1				1	4			1			1		24	
A. inermis	64	73	48	33	90		36	65	15			44	170	18	46	9	5	4	20	265	76	152
Oithona spp.	12	72	4	1	3	2	12	11	7	5	2	9	39	8	39	2	1	8	11	28	14	34
Harpacticoids	24	35	18	17	11	4	9	14	19	25	4	4	6	5	10	80	9	24	7	6	12	16
Mysids													2								2	
Cumaceans	4	8		1		1	2	5		4				2	9			4	1	1	2	
L. dubia	3	9	7	3			14	1			2	19	43	92	44	14	4	23	6	11	32	10
Amphipods	49	14	5	2	3		12	3			1	4	4	7		5	3	6		1	1	1
Shrimp larvae	2	1	1	1				2			1	1		20		6	38	1	1		7	
Crab larvae		1		1				2								2	119					
Tunicate larvae													2			1						
O. diocia		8										2	7		2		2		6	2	6	7
Fish larvae		1										1	3									
Miscellaneous		2					2	3				1					1	1	2	1		
TOTAL	164	235	88	153	158	11	92	117	166	43	11	90	284	156	169	886	983	77	60	318	236	270

Appendix

Table 3. Microfauna collected from *Montipora verrucosa* substrate.

Taxon	May 28	May 28	June 01	June 01	June 03	June 03	June 15	June 15	June 23	June 25	June 30	June 30	July 02	July 02	July 12	July 12	July 17	July 19	July 19	July 21	July 21	July 24	July 24
Coral Planulae												2						21	21	10	1	9	1
S. enflata			1						5					9				1	26	37	2	2	
Polychaetes	4	6	6	11	2		1	1		6	5	3	5	6			2	2		4	4	2	
Bivalves	1		1			1		1	2				22			1	1	3	48	10			
Gastropods																			3	1			
A. inermis	30	60	12	75	32	50	5	7	14	1	22	80	135	88		46	7	14	98	265	70	1	2
Oithona spp.	2	4	2	14	2	20	13	2	19	6	1	12	26			2	4	10	5	24	18	4	
Harpacticoids	15	87	24	16	13	7	39	13	46	3	12	5	22	2	4	34	21	6	3		3	25	21
Mysids												2						1			10		
Cumaceans	1	27	2	7		1	2		1				6		1	12	3	6			3	2	
L. dubia	6	5		1	1	1	13	14	6			40	52	4	9	12	9	30			11	18	25
Amphipods		54	1	14	5	4	7	5	1		1	3	6	6	5	23	3			2	2	7	2
Shrimp larvae	3	2	1	3					3	10			1	3		1		1		15			
Crab larvae		1	5							3								3		1			43
Tunicate larvae		2	1			2	2	3		1	2				1				24		1		1
Q. diocia	6			1									1	1			2	4	32	37	3	3	1
Fish larvae		2																1		305			1
Miscellaneous								1					1					2	1				
TOTAL	62	245	51	156	55	85	83	47	93	34	42	153	277	119	20	131	52	103	261	711	128	73	97

Appendix

Table 4. Microfauna collected from sand substrate.

Day	July 5	5	6	6	8	8
Taxon						
Medusae						
Coral planulae						
S. inflata					1	5
Polychaetes	3	1			3	2
Bivalves						4
Gastropods	1					
A. longiris	6	1	23	20	2	18
Oithona spp.	5	1	2	2	15	8
Harpacticoids	5	9	1	11	3	12
Mysids						1
Cumaceans	2	1	6	1	4	5
L. dubia	5	36	4		75	17
Amphipods	4	2	3	1	9	11
Shrimp larvae					1	1
Crab larvae						1
Tunicate larvae						
O. diocia						2
Fish larvae						
Miscellaneous	5					
TOTAL	36	51	39	35	113	87

A preliminary study on the emergence patterns of microfauna in Kaneohe Bay, Hawaii.

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Abstract

Emergent microfauna were collected over two Porites compressa heads and two Montipora verrucosa plates on a fringing reef adjacent to Coconut Island, Oahu, Hawaii, during full moon (July 24-25) and new moon (August 8-9) 1983. Four demersal traps (.25 m², 0.25 mm mesh) were sampled over a 27 h period at approximately 30 min intervals during crepuscular periods and 3 h intervals the remaining periods. A final 48 h sample was collected to determine the efficiency of this collecting method.

The total number of microfauna represented mainly by the calanoid Acrocalanus inermis (48% of total microfauna) were generally available to the reef at any time interval, however they were emerging at the greatest rates at dusk, (78/trap/h) and dawn (69/trap/h) crepuscular periods, with a maximum of 165/trap/h. The predominant and most effectively captured microfauna were holoplanktonic (A. inermis, Oithona simplex, O. nana, Sagitta enflata, Oikopleura dioica, and medusa). O. simplex showed a strong dusk crepuscular emergence, independent of the day or the coral. The total number of microfauna emerging from each coral species on each day did not differ. However specific groups emerged in greater numbers over P. compressa heads (harpacticoids, Leptocheliа dubia , crab zoea, tunicates, mysids, and P. compressa eggs), during new moon (harpacticoids, L. dubia, amphipods, shrimp larvae, protozoans and mysids), and during full moon (S. enflata, bivalves, gastropods, crab larvae, and P. compressa eggs). Several epibenthic microfauna (harpacticoids, L. dubia, amphipods, polychaetes) were neither significantly depleted or effectively trapped.

Introduction

Microfauna associated with live corals are an inherent component of and a potential energy source for the reef community, yet little is known about their availability to the reef community, especially for different species of coral. An examination of diel emergence would further the understanding of their ecological significance.

The microfauna are comprised of four groups: (1) holoplankton, (2) meroplankton (released by the coral itself as sex products or by macrofauna; e.g. symbionic crabs and sbrimps); (3) epifauna, and (4) benthic fauna. Presently, no available collection trap can quantitatively account for all four of these groups. This study will examine which groups can be quantified using the trap design of Hobson and Chess (1978) as modified by Birkeland and Smalley (1981).

The main objective of this study was to examine the emergence of the total microfauna 1 meter above two species of coral heads at given time intervals and thus, to determine when microfauna associated with these corals are available to the reef community.

Materials and Methods

The four demersal traps (0 .25 m², 0.25 mm mesh), were identical to the traps described by Birkeland and Smalley (1981) as modified from Hobson and Chess (1978). These were placed over two Montipora verrucosa and two Porites compressa heads. The same pairs of corals were used each day. The M. verrucosa plates were at 7.0 m depth (M-1) and 7.05 m depth (M-2), the surface area sampled was approximately equal to the dimensions of the traps (50 cm X 50 cm) since the traps were set on top of each plate. Bungie cords were used to wrap the skirts of each trap underneath the plate. The P. compressa heads were at 6.8 m depth (P-1) and 7.2 m depth (P-2). The heads had dimensions of 47 cm X 32 cm X 13 cm

Table 2 shows the species or groups of animals that were significantly depleted in numbers from a coral species or not adequately sampled by the exchange bottles. A species was categorized as depleted from a coral head (YES) if less than 5% of the total number were collected 24 h after the final sampling (1600 h). The trap was categorized as effective (YES) if less than 5% of the total number of a group or species collected 24 h after the final sampling (1600 h) was found within the inner portion of the trap. The number in parenthesis is the frequency of Yes (>5%) or No (<5%). A total frequency less than 8 (the total number of samples) occurred when no animals were collected during the 48 h period for a particular coral head. Simple probability was used to test for significance. The chance of getting more or less in the exchange bottle or within the net 24 h after the main study is 0.5 and the maximum frequency is 8 (e.g. $(0.5)^8 = .004$). Therefore: +++ = $p>.004$, ++ = $p>.008$, and + = $p>.016$. The results of this test for each group or species of zooplankter are as follows:

The medusae and S. conflata were both effectively captured but not significantly depleted.

Shrimp larvae, tunicate larvae, and A. inermis were also not significantly depleted but tended to be effectively collected.

P. compressa planulae and eggs were effectively collected and tended to be depleted.

Oithona simplex and Oikopleura dioica were effectively collected and significantly depleted. Fish larvae were effectively trapped and tended to be depleted.

Gastropods tended to be effectively trapped and were significantly depleted. The emergence patterns for harpacticoids amphipods, Leptocheliа dubia, polychaetes, and cumaceans must be considered only qualitatively since they were not effectively collected. Harpacticoid copepods, amphipods, and L. dubia were neither significantly depleted or effectively trapped.

Polychaetes were not effectively trapped and tended to be depleted.

Cumaceans were not effectively trapped. The emergence patterns for these groups must be considered only qualitatively since they were not effectively collected.

B. Experimental Results

Emergence patterns for the total zooplankton indicate no significant difference between corals (P. compressa and M. verrucosa) or between days (new moon and full moon). This largely reflects the emergence pattern for A. inermis, which represents 48% of of the total zooplankton collected (Table 3). The only significant variation in the abundance of the total zooplankton collected at any time interval was between the initial collection (1300-1700) and between (0500-0530). The variance of the mean abundance does not overlap. However, the rate of emergence (no. per hour) is greatest during the crepuscular periods (1900-2100 and 0430-0630).

For individual species, the Wilcoxon's matched pairs signed ranks test (Sokal and Rohlf, 1969) was used to test the null hypothesis that the mean abundance of a given species of zooplankton emerging at a specific time interval was equal to the mean abundance of that same species emerging at the same specific time regardless of the coral species or day.

Paired comparisons were done for each species or group of zooplankton between corals within days and between days within corals. No significant difference was found between corals within days, so the corals were lumped to compare days and the days were lumped to compare corals.

Based on these tests, the individual species were grouped into the following four categories of species emergence 1) independent of coral or day, 2) independent of day and dependent upon coral, 3) independent of coral and dependent on day, and 4) dependent on coral and day.

(P-1) and 48 cm X 30 cm X 15 cm (P-2). The traps completely covered each Porites head, with weights completely surrounding the skirts.

The following method was used to test for any initial contamination while bringing the traps through the water column to the bottom. Four traps were sequentially brought to the bottom. Each trap was carried in a vertical position (to avoid contamination) and secured to the bottom. The plug was removed and replaced within a one minute period. The trap was brought to the surface, rinsed throughly four times and the sample preserved. This sampling was conducted from 1300-1400 h during the new moon.

The traps were initially set at 1300 h and sampled at approximately 3 h intervals thereafter. During 1900-2100 h and 0430-0630 h the traps were sampled at 30 min intervals. At the end of the 24 h sampling periods, the traps were left another 24 h period and then retrieved. The contents within each sampling cod end alone and the contents within each trap were collected.

To minimize contamination, the cod end was replaced by removing it from the trap while a plug was quickly placed into the trap opening and the cod end was screwed closed with a fitted cap. This was done simultaneously to avoid loss. The cod end was brought to the surface where on the boat, the sample was placed in 4% formalin solution after 4 rinses of the cod end. The cod end was then sealed and returned to the trap. At night, pairs of divers collected samples, using a small night light to locate the traps. The lights were faced away from the trap during collection. Each diver reported approximate fish counts near traps during the 1900-2100 and 0430-0630 collections. Total numbers of zooplankters were counted and identified as to species or major groups for each sample.

Results

A. Methodology

Table 1 summarizes the total numbers and groups or species of animals collected during the control experiments that tested for the capture efficiency. Initial contamination may represent animals trapped under or around the trap as it was passing through the water column, and also animals actively emerging or just moving over the coral during the time of this test (1300-1400) which were trapped during the 30 sec time interval when the plug was removed and replaced. No significant difference (all variances from the mean for each group or species overlapped) was found between the sand and the P. compressa heads. Acrocalanus inermis and Oithona nana were collected in larger numbers than other zooplankters; both are predominant species at the study site. The significantly greater initial abundance of A. inermis during the study may be partially a result of this contamination.

Table 1. Total numbers of animals collected from coral heads vs. sand and the mean and standard deviation for similar substrates.

	Sand	Sand	Mean	P. compressa	P. compressa	Mean
A. inermis	14	24	19.0±7.07	37	2	19.5±14.48
Oikopleura diocia	2	2	2.0±0	4	1	2.5±2.12
Oithona nana	5	18	11.5±9.19	12	10	11.0±1.4
Cumaceans	1	6	3.5±3.5	1	0	0.5±0.7
Leptocbelia dubia	0	5	2.5±3.5	3	1	2.0±1.4
Amphipods	0	1	0.5±0.7	2	0	1.0±1.4
Polychaetes	0	0	0	1	0	0.5±0.7

Cumaceans and tanaids were collected over both substrates, especially over sand. The higher abundance of these two groups (and probably amphipods also) over P. compressa may be a result of their high abundance in sand immediately surrounding the P. compressa, while the M. verrucosa are shelf-like plates suspended off the sandy bottom.

Table 2. The effective capture of each group or species of zooplankton over each coral head during the 24 h period.

Taxon	Depleted			Effective Collection		
	No	Yes	P	No	Yes	P
Protozoans	0	4		2	2	
Medusae	8	0	+++	0	8	++
Coral planulae	5	2		1	6	
S. enflata	6	2	+	1	6	
Polychaetes	5	2		8	0	++
Bivalves	5	3		4	4	
Gastropods	1	6	+	2	5	
A. inermis	6	2	+	4	4	
Oithona nana	4	4		5	3	
O. similis	0	8	+++	0	8	++
Harpacticoids	6	1	+	6	0	
Mysids	8	1		4	4	
Cumaceans	0	1		5	0	
Leptochelia dubia	6	2	+	6	2	
Amphipods	8	0	+++	6	1	
Shrimp larvae	7	1	++	5	3	
Crab larvae	2	3		2	3	
Tunicate larvae	7	1	++	4	3	
O. dioica	1	7	++	1	7	+
Fish larvae						

\+ p>.016
++ p>.008
+++ p>0.004

Differences in emergence intervals for species within each category will be described as significant only if the standard deviation from the mean doesn't overlap with any other time interval. Table 4 represents the emergence rates for the significant groups of animals emerging during each time interval for each day and each coral.

Apparent trends in the data are as follows:

1. Emergence independent of coral or day (Tables 3, 4).

A. inermis emerged in greater numbers initially (1300-1600) and during the crepuscular periods (1900-2100, 0430-0630). The dawn (0430-0630) crepuscular emergence was significantly greater than emergence during the day (0700-0400), but not significantly greater than late afternoon through the night (1600-0430).

O. nana emerged in significantly greater number during the crespuscular periods than in morning daylight (0700-1300).

O. simplex emerged in significantly greater numbers at dusk (1900-2100).

Medusae - emerged in significantly greater numbers at the dusk crepuscular period than in the late morning through the afternoon (0900-1600).

Polychaetes - with the exception of one species, (which abruptly emerged at dawn crepuscular (0400-0500) on full moon over one M. verrucosa head, all the polychaetes emerged in significantly greater numbers during the dusk crepuscular period.

Fish larvae - emerged randomly throughout the study.

2. Emergence independent of coral and dependent upon the day.

Amphipods - emerged in significantly greater numbers (Ts=0) during new moon. Significantly more emerged at dawn crepuscular (0430-0530) during new moon over P. compressa.

Shrimp larvae - emerged in significantly greater numbers during new moon. No significant difference in emergence between time intervals was found. Although 94% of the total number emerged at night.

Bivalve larvae - emerged in significantly greater numbers during full moon, especially over P. compressa. No significant increase in emergence occurred between time intervals.

Protozoans - emerged in significantly greater numbers during new moon. Most of the emergence occurred at dusk crepuscular (89% of total abundance).

3. Emergence dependent on the coral and independent of day (Tables 3, 4).

O. diocia - emerged in significantly greater numbers over M. verrucosa during new moon. Emergence occurred randomly throughout the study.

Sagitta enflata - emerged in significantly greater numbers over P. compressa during full moon. No significant difference in the number emerging between days over M. verrucosa was found, however more (75% of total) emerged from M. verrucosa of which significantly more (40% of total) emerged from 2100-0430.

4. Emergence dependent upon the coral and the day (Tables 3, 4).

Harpacticoidcopepods - emerged in significantly (Ts=8) greater number (87% of the total number) during new moon for both the coral species, of which significantly more (Ts=0) emerged over P. compressa (75% of the total number). Emergence was random throughout the study.

Leptochelia dubia emerged in significantly (Ts=0) greater numbers (77% of the total number) during new moon for both coral species, of which significantly, more (ts=15.5) emerged over P. compressa (84% of total number). Emergence was random throughout the study.

Table 4. The total mean emergence rate (no./.06 m^2/h) (±SD) of each taxon during both moon phases over both coral species for the five major sampling periods. (n = number of samples during that sampling period).

	1300-1900 (n=2)	1900-2100 (n=4)	2100-0430 (n=2)	0430-0630 (n=4)	0630-1600 (n=3)
Protozoans		.27(.73)			
Medusa	.41(.34)	1.03(.39)	.16(.15)	.75(.48)	.24(.22)
Coral eggs and planula	.02(.04)	.03(.09)	.01(.02)	.97(2.36)	.37(.65)
Sagitta enflata	.45(.26)	.84(.92)	1.15(1.92)	2.28(1.80)	.36(.41)
Polychaetes	.02(.04)	.65(.64)	.15(.28)	.12(.35)	.01(.02)
Bivalves	.54(.36)	1.53(1.69)	.13(.07)	.69(.53)	.13(.17)
Gastropods	.08(.14)	.16(.24)		.06(.18)	.05(.08)
Acrocalanus inermis	7.21(5.40)	13.38(5.81)	4.06(2.71)	12.62(4.85)	2.94(.82)
Calanoid sp.		.03(.09)	.32(.47)	1.81(3.07)	.16(.41)
Oithona nana	.98(.65)	4.41(3.06)	.76(.56)	4.90(2.94)	.86(.52)
O. similis	.06(.59)	9.44(3.95)	.71(.60)	4.16(3.00)	.48(.50)
Harpacticoids	.26(.33)	1.50(1.76)	.55(1.10)	1.34(2.92)	.53(.50)
Mysids	.06(.12)	.06(.18)	.02(.04)		
Leptochelia dubia	.04(.08)	.25(.36)	.94(.23)	.97(2.54)	.08(.20)
Amphipods	.95(.21)	.13(.19)	.08(.06)	.28(.43)	
Shrimp larvae		.72(1.32)	.26(.46)	.38(.65)	.02(.06)
Crab larvae		1.94(5.48)	.42(1.12)	.28(.80)	
Tunicate larvae sp. A	.01(.03)	.03(.09)	.20(.50)	1.38(1.92)	.16(.13)
Tunicate larvae sp. B	.02(.04)				.12(.21)
Oikopleura diocia	.71(.61)	.88(.42)	.26(.21)	1.84(.76)	.66(.50)
Fish larvae	.01(.03)	.04(.09)	.01(.02)		.01(.02)
TOTAL	12.18(5.14)	36.03(13.99)	9.97(2.27)	38.60(10.94)	7.29(2.02)

Table 3. The total mean number (n=30) of zooplankton emerging per .06 m² (±SD) throughout the two 24 h periods. The tx values for the probability that the two treatments: coral (Ts coral) and day (Ts day) were significantly different was determined with the Wilcoxon's matched pairs signed ranks test (t..005<15> = 15, t.01<15> = 19, t.025<15> = 25, if t≥ 25, then nonsignificant (ns).

		New Moon			Full Moon		
Ts coral	Ts day	Porites compressa	Montipora verrucosa	mean	Porites compressa	Montipora verrucosa	mean
Medusae							
ns	13	.55(.58)	.90(.80)	.70(.85)	.55(1.1)	.40(.55)	.55(1.1)
Coral Planulae							
0	0	.35(.58)	0	.15(.66)	1.3(3.2)	.05(.10)	.65(2.3)
S. enflata							
15	7	.40(.60)	1.1(1.5)	.70(1.7)	.95(1.1)	3.0(6.0)	2.0(4.2)
Polychaetes							
ns	12	.30(.50)	.15(.25)	.20(.40)	.30(1.0)	.10(.20)	.20(.70)
Bivalves							
ns	12	.55(.75)	.45(.70)	.50(.70)	.95(1.8)	.75(.85)	.85(1.0)
Gastropods							
11	0	0	.15(.35)	.10(.25)	.45(.95)	.20(.45)	.30(.75)
A. inermis							
ns	ns	13(18)	12(12)	13(15)	8(6)	10(9)	9(8)
Oithona nana							
ns	ns	2.0(1.3)	2.1(1.6)	2.0(1.5)	4.1(4.3)	5.5(11)	4.5(8)
O. simplex							
ns	ns	2.0(2.6)	2.1(2.0)	2.1(2.2)	3.1(4.2)	4.0(3.5)	3.5(3.8)
Harpacticoids							
8	0	1.9(2.3)	1.8(1.6)	1.3(2.1)	.25(.40)	.10(.30)	.20(.35)
Mysids							
0	0	.20(.35)	.05(.10)	.10(.30)	0	0	0
Leptochelia dubia							
0	19	.95(1.6)	.05(.20)	.50(1.2)	.15(.40)	.10(.20)	.10(.30)
Amphipods							
ns	4	.25(.40)	.20(.65)	.20(.55)	.05(.15)	.05(.10)	.05(.30)
Shrimp larvae							
ns	13	.60(1.3)	.45(1.3)	.75(2.3)	.10(.40)	.05(.10)	.05(.30
Crab larvae							
0	0	.05(.10)	0	.05(.05)	1.9(5.3)	.15(.60)	1.1(3.8)
Tunicate							
ns	24	.30(1.6)	1.0(2.6)	.65(2.0)	.15(.35)	.10(.25)	.15(.30)
O. diocia							
7	ns	.95(2.6)	1.6(2.4)	1.1(1.9)	1.5(1.9)	1.7(2.2)	1.7(1.9)
Fish larvae							
15	ns	.05(.15)	.05(.15)	.05(.15)	.05(.10)	.05(.20)	.05(.20)
Protozoans		.40(2.0)	.50(2.2)	.50(2.1)			
TOTAL		26(19)	25(18)	25(18)	17(10)	29(16)	23(13)

P. compressa planula and eggs - emerged in significantly (Ts=0) greater numbers (79% of total number) during full moon. Most of the emergence (97%) occurred during sunlight periods (0600-1600).

Crab larvae - emerged in significantly (Ts=0) greater numbers during full moon (98% of total number) for both coral species. Significantly (Ts=0) more (92% of total number) emerged over P. compressa. Most of the emergence (91% occurred during the night (2000-0500) over one P. compressa head.

Gastropod larvae - emerged in significantly (Ts=11) more numbers (68%) over P. compressa during full moon. Most of the emergence (59%) occurred at night.

Mysid sp. - emerged only during new moon (Ts=0) with significantly more (85%) of total) emerging over P. compressa. Emergence was random throughout the study.

Tunicate sp. A. - emerged significantly (Ts=0) more (88% of total number) during new moon over P. compressa. Most of the emergence (85%) occurred from 0500-0700.

Tunicate sp. B. - emerged only over P. compressa in significantly (Ts=0) greater numbers (95% of the total) in the late morning through afternoon (1030-1600), during new moon (81% of total).

Discussion

A. Methodology

The predominant and most effectively captured microfauna collected during this study were 'holoplanktonic' species (A. inermis, O. nana, O. simplex, S. enflata, O. diocia). In a similar study done in the Philippines (Walter and Pasamonte, 1981), great numbers of 'holoplanktonic' calanoids (Calanopia and Acartia) were also collected. They concluded that holoplankters have a wider range of habitat and are not contaminants. My results support their conclusions.

The frequency of bottle exchange during this study may be criticized as a potential source of contamination by holoplanktonic forms into the trap or bottle. No method was used to quantify loss or gain of animals during the exchange of bottles. The height of the traps (92 cm) may be too great to capture certain groups of plankton. Alldredge and King (1980) found a significant decrease in the number of amphipods and polychaetes captured in traps 63 cm above the substrate compared to 5 cm above the substrate. Thus, several epibenthic forms of microfauna may not emerge very far from the substrate and should not be quantitatively studied using this trap design.

Emergence Patterns. Most of the emergence patterns were dependent upon the coral or the day. Only one species (O. simplex) and one group (polychaetes) showed significantly greater emergence at dusk regardless of the coral or day. Polychaetes showed a similar strong dusk emergence in another study (Alldredge and King, 1980).

More species or groups of microfauna emerged over P. compressa (tunicates, mysids, gastropods, crab larvae, L. dubia, harpacticoids and P. compressa planulae and eggs) than over M. verrucosa (O. diocia). The P. compressa is structurally more complex and was closer to the sandy substrate. The greater abundance of epibenthic fauna (Leptochelia dubia, harpacticoids, mysids) may be caused by emergence of these groups from the sands. Some of the adult or larval forms may also seek shelter within P. compressa because it has more available interstices than M. verrucosa. Porites planula and eggs may provide an energy source for some of these animals as well. The significant depletion and capture of O. diocia suggests that it may be a more transient species, temporarily hovering over M. verrucosa. The physical effect of wash up of deep channel organisms onto shallow coral may be a physical phenomenon rather than biological.

B. Experimental

1. Emergence on new moon. Certain groups of microfauna (shrimp larvae, amphipods, L. dubia, harpacticoids, protozoans and mysids) emerged in significantly greater numbers during new moon. Since most of these relatively large crustaceans

emerged at night, they may be avoiding moonlight. Intensive predation by visually orientated diurnal predators (e.g. reef fish) has been considered a selective pressure resulting in vertical migration of zooplankton (reviewed, Alldredge and King, 1980). Based on this supposition, a qualitative estimate of fish activity was made during each crepuscular period, a period of higher fish activity (Hobson and Chess, 1978). Visual estimates showed that greater fish activity occurred during full moon than new moon with peak fish activity at 1930 and 0423 during new moon and 1900-2000 and 0500-0600 during full moon. Therefore, qualitatively, the rate and duration of fish activity was greater during full moon. Thus, it would be selectively advantageous to emerge on moonless night to avoid predation, especially for larger, less mobile groups (cumaceans, tanaids, amphipods).

Tunicate larvae and O. diocia also emerged in significantly greater numbers during new moon, but during the day. These more transparent group and species may be less susceptable to predation during the day.

2. Emergence during full moon. In general, the microfauna that emerged in significantly greater numbers during full moon (gastropods, bivalves, crab larvae, P. compressa eggs and S. enflata) or emerged in significantly greater numbers at dusk crepuscular periods regardless of the moon phase (O. simplex, polychaetes, and medusae) were not of epibenthic forms. Most were small sized (O. simplex, bivalves, gastropods, and P. compressa planulae and eggs) or transparent (S. enflata and medusae) species. Thus, visually orientated predators would have difficulty focusing in on these potential prey. Two larger sized, more opaque groups (polychaetes and crab larvae) had greater dusk emergence, which was probably a result of spawning activity; where gamete exchange by the polychaetes is more essential than predator avoidance. The crab larvae may also be abundant because of an adult breeding cycle. P. compressa planulae and eggs, a potential food source for many marine organisms, emerged in greater numbers throughout the daylight period. None were present during the crepuscular periods. S. enflata also had significant emergence during 2100-0430, rather than crepuscular emergence. In Guam, a significant early morning (0200-0300) abundance of S. enflata near the surface was also observed during four diurnal studies (Hillmann - Kitalong, M.S. Thesis).

The fact that S. enflata and the medusa were effectively captured but not depleted suggests that these species may be regularly migrating from the coral head. This is certainly true for P. compressa planulae and eggs. Cubo medusa were directly observed emerging in great numbers from underneath and within coral heads during a two hour interval on full moon, which suggests that the coral heads may act as a refuge during the day (personal observation, 1981). The mean length of S. enflata was 0.364 ± 0.15 for full moon, and the adults were 0.70 - 1.00 cm long. Thus, this predominantly juvenile population may also be seeking refuge under or within the coral heads and migrating up during periods of less predation.

Interactions. Interactions between groups or species of microfauna not apparent from the samples. The guts of both potential predators: medusae, and S. enflata, were empty. However, some of the emergence patterns discussed may be affected by interactions with fauna outside the trap that may be reentering the coral, or predators surrounding the corals. A trap design with both a reentry and an emergence opening and direct observations in the field or laboratory (or at least large sized groups) would enhance our understanding of these possible interactions.

Conclusion

The total microfauna, represented mainly by the calanoid A. inermis, are generally available to the reef community at any time interval, however, they are emerging at greater rates during the crepuscular periods. The species or group of microfauna most available are 'holoplanktonic species'. Although many groups or species of microfauna emerged in greater numbers over P. compressa during new moon, these species represented a small proportion of the total microfauna. O. simplex was the only predominant group exhibiting a strong dusk crepuscular emergence regardless of coral or day. The emergence of medusa and S. enflata suggest a broader habitat for these two species than previously thought. The emergence of P. compressa planulae and eggs may be an important energy source available to the community in larger quantities especially during seasonal spawning peaks.

The more epibenthic species or groups were inadequately sampled with the exchange bottles. These species may not emerge high enough into the water column. Thus, the design of a trap has a significant affect on the types of microfauna collected.

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Glutamine synthetase activity in the symbiotic dinoflagellate *Symbiodinium microadriaticum*

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Abstract

Few studies on the nitrogen metabolism of coral-zooxanthellae symbioses have examined the zooxanthellar enzymes involved. The purpose of this study was to examine the activity of the ammonium assimilating enzyme glutamine synthetase in freshly isolated and cultured zooxanthellae. Glutamine synthetase activity was found in both freshly isolated *Pocillopora damicornis* zooxanthellae and cultured *Zoanthus* zooxanthellae. Attempts to determine the Km for ammonium for glutamine synthetase were unsuccessful. The addition of methionine sulfoximine, an irreversible inhibitor of glutamine synthetase, to chamber incubations of intact *P. damicornis* symbioses completely inhibited the uptake of ammonium by the symbiosis and resulted in the excretion of ammonium into the medium by the coral. These results indicate the enzyme glutamine synthetase plays an important role in the nitrogen metabolism of coral-algal symbioses.

Introduction

Most studies on the nitrogen metabolism of coral-zooxanthellae symbioses focus on the uptake of exogenous inorganic nitrogen by the symbiotic association (Kawaguti, 1953; Franzisket, 1973; D'Elia and Webb, 1977; Muscatine and D'Elia, 1978; Webb and Wiebe, 1978; and Muscatine et al., 1979). D'Elia and co-workers (D'Elia and Webb, 1977; D'Elia et al., 1983; and Domotor and D'Elia, in press) studied in detail the kinetics of nitrate and ammonium uptake from seawater by freshly isolated zooxanthellae, cultured zooxanthellae and intact coral-zooxanthellae symbioses. They showed that the nutrient uptake kinetics of freshly isolated and cultured zooxanthellae are similar to those of free living marine phytoplankton, and follow Michaelis-Menten kinetics. Uptake by intact coral symbioses, however, is best described by a modified Michaelis-Menten expression with an additional term representing a diffusive component of the uptake process.

In addition to the uptake of nutrients from seawater, it has been proposed that nitrogenous waste from the coral host may provide a second route by which zooxanthellae obtain nitrogen. Yonge and Nicholls first suggested in 1931 that zooxanthellae take up ammonium waste products from the coral. Lewis and Smith (1971) proposed that the zooanthellae convert this ammonium into amino acids which are then translocated to the coral host. ^{14}C labelling experiments with isolated zooxanthellae and intact coral-zooxanthellae symbioses show alanine is the amino acid translocated to the coral host and preincubation of corals with 5 mM ammonium increases the fraction of alanine translocated (Lewis and Smith, 1971).

Less attention has been given to the zooxanthellar enzymes involved in the assimilation of inorganic nitrogen. Crossland and Barnes (1977) reported high activities of nitrite reductase and glutamate dehydrogenase and low but consistent nitrate reductase activity in zooxanthellae isolated from two Australian reef corals. Using ^{15}N- labelled ammonium chloride, sodium nitrate and urea, Summons and Osmond (1981) were able to demonstrate incorporation of ^{15}N into the amino acid pool of isolated zooxanthellae. They also found that the pathway of this incorporation was via the enzymes glutamine synthetase (GS) and glutamate synthase (GOGAT).

Presented in this paper are the first measurements of the activity of glutamine synthetase in zooxanthellae freshly isolated from *Pocillopora damicornis* and in zooxanthellae cultured from the Caribbean zoanthid *Zoanthus sp.*, and the effect of an irreversible inhibitor of glutamine synthetase, methionine sulfoximine (Ronzio et al., 1969; and Tate and Meister, 1973), on ammonium uptake by intact coral heads are also reported.

Materials and Methods

Culture of Zooxanthellae

Zooxanthellae isolated from the Caribbean zoanthid Zoanthus sp. were maintained in 150 ml batch cultures bubbled with air. Air-bubbling prevented the zooxanthellae from growing in sheets adhering to the glass walls of the culture containers and results in thick homogenous cell suspensions. Cells were grown in 0.22 micron Millipore filtered 33‰ artificial seawater enriched with Provasoli's ES-I media with sodium nitrate as the sole nitrogen source (Provasoli, 1968). Cultures were maintained in an Environator growth chamber at 27°C with 75 μEm^{-2} s^{-1} illumination provided by GE cool white fluorescent lights on a 12:12 h light:dark cycle. Light intensities were measured with a Biospherical Quantum Irradiance Meter (San Diego, Ca.).

Isolation of Zooxanthellae

Colonies of Pocillopora damicornis were collected just prior to use from the south fringing reef of Coconut Island, Hawaii in 1-2 m of water. Coral heads were cleaned of commensal crabs and gently rinsed with 0.45 micron Millipore filtered seawater (MFSW). The coral tissue and zooxanthellae were stripped from the corallum using the Water Pik method (Johannes and Wiebe, 1970) and filtered through 2 layers of surgical guaze and then through a layer of 20 micron Nitex screening. The resulting coral-zooxanthellae suspension was centrifugally washed (1000 rpm for 3 min in an IEC International Portable Refrigerated Centrifuge PR-2) 8-10 times with 0.45 micron MFSW. Prior to assay for glutamine synthetase activity, freshly isolated zooxanthellae or cultured Zoanthus zooxanthellae were centrifugally washed (1000 rpm for 3 min) 3 times in a 0.3 M sucrose and 1 mM Hepes, pH 7.8, solution and resuspended in the same solution to a concentration of approximately 3 μg Chl a ml^{-1}.

Glutamine Synthetase Assay

Whole cell glutamine activity was determined using the biosynthetic radioactive assay modified from Prusiner and Milner (1970) which follows the conversion of ^{14}C-glutamate plus ammonium to ^{14}C-glutamine. Zooxanthellae and water controls were incubated with 50 mM glutamate; 100 mM magnesium chloride; 20 mM ATP; 1.0% Nonidet P 40, a cell permeabilizing agent; 10 mM ammonium chloride; and 0.18 μCi of L-(U-^{14}C)-glutamate (in Hawaii : ICN Pharmaceuticals, Inc., Irvine, Ca. and at The Pennsylvania State University (PSU): New England Nuclear, Boston, Ma.) for 10 min at 27° C. The reaction was stopped by the addition of 2.0 ml ice-cold water and the reaction mixtures were placed on Dowex 1 x 8 Cl^- form (Sigma Chemical Co., St. Louis, Mo.) ion exchange columns. The eluant was collected and after the addition of 10 ml scintillation cocktail, the activity of ^{14}C-glutamine was counted (in Hawaii on a Beckman LS-230 Liquid Scintillation Counter and at PSU on a Unilux II Liquid Scintillation System, Nuclear-Chicago Corp., Des Plaines, Ill.).

Nutrient Uptake Experiment with an Inhibitor of Glutamine Synthetase, Methionine Sulforimine

Coral heads for nutrient uptake experiments in the presence or absence of methionine sulfoximine (MSX), an inhibitor of glutamine synthetase, were carefully collected and cleaned, as above, just prior to use. The coral heads were then placed on a raised perforate platform inside a 7.0 liter capacity plexiglass chamber filled with 0.45 micron MFSW. A magnetic stir bar under the platform provided vigorous mixing. The entire chamber was set in a cooled waterbath which maintained the temperature inside the chamber at 27 ± 1° C. Illumination of 80 μEm^{-2} s^{-1} was provided by a 1150 W flood light suspended directly over the chamber. The coral heads were allowed to acclimate in the chamber for 30 min prior to the start of the experiment. The seawater in the chamber was enriched with 5 μM nitrate and 5 μM ammonia at the start of the experimental period and duplicate seawater samples for auto analysis of nitrate and ammonia were taken at 30 min intervals through a small port one inch from the base of the chamber.

Nutrient Analyses of Seawater Samples

Seawater samples obtained as above were filtered through precombusted (500 ° C for 4 h) GFC glass fiber filters and stored and frozen immediately in linear

polyethylene bottles. Auto analysis for nitrate and ammonia was done on a Technicon AA II Auto Analyzer (Technicon Industrial Methods Systems, Tarrytown, N.Y.) following the Technicon Industrial Methods for seawater analysis with some modifications. Nitrate + nitrite was measured by the Cu-Cd reduction method (auto analyzer precision ± 0.03 µM ammonia).

Chlorophyll a Determination

In Hawaii, chlorophyll a was measured by extracting samples in 100% Acetone (24 h, 4°C) in the dark. Absorbances were measured on a Beckman DB-G Grating Spectrophotometer and chlorophyll a concentrations calculated using the equation of Jeffrey and Humphrey (1975). Chlorophyll a determinations on Zoanthus zooxanthellae were done at PSU using 4:1 (v:v) methanol: tetrahydrofuran to extract the pigments. Absorbances were measured on a Aminco DW-2a Spectrophotometer (Travenol Laboratories, Inc., Silver Springs, Md.) and chlorophyll a concentrations calculated using the following equation (R. Summons, personal communication):

$$\mu g \text{ Chl a } ml^{-1} = 11.6\ A(663) - 0.6\ A(630)$$

Results

Zooxanthellae freshly isolated from Pocillopora damicornis yielded consistent glutamine synthetase activity at one half the rate measured in cultured zooxanthellae from Zoanthus spp. (see Table 1). Controls of animal tissue from the aposymbiotic coral Tubastrea coccinea and the isolated animal fraction from P. damicornis showed no GS activity.

Table 1. Glutamine synthetase activity from various sources. NA = no activity detected.

Source	GS Activity (µM Gln produced per g Chl a $^{-1}$ h^{-1})
Zoanthus sp. zooxanthellae	0.41
Pocillopora damicornis zooxanthellae	0.19
Pocillopora damicornis animal	NA
Tubastrea coccinea animal	NA

During initial attempts to determine the Km of glutamine synthetase in Zoanthus zooxanthellae for ammonium it was found that the GS activity was relatively constant irregardless of the concentration of ammonium supplied in the assay mixture. Even with no added ammonium GS activity was 60-85% of the maximum activity obtained with the addition of 10 mM ammonium. This problem of high GS activity with no ammonium present in the assay mixture was believed to be due to a high endogenous level of nitrogen in the zooxanthellae. In an attempt to reduce the endogenous pool of nitrogen, the Zoanthus zooxanthellae were transfered to nitrogen-free media and were assayed for GS activity with zero added ammonium and with 10 mM added ammonium. It was found that the level of GS activity measured was 30-40% of the maximal activity obtained with 10 mM ammonium even after 24 h starvation in nitrogen free media. The activity with 10 mM ammonium added remained the same. It proved impossible to determine a Km for ammonium for the enzyme in Zoanthus zooxanthellae. Pocillopora damicornis zooxanthellae appeared to also contain high levels of endogenous nitrogen and attempts to starve them were unsuccessful. GS activity declined rapidly when the P. damicornis zooxanthellae were incubated in nitrogen-free seawater, indicating the freshly isolated zooxanthellae did not remain healthy under these conditions.

Nutrient uptake experiments on whole P. damicornis coral heads in the presence of 0.5 mM methionine sulfoximine show that ammonium uptake is rapidly and completely inhibited by the glutamine synthetase inhibitor (results in Fig. 1). Ammonium uptake is completely stopped within 60 min of the addition of MSI and ammonium excretion occurs after that time. Control corals with no added methionine sulfoximine continued to take up ammonium and nitrate at an almost linear

rate throughout the entire incubation period. Methionine sulfoximine had no effect on the uptake of nitrate.

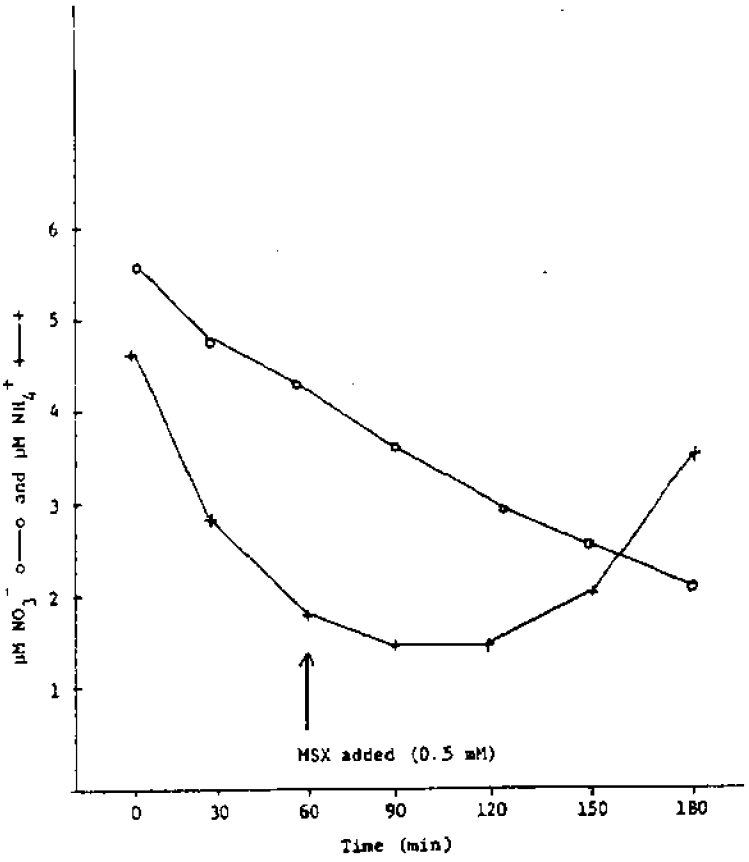

Fig. 1. Nitrate and ammonium concentrations in the medium during incubations of Pocillopora damicornis. Methionine sulfoximine, an irreversible inhibitor of glutamine synthetase, added at t = 60 min.

Discussion

Cultured Zoanthus zooxanthellae and zooxanthellae freshly isolated from Pocillopora damicornis appear to have high endogenous level of nitrogen which interferes with the determination of a Km for ammonia of glutamine synthetase. It is possible to reduce the endogenous level of nitrogen in cultured cells by transferring them to nitrogen-free seawater and starving them for at least 24 h but residual GS activity with no added ammonium remains. Zooxanthellae freshly isolated from P. damicornis and transfered to nitrogen-free seawater did not remain healthy and it was not possible to starve them for nitrogen or determine a Km for ammonium. Wilkerson and Muscatine (in press) also reported negative cooperativity of Aiptasia pulchella zooxanthellae GS for ammonium, even after dialyzing the enzyme extract against MFSW. They also attribute the residual GS activity with no added ammonium to high endogenous levels of ammonium in the enzyme preparation. Recent work indicates that a second enzyme activity may be interfering with the GS assay making it impossible to determine a Km for ammonium. However, further experimentation is needed to confirm this possibility.

That no GS activity was detected in the animal fraction from P. damicornis or the aposymbiotic coral Tubastrea coccinea may be a function of the assay system used. The biosynthetic radioactive assay used here, while one of the most sen-

sitive assays for GS activity, has specific requirements for pH and metal ion cofactors. The assay conditions used here were optimized for zooxanthellae, and it is possible the animal enzyme may have different pH optima and metal ion requirements. It would be premature to rule out the presence of glutamine synthetase in the tissues of corals based on the data presented in this paper.

Preliminary experiments show that ammonium uptake by the intact P. damicornis symbiosis is readily inhibited by the glutamine synthetase inhibitor methionine sulfoximine, but the inhibitor had no effect on the uptake of nitrate. That ammonium uptake can be inhibited by methionine sulfoximine indicates glutamine synthetase plays an important role in the nutrition of symbiotic corals. Methionine sulfoximine should prove to be a useful tool in further studies of coral nutrition.

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Effect of varying solar radiation intensities and ultraviolet radiation on growth rates of *Symbiodinium microadriaticum* isolated from different hosts

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Abstract

Growth rates of zooxanthellae isolated from five different hosts were determined at five levels of incoming solar radiation. The various strains differed significantly in their growth rates, as well as in their abilities to adapt to low and high irradiance did not appear to be correlated with solar radiation intensities in the environments from which they were isolated. The effect of UV radiation on zooxanthellae growth rates was also monitored. Full incoming UV radiation was shown to completely inhibit growth in three of four strains tested.

Introduction

A wide range of marine invertebrates, spanning several phyla, harbor dinoflagellate endosymbionts commonly called zooxanthellae (McLaughlin and Zahl, 1966; Trench, 1979). The majority of these symbionts belong to the gymnodinioid species *Symbiodinium* (=*Gymnodinium*) *microadriaticum*. It was once believed that a universal algal species was distributed among the various host taxa (Taylor, 1972; Kevin, et al., 1969); however, recent evidence including isoenzyme patterns (Schoenberg and Trench 1980 a,b,c), sterol composition (Withers et al., 1982), and effect on growth rates of experimentally infected hosts (Kinzie and Chee, 1979) indicates considerable genetic diversity among *S. microadriaticum* isolated from various hosts. Since zooxanthellae are associated with their hosts for a large part of the life cycle in some species and the entire life cycle in others, the genome of the symbiont contributes significantly to the genetic potential of the consortium (Karakashian and Siegel, 1965; Margulis, 1976). In effect, the establishment of a symbiosis may be viewed as a parasexual event involving the recombination of genes, thus allowing one or both of the partners to exploit previously unavailable habitats (Margulis, 1980). Conversely, the metabolic needs of a symbiont may render some previous host environments unsuitable. Therefore genetic diversity in zooxanthellae may influence under what conditions their hosts can live.

The ability of different strains of *S. microadriaticum* to adapt to varying light regimes may be a trait which has such an ecological effect. One possibility is that animal species which live only in high light environments are restricted due to the inability of their zooxanthellae to adapt to low irradiances found in shaded areas or deep water. Since it has been demonstrated that zooxanthellae contribute significantly to the nutrition of their hosts via translocation of photosynthate (Muscatine and Porter, 1977; Muscatine et al., 1981), animals which inhabit low light environments could suffer from a lack of reduced carbon if zooxanthellar photosynthesis decreased with decreasing irradiance. However, several marine phytoplankton have been shown to adapt to low irradiances to varying degrees by increasing the concentration of photosynthetic pigments, allowing maximum gross photosynthesis and growth rate to remain constant in the face of decreasing irradiance (Chan, 1978; Prezelin and Sweeney, 1978; Falkowski, 1980). Studies on low light adaptation in *S. microadriaticum* have been done primarily on intact coral symbioses, and have yielded conflicting results. Wethey and Porter (1976 a,b) demonstrated that maximum gross photosynthesis remains almost constant in the coral *Pavona praetorta* Dana collected from 10 and 25 m, while McCloskey and Muscatine (ms.) found a very large decrease in algal production between colonies of *Stylophora pistillata* Esper from 3 and 35 m. Other workers have documented increases in the amount of photosynthetic pigments in corals kept at low light in the laboratory (Redalje, 1976), collected from shaded environments (Falkowski and Dubinsky, 1981; Titlyonov et al., 1980), and collected from deep water (Dustan, 1979; Titlyonov et al., 1980) relative to their high light and shallow water counterparts.

However, work by Titlyanov et al. (1980) and unpublished observations of R. Warnock, R. Fitt and J. F. Battey (in Trench, ms.) revealed constant or decreasing pigment concentrations with depth in other species. In the only study to compare species with different depth ranges, Rodalje (1976), using a series of decreasing irradiances, showed that zooxanthellae from Leptoseris incrustans, a deep water species, could increase their chlorophyll content under low irradiances at which the shallow species, Cycloseris ocellina could no longer adapt. This supports the hypothesis that different strains of S. microadriaticum have different capacities for photoadaptation, thereby setting limits on host bathymetric range.

A second possibility is that animals living in low light environments may have to tolerate lowered photosynthetic rates due to an inability to withstand high irradiances, especially in the ultraviolet region of the spectrum (280-400 nm). Ultraviolet radiation (UV) which penetrates clear tropical ocean water (Jerlov, 1950) is harmful to many organisms (Urbach, 1969), although some appear more resistant than others (Jokiel and York, 1982). Jokiel and York (1982) have shown that zooxanthellae isolated from the "sunloving" species Cassiopea sp. exhibit a faster growth rate under high UV than do those from Aiptasia sp., a species which favors low light environments, while without UV their growth rates were almost identical. Again, response of zooxanthellae to irradiance appears to affect preferred host environments.

In this study, the photoadaptive abilities of S. microadriaticum isolated from several hosts with different preferences for high and low light environments were assessed, and attempts made to correlate this ability with host habitat. Growth rates (u) were used as a measure of productivity. Growth rates of five strains of S. microadriaticum in culture were compared at varying solar radiation intensities. Four of the five strains were examined for growth rates with and without UV.

Materials and Methods

Cultures of S. microadriaticum were generously provided by Richard York of the Hawaii Institute of Marine Biology. All strains had been in culture for at least 2 years. Host species, location of collection, algal clone number, and irradiance preference of the hosts are listed in Table 1.

Table 1. Strains of S. microadriaticum used.

Host Species	Location of collection	Clone #	Irradiance preferences[1]
Aiptasia pulchella (anemone)	Kaneohe Bay, Oahu, HI	KBB	low
Cassiopea medusa (schyphozoan)	Kaneohe Bay, Oahu, HI	KB6	high
Melibe pilosa (nudibranch)	Oahu, HI	not a clone	low
Montipora verrucosa (scleractinian coral)	Kaneohe Bay, Oahu, HI	KB12	wide range
Tridacna maxima	Enewetak	not a clone	high

[1]Determined from site of host collection and field observations.

Experiments were conducted in a continuous flow water bath maintained at 24.5±1°C under full natural solar irradiance. The water bath was subdivided into 12 compartments which were covered with various materials in order to produce the desired light regimes. Throughout each experiment, incoming solar radiation was continuously measured near the test site using an Epply pyrheliometer.

For the first experiment, which tested growth at various intensities of visible light only, compartments were covered with UV stabilized polycarbonate (Rohm and Hass Tuffack) sheets, which had been darkened with varying amount of black spray paint. Polycarbonate blocks almost all UV but is highly transparent to visible light (Fig. 1). Panels with transmittances of 6.6, 14.5, 20.6, 29.1, 43.5, and 88.5 percent were prepared in duplicate. Percent transmittance as measured with a Lambda Instruments LI-185 Quantmeter varied an average of ± 1.43% (range ± 0.4 to 3.8%) within a panel and 0.75% (range ± 0.1 to 1.7%) between duplicates. Positions of the panels on the water bath were randomly assigned. Algae were grown in half strength "f" medium (Guillard and Rhyther, 1962). Counts of each culture were made and densities adjusted to approximately 10^4 cells ml^{-1}. Thirty replicate counts were made to determine starting densities, and 6 ml. aliquots dispensed into sterile acid-rinsed screwcap test tubes (13x100 mm). The caps were screwed on as tightly as possible and the tubes placed horizontally in submerged racks in order to prevent shading which may have occurred had they been placed upright in test tube racks. Three replicates of each of the five zooxanthellae cultures were placed in each of the 12 compartments, giving a total of six replicates of each combination of algae and light. At the end of 12 days, the tubes were collected and cell densities determined using a Spiers-Levy eosinophil counter. Doublings day^{-1} were calculated according to the equation:

$$\text{doublings day}^{-1} = \frac{(\ln n^2 - \ln n1)/\text{no. days}}{\ln 2}$$

Eight replicate counts of each tube were made.

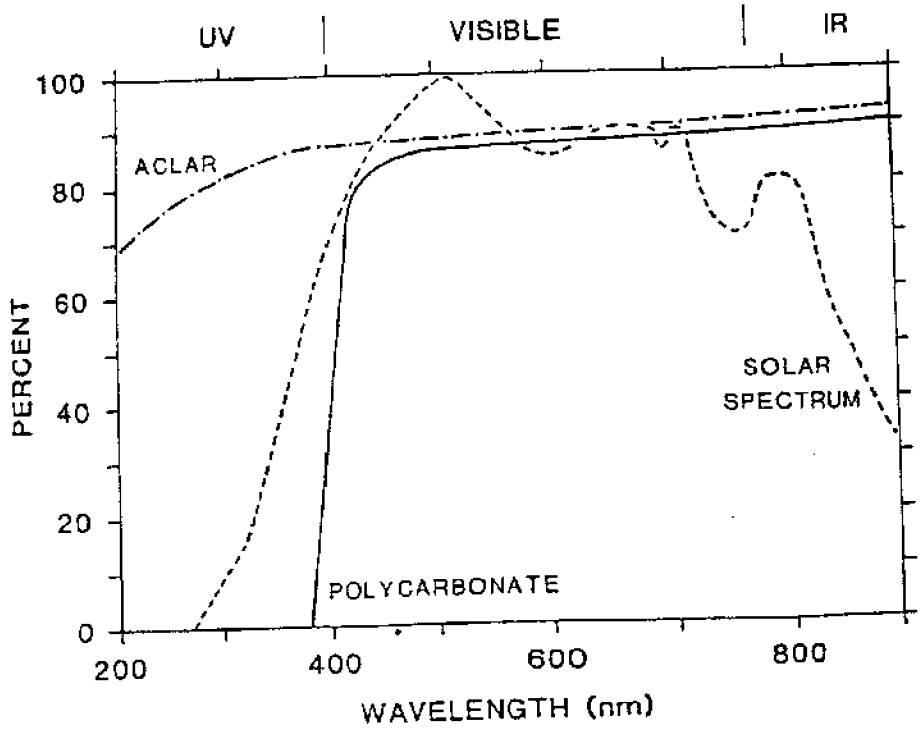

Fig. 1. Absorption characteristics of filters used in the experiment. Dashed line represents relative distribution of solar radiation at the surface of the earth.

The second experiment was designed to verify patterns of low light adaptation found in Experiment 1. One "sunloving" strain (C. medusa), one "shadeloving" strain (A. pulchella), and the strain with a wide irradiance tolerance (M. verrucosa) were used. Four tubes of each strain were grown at 6.6 and 43.5% incident irradiance. Since in the first experiment growth remained almost constant in all strains between 20.6 and 43.5%, 43.5% was chosen in order to produce a maximum growth rate against which to scale growth inhibition at low irradiance. Cultures were prepared as in the first experiment, except that starting densities were approximately 10^5 cells ml^{-1}. Also, due to diatom contamination in 5% of the tubes in the first experiment, which was thought to have been introduced throughout the water bath, tubes were incubated in a upright position with their caps out of the water. Since there were fewer tubes in this experiment and they were widely spaced within each compartment, shading was minimized. Again, tubes were collected and cells counted after 12 days.

Variations in UV tolerance between the strains of S. microadriaticum were also tested. For this experiment, one portion of the water bath was covered with clear polycarbonate to block out the majority of UV radiation, and the other part covered with UV transparent Aclar (Allied Chemical Corp.) which is highly transparent to all UV and visible wavelengths. Spectral transaission curves for both materials as measured in a Beckman DB-G Spectrophotometer are shown in Fig. 1. The level of photosynthetically available radiance was the same in both treatments (Jokiel and York, 1984 in press). After adjusting culture densities to approximately 10^5 cells ml^{-1}, 10 ml aliquots of each culture were dispensed into sterile UV transparent quartz tubes and the tubes stoppered with cotton and capped with parafilm. Since a lack of the expensive quartz tubes prevented testing all five strains, M. verrucosa was omitted. After innoculation, the tubes were placed in their respective treatment chambers in racks slanted at approximately a 60° angle. Tubes were collected and cells counted after 15 days. Data were analyzed using a standard analysis of variance followed by either Scheffe's multiple-comparison procedure or Duncan's multiple range test.

Results

Different strains of zooxanthellae exhibited significantly different responses to the range of solar radiation intensities to which they were exposed, despite a high degree of variability (Fig. 2). During the first experiment, average daily incoming solar irradiation was 471.56 cal cm^{-2} day^{-1}. Growth rates were essentially constant at all light levels between 14.5 and 43.5%, except for zooxanthellae from M. pilosa which showed a significant ($p<.05$) decreases at 14.5%, and those from M. verrucosa whose growth rate decreased at 20.6% compared to 43.35%. The latter decrease may be an aberrant point since it seems unlikely that there would be a decrease at an intermediate light level. Algae from A. pulchella, C. medusa, and M. pilosa displayed lower growth rates ($p<.05$) at the highest light level tested, while those from M. verrucosa and T. maxima did not appear to be photoinhibited by 88.5% incident irradiance. All strains except M. verrucosa grew at significantly ($p<.05$) lower rates under 6.6% incident light, however the data for C. medusa must be just within the limits of significance, as the percent decrease at low light for this strain is very similar to that of M. verrucosa algae (Table 2). Table 2 presents the rate of doubling day^{-1} for each strain of S. microadriaticum at 6.6 and 88.5% relative to that at 43.5%, which was arbitrarily chosen to represent maximum growth rate.

All maximum growth rates proved to be significantly different from one another ($p<.05$) except in the comparison of zooxanthellae from T. maxima and C. medusa. The latter two strains had the fastest maximum growth rates, followed by M. pilosa, A. pulchella, and M. verrucosa algae.

In the second experiment, involving only zooxanthellae from A. pulchella, C. medusa, and M. verrucosa and light levels of 6.6 and 43.5 percent incident irradiance, doubling day^{-1} were much lower in general than those in the first experiment due to the high starting densities of the cultures. Average daily irradiance for this period was only slightly lower than during the first experiment (391.21 cal cm^{-2} day^{-1}). Nevertheless, similar results were obtained for the A. pulchella and C. medusa strains. Again, growth of A. pulchella algae was greatly inhibited by low light, while that of the C. redusa algae was not (Tables 2 and 3). Zooxanthellae from M. verrucosa showed more low light inhibition in this experiment than in the previous one. This may have been due to a reduction in the actual irradiance "seen" by the algae, which would have been lowered compared to the first experiment by self-shading. These algae may show a steep slope in the growth rate vs. irradiance curve when irradiances lower than those

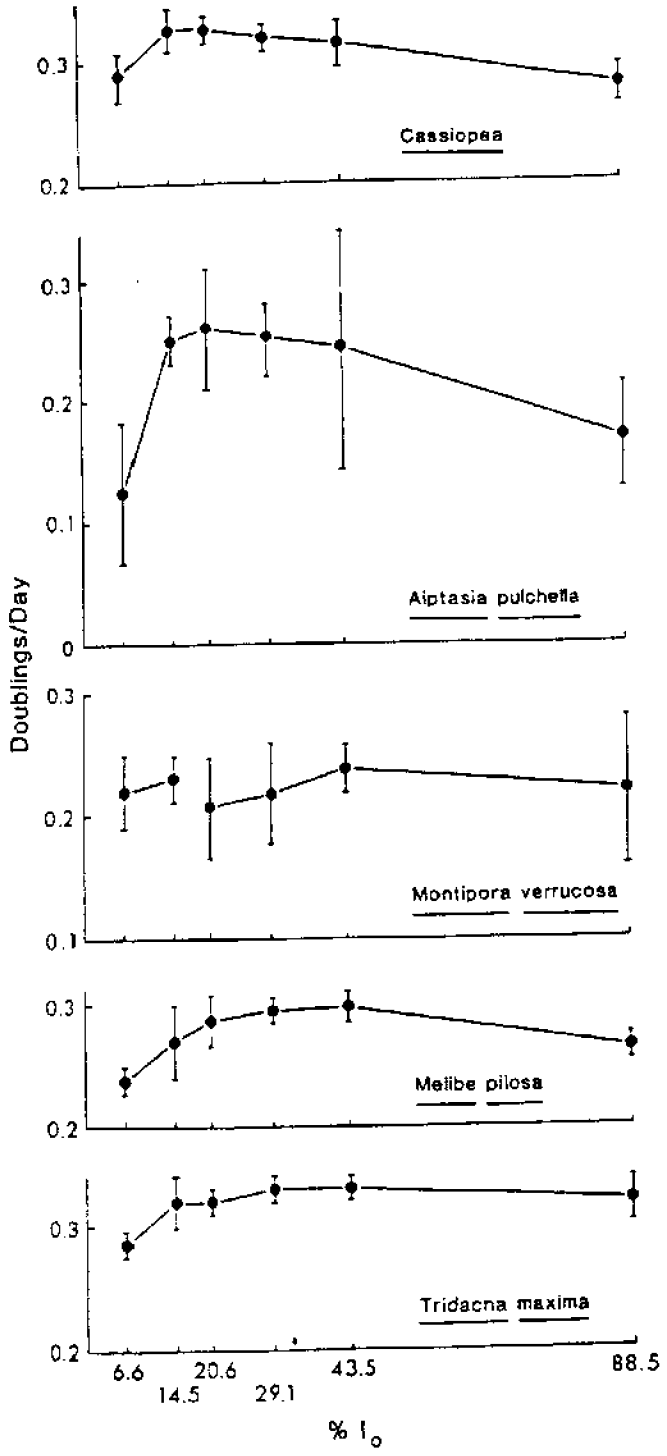

Fig. 2. Comparison of growth rates of zooxanthellae isolated from various hosts under different intensities of solar irradiance.

used in these experiments are included, causing a small decrease in light to produce a sharp drop in growth rate. Another discrepancy between the second and first experiments is the relative rate of growth of A. pulchella and C. medusa algae at 43.5% incident irradiance. Whereas in the first experiment A. pulchella grew more slowly than C. medusa, in the second the growth rate of C. medusa was slightly lower than A. pulchella. This may be easily explained by the portion of the growth curve of the algae over which these experiments were performed. That is, since the second experiment began at densities much closer to the maximum density, the results imply that A. pulchella zooxanthellae have a slower growth rate than those from C. medusa, but reach a similar or slightly higher maximum density.

UV radiation had a profound effect on the growth of all strains of S. microadriaticum. While all strains grew at very similar rates when not exposed to UV, only algae from M. pilosa, grew at all when full UV was present (Table 4). The growth rate of these algae under UV was 22.5% of that without UV exposure. In addition, the cells of all strains were much larger in the cultur , grown with UV than in those grown with visible light only.

Table 2. Growth of S. microadriaticum strains under high and low irradiance. Low = μ at 6.6% incident irradiance/μ at 43.5% incident irradiance X 100. High = μ at 88.5% incident irradiance/μ at 43.5% incident irradiance X 100.

Host	Low		High
	First exp.	Second exp.	
A. pulchella	52.0%	62.1%	69.0%
C. medusa	92.0%	91.1%	88.6%
M. pilosa	79.6%	----	88.6%
M. verrucosa	93.3%	76.3%	92.4%
T. maxima	85.5%	----	97.6%

Table 3. Experiment 2: Growth rates (doublings/day).

Host	6.6% incident irr.	43.5% incident irr.
A. pulchella	0.082±0.014	0.132±0.009
C. medusa	0.113±0.018	0.124±0.023
M. verrucosa	0.087±0.024	0.114±0.015

Table 4. Growth with and without UV radiation (doublings/day).

Host	visible only	visible + UV
A. pulchella	0.121±0.017	0.00
C. medusa	0.121±0.010	0.00
M. pilosa	0.120±0.009	0.027±0.013
T. maxima	0.129±0.010	0.00

Discussion

Photoadaptive capacities of zooxanthellae were not shown to be correlated with host habitat. In general, algae from "shade-loving" animals had a higher percent decrease in growth rate at low irradiance levels than those from "sun-loving" animals. Since in intact symbioses, algal growth rate is rigidly controlled (Trench, 1979), changes in growth rates of algae in culture are likely to appear as variation in amount of organic material translocated to the host and/or stored in the algae. Indeed, it has been shown (McCloskey and Muscatine, ms.) that the percentage of fixed carbon translocated decreases from 39% to 11% in S. pistillata from 3 and 35 m, respectively, while maximum gross photosynthesis also decreased. My results suggest that animals which live at low irradiances, in the evolution of their symbioses, have not selectively chosen algae which are better adapted to low light levels. Thus, those associations which are often found at low irradiances may possess other mechanisms for low light adaptation besides those of the zooxanthellae for keeping photosynthetic rate constant.

Adaptations to decreasing irradiances, and thus most likely decreasing translocation, may include a drop in algal and/or animal respiration rate and increased heterotrophic feeding. That respiration rates of corals decline with depth has been well documented (Zvalinskii, et al., 1980; Spenser-Davies, 1980; McCloskey and Muscatine, ms.). This may be explained by the observations of Fitt, et al. (in press) and Svoboda and Porman (1980) who have shown that respiration rate in anemones is correlated with the amount of exogenous nutrients. Both McCloskey and Muscatine (ms.) and Zvalinskii, et al. (1980) however, found that the decline in coral respiration was not enough to compensate for the lowered photosynthetic rate. This implies, then that heterotrophy must be increasing with depth in these animals. It has been established that many of these invertebrates can feed heterotrophically on zooplankton (Porter, 1974; Johannes, et al., 1970) and bacteria (DiSalvo, 1971; Sorokin, 1973) and can assimilate dissolved organic carbon (Murdock and Lenhoff, 1968; Trench, 1974; Sorokin, 1973). Therefore, a shift in the autotrophy:heterotrophy ratio may be accomplished with such ease that animals have not had to distinguish between zooxanthellae which perform differently at low irradiances. Changes in the algal density per animal tissue may also occur at low irradiances, although a clear trend in this area has not been established. Several workers have found no differences in algal numbers with irradiance (Pedalje, 1976; Svoboda and Porman, 1980; Falkowski and Dubinsky, 1981), others have found increased numbers (Titlyonov et al., 0981; Rouck, 1978; Scelfo, this volume), while still others have shown a decrease (Dustan, 1979; McCloskey and Muscatine, ms.). A decrease in algal density at low light levels could help to keep photosynthetic rate constant by reducing self-shading.

There also appeared to be no correlation between habitat preference of hosts and growth inhibition of zooxanthellae by high irradiance levels, as M. pilosa algae responded similarly to the two "sun-loving" strains. The photoinhibition which did occur was, except for C. medusa algae, less than growth inhibition by low light, and so can probably be explained by the same adaptations on the part of the host.

Tolerance of UV radiation by the different strains of zooxanthellae also did not appear in this study to be related to host habitat, since the only strain able to grow in the presence of UV was the "shade-loving" M. pilosa zooxanthellae. Had beginning cell densities been lower, a finer resolution of UV tolerance among the strains might have been perceived. Ability to withstand high levels of UV has been linked to the pigment S-320, so called because of its absorption peak at 320 nm (Shibata, 1969; Jokiel and York, 1982). S-320 has been detected in the corals Pocillopora sp. and five species of Acropora (Shibata, 1969), P. damicornis (Jokiel and York, 1982), and M. verrucosa (Scelfo, this volume), and in a cyanobacterium (Shibata, 1969). In addition, increasing S-320 concentration in shallow water has been reported for P. damicornis (Jokiel and York, 1982) and M. verrucosa (Scelfo, this volume), and so is thought to function as a UV shield. Whether it is produced by the animal or algal partner of the corals has not been ascertained. If it is produced by the animal, and so protects both partners, this may explain why zooxanthellae show such severe UV inhibition in culture (Jokiel and York, in press). Furthermore, differential production of S-320 by different invertebrates could account for some of the differences in UV tolerance between strains of S. microadriaticum. In other words, although M. pilosa generally inhabits low

light environments, if the animal produces no UV protectant, then the algae may require more UV resistance than algae in a "sun-loving" animal which does produce a UV screen. The observation that cell size is greatly increased in UV exposed cells suggests that not only photosynthesis but cell division may be inhibited.

To thoroughly assess the effect of low irradiances on marine invertebrate-alga associations, changes in productivity, translocation, respiration of algae and animal, number of algae per host tissue area, and heterotrophic feeding must be examined. The results of this study imply that although zooxanthellar productivity is kept constant over a wide range of irradiances, animals which are found in shaded or deep water environments may be exercising other photoadaptive mechanisms as well. Resistance of zooxanthellae to UV is low, and may have evolved in response to the amount of UV protection afforded by the host. This problem requires further examination. In summary, although strains of S. microadriaticum isolated from different hosts do exhibit different responses to varying solar radiation intensities and UV radiation, these differences may not be of critical importance to the host in symbiont selection.

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Relationship between solar radiation and pigmentation of the coral Montipora verrucosa and its zooxanthellae

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Abstract

Colonies of the reef coral Montipora verrucosa were transplanted from moderate (3 m) and deep (10 m) depths to a shallow aquaria (20 cm). Corals were exposed to solar radiation with and without ultraviolet (UV) under full intensity and shaded conditions. M. verrucosa collected from 3 m had a much higher concentration of a UV absorbing pigment (S320) than the colony taken from 10 m. The 10 m colony did not survive at shallow depth in full sunlight, whereas M. verrucosa transplanted from moderate depth was capable of tolerating the increase in light intensity and UV radiation. A significant increase in the concentration of UV absorbing pigment was evident for all surviving corals and was greater for corals in full sunlight than for those in the shade. Corals exposed to ultraviolet radiation had at least double the amount of S320 pigment as corals receiving the same intensity of solar radiation but without UV.

Introduction

Hermatypic corals must inhabit shallow warm water in order to receive adequate sunlight for their endosymbiotic zooxanthellae (Symbiodinium microadriaticum). In shallow water, the corals often are exposed to substantial amounts of solar ultraviolet radiation because the clear tropical oceanic waters covering the reefs are highly transparent to short wavelengths. In some cases, 80% of the surface UV irradiance penetrates to a depth of one m, decreasing to 11% at 10 m (Jerlov, 1950, 1968). Ultraviolet radiation is detrimental to many organisms, as these wavelengths damage DNA and chloroplasts and denature proteins (Giese, 1964; Steeman Nielsen, 1964; Halldal et al., 1972). The ability of hermatypic corals to tolerate solar UV radiation suggests that these organisms have evolved a protective mechanism (Jokiel, 1980).

Pigments which reflect, floresce or absorb ultraviolet radiation may effectively protect the coral and its endosymbionts. Shibata (1969) extracted from several species of corals, a water soluble pigment (S320) having an absorbance maximum at 320 nm. Jokiel and York (1982) demonstrated that the production of this pigment is in direct response to UV and may serve a protective function. They observed an increase in growth rate and a decrease in S320 concentration for Pocillopora damicornis when solar UV was blocked. Siebeck (1981) found that the UV tolerance of several schleractinian corals varied between and within species, in relation to the location of the individuals' habitat. His study showed that UV tolerance decreases as the depth of habitat increases. Other researchers have found that the concentration of S320 decreases with depth (Maragos, 1972; Chalker, personal communication).

The purpose of the present study was to investigate the photoadaptive capabilities of the coral Montipora verrucosa collected from different depths and to determine the effects of solar UV radiation upon the production of the UV absorbing pigment (S320). The effect of solar UV radiation upon the endosymbiotic zooxanthellae was also assessed.

Materials and Methods

This study was conducted on Coconut Island in Kaneohe Bay, Oahu, Hawaii (21° 26' N, 157° 48' W) during July and August of 1983. The effect of ultraviolet radiation upon Montipora verrucosa colonies taken from different depths was determined by measuring changes in pigment concentration (S320 and chlorophyll a). Two large colonies were collected from moderate (3 m) and deep (10 m) depths and transplanted to a shallow aquaria (20 cm). Each colony was broken into smaller colonies, which were then randomly divided and placed into different light

treatments. Corals were exposed to solar radiation with and without ultraviolet under full intensity and shaded conditions.

The experiment was conducted in continuous flow aquaria located in full sunlight. One aquarium was covered with UV-stabilized polycarbonate filter (Rohm and Hass Truffak brand). This material blocked UV radiation (<400 nm) but transmitted approximately 90% of visible light energy. The other aquarium was cover with Allied Chemical Corp., Aclar brand fluorohalocarbon film which transmitted both UV and visible wavelengths at about 90%. The spectral curves for these filters were measured with a Beckman DB-G grating spectrophotometer and are illustrated in Fig. 1 (Jokiel, 1982). Neutral density screen was used to shade half of each aquarium, reducing the light intensity to approximately 40%.

Photosynthetically active radiation (PAR) was measured with a Li-Cor Li 188 B integrating quantum meter. Simultaneous light measurements were taken within each treatment and above the aquaria. The precent surface irradiance of PAR for the shaded treatment receiving UV ($\bar{x}$=38%, SD=3%) was comparable to the treatment lacking UV ($\bar{x}$=39%, SD=2%). A two sample t-test (Zar, 1974) indicated that the sample means for the two treatmens were not significantly different ($0.2>p>0.4$). The percent surface irradiance of PAR for the full intensity sunlight treatment receiving UV ($\bar{x}$=61%, SD=17%) was not significantly different from the full sun treatment without UV ($\bar{x}$=65%, SD=16%) ($0.5>p0.9$).

The percent surface irradiance was also determined in the field at several depths along the reef slope near the collection sites. Measurements were taken along a vertical depth transect at 0.25 m, 0.55 m, 3.0 m, 4.5 m and 7.5 m. A linear regression analysis using arc sine transformed data indicated that the slope was not equal to zero ($p<0.0001$). The percent surface irradiance for the 10 m site was inversely predicted, however, the extrapolation of points is considered invalid. The percent surface irradiance of PAR for the 3 m and 10 m sites were determined to be 44% and 1.3% respectively. The linear regression curve for the % irradiance along the coral reef slope is illustrated in Fig. 2.

Samples were taken on five occasions during a 36 day period, and were analyzed immediately. In preparation for analysis, the coral was first rinsed thoroughly with filtered seawater. A 1 cm diameter core borer was used to obtain the sample plugs, which were then trimmed and placed in a test tube with the appropriate extraction solvent.

To extract the S320 pigment, the coral plugs were placed in 10 ml of deionized water (Shibata, 1969). The pigment extractions were conducted in dim light at 4° C and allowed to extract for 16 hours. Samples were centrifuged for 5 minutes at 1500 RPM at 4° C. The supernatent was analyzed in a Beckman DB-G grating spectrophotometer using a 1 cm quartz cuvette.

Samples analyzed for chlorophyll a content were prepared in the same manner as described above, except were place in 5 ml of 100% acetone and crushed in a glass tissue grinder to improve extraction (Maragos, 1972). These data were then converted to pigment concentrations using the equations of Jeffrey and Humphrey (1975).

Results

UV Absorbing Pigment

Montipora verrucosa collected from moderate depth (3 m) had an initial S320 concentration ($\bar{x}$=0.047 absorbance units cm^{-2}, SD=0.02) 9 times greater than the deep colony (10 m) ($\bar{x}$=0.0005 absorbance units cm^{-2}, SD=0.001). A student's t-test indicated that the difference between sample means was very significant ($0.001<p<0.05$).

There was 100% mortality for M. verrucosa transplanted from 10 m and placed in full intensity sunlight. The corals exposed to the full solar spectrum (with UV) bleached and died within two days, whereas the corals receiving the same intensity PAR, but without UV, survived for three weeks. Corals in the shaded treatments showed a very significant increase in S320 concentration ($p<0.001$); corals receiving UV were significantly higher ($p<0.001$) than those not receiving UV. Fig. 3 shows the change in S320 concentration for the 10 cm colony in the different light treatments. The absorbance values are given in Table 1.

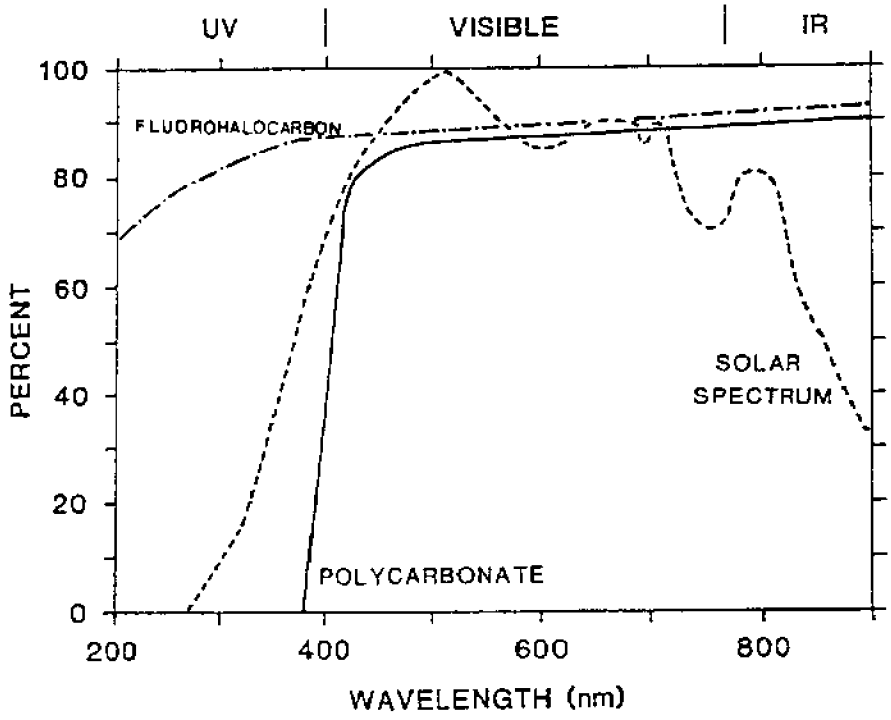

Fig. 1. Percent spectral transmission for the fluorohalocarbon and polycarbonate filters. Also shown is a spectral irradiance curve for incident light at the earth's surface.

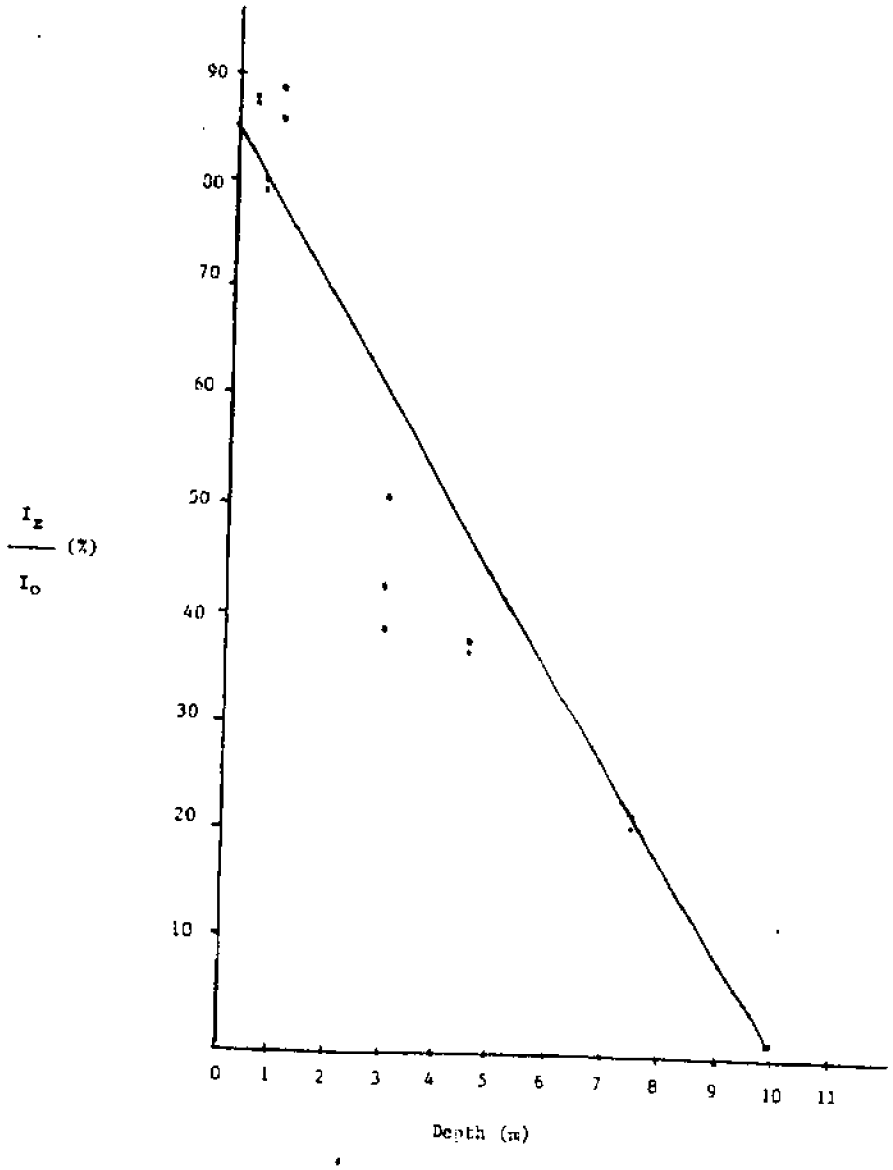

Fig. 2. Depth profile for light measurements at field collection site.

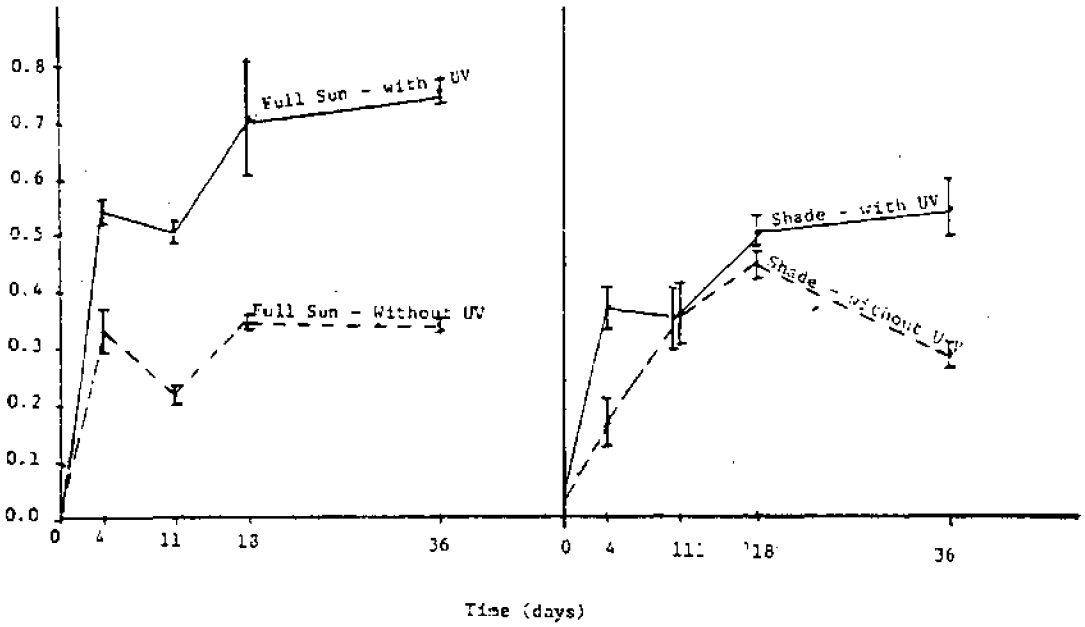

Fig. 3. Montipora verrucosa transplanted from deep depth (10 m) to shallow aquaria. Change in S320 concentration under different light treatments.

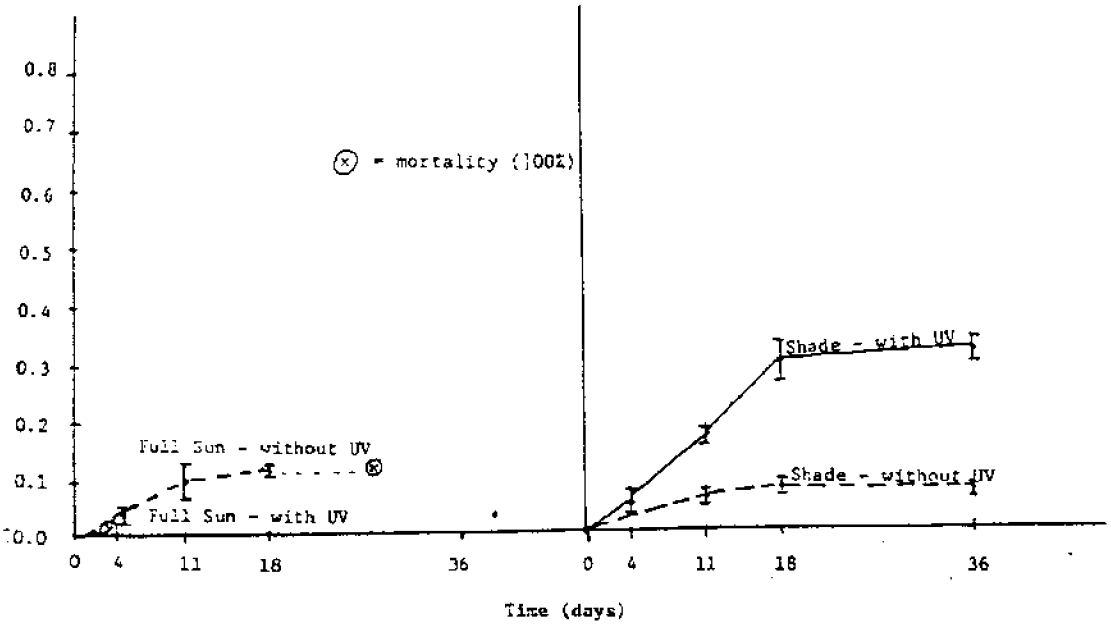

Fig. 4. Montipora verrucosa transplanted from moderate depth (3 m) to shallow aquaria. Change in S320 concentration under different light treatments.

Table 1. S320 pigment (absorbance units/cm²) for the corals transplanted from moderate (3 m) and deep (10 m) into the shallow aquaria (mean ± SD) (n=4).

	Colonies from 3 m				Colonies from 10 m			
	Full Sun		50% Sun		Full Sun		50% Sun	
Time (Days)	With UV	Without UV	With UV	Without UV	With UV	Without UV	With UV	Without UV
0	0.047±0.02				0.0005±0.001			
4	0.548 ±0.017	0.338 ±0.045	0.374 ±0.036	0.172 ±0.045	--	0.041 ±0.013	0.057 ±0.019	0.033 ±0.015
11	0.512 ±0.019	0.220 ±0.014	0.360 ±0.057	0.357 ±0.055	--	0.104 ±0.033	0.172 ±0.017	0.064 ±0.008
18	0.710 ±0.102	0.349 ±0.015	0.506 ±0.034	0.446 ±0.037	--	0.118 ±0.001	0.297 ±0.037	0.080 ±0.018
36	0.758 ±0.023	0.343 ±0.055	0.553 ±0.050	0.290 ±0.022	--	--	0.316 ±0.025	0.073 ±0.004

Table 2. Results of two level ANOVA applied to change in S320 pigment concentration for moderate depth colony relative to light intensity and UV.

Source of Variation	SS	DF	MS	F	Significance
Light Intensity	0.066	1	0.182	90.30	p<0.0001
UV treatment	0.458	1		279.97	0.0001
Intensity*UV treatment	0.023	1		14.26	0.0026
Error	0.020	12	0.002	--	-
TOTAL	0.567	15	--	--	-

Table 3. Results of two level ANOVA applied to change in S320 pigment concentration in M. verrucosa colonies in shaded treatments relative to original habitat depth and UV.

Source of Variation	SS	DF	MS	F	Significance
Original Depth of Coral	0.1380	1		152.91	p<0.0001
UV	0.2565	1		284.23	0.0001
Depth*UV	0.0003	1	0.132	0.34	0.5710
Error	0.0110	12	0.001	--	--
TOTAL	0.567	15	--	--	.5901

M. verrucosa transplanted from moderate depth showed a highly significant increase in S320 concentration for each treatment ($p<0.001$). Light intensity and UV have a significant effect as indicated by a two level ANOVA (Table 2). There is evidence of an intensity x UV interaction. Corals in full sunlight attained higher concentrations of S320 than those in shaded treatments and were higher for colonies exposed to UV than for those receiving PAR only. The change in pigment concentration during the experimental period is shown in Fig. 4 and the absorbance values are given in Table 1.

A comparison of the corals maintained in reduced sunlight showed that the colonies from moderate and deep depths respond differently and that the reponse also varies with respect to the presence or absence of ultraviolet radiation. UV appears to effect the two colonies equally, for here is insufficient evidence of a colony depth x UV interaction. These effects are indicated by a two-level ANOVA (Table 3).

The relative increase of pigment concentration for both colonies in each treatment was obtained from the ratio of final S320 concentrations to initial concentration. The greater increase in pigment concentration was observed for the colony transplanted from 10 m to the reduced sunlight treatment with UV (63 fold increase). The 3 m colony showed the least amount of increase in both treatments lacking UV radiation. A six fold and seven fold increase was measured for the shaded and full sunlight conditions, respectively. These results are summarized in Table 4.

Photosynthetic pigment

Montipora verrucosa collected from 10 m had a higher chlorophyll a (chl a) content ($\bar{X}$=1.8 pg cm^{-2}, SD=0.023) than the 3 m colony ($\bar{X}$=1.116 pg cm^{-2}, SD=0.032). A student's t-test indicated that this difference was highly significant ($0.002<p<0.001$).

M. verrucosa colonies transplanted from 10 m to full intensity sunlight bleached and died. The bleached color indicated chloroplast damage and is a sign of zooxanthellae death. Corals in the UV treatment lost their algal symbionts immediately while the corals not exposed to UV took approximately 10 days for loss to occur. Having lost their endosymbionts, coral death quickly ensued. 10 m corals placed in the shaded treatments showed an initial decline in chl a content, but increased again after two weeks. By the end of the experiment, no net change in chl a concentration was evident for the corals in the no-UV treatment ($0.2<p<0.1$), while the corals exposed to UV decreased significantly ($p<0.001$).

In full intensity sunlight, the 3 m colony showed no significant change in chl a concentration when in the treatment receiving UV ($0.1<p<0.5$), but decreased slightly when UV was blocked ($0.05>p>0.02$). Under shaded conditions, chl a content increased for both the with- and without-UV treatments; ($0.01>p>0.001$ and $0.02>p>0.01$, respectively). A two level ANOVA indicates that light intensity and UV effect the chl a concentration of the moderate depth and colony (Table 5). There is not an intensity UV interaction - and consequently no synergistic effects of intensity and UV. Fig. 5 illustrates the change in chl a concentration for both coral colonies in the various treatments. The concentration values are given in Table 6.

A two level Anova applied to the change in chl a concentration in M. verrucosa colonies in shaded treatments indicates that there is a significant difference in response relative to colony type (moderate vs deep habitat depth) and UV. There is evidence of an interaction between habitat depth of coral x UV suggesting that UV effects chl a production of the colonies differently. These results are given in Table 7.

Discussion

Montipora verrucosa is most abundant between 2 and 10 m. Light intensity and UV penetration decrease with depth, thus colonies at different depths are exposed to very different light conditions. The responses of M. verrucosa and its zooxanthellae to transplantation suggests that colonies have certain photoadaptive capabilities. Zooxanthellae can photosynthesize over a wide range of light intensities and spectral qualities, thus extending the depth range of the coral

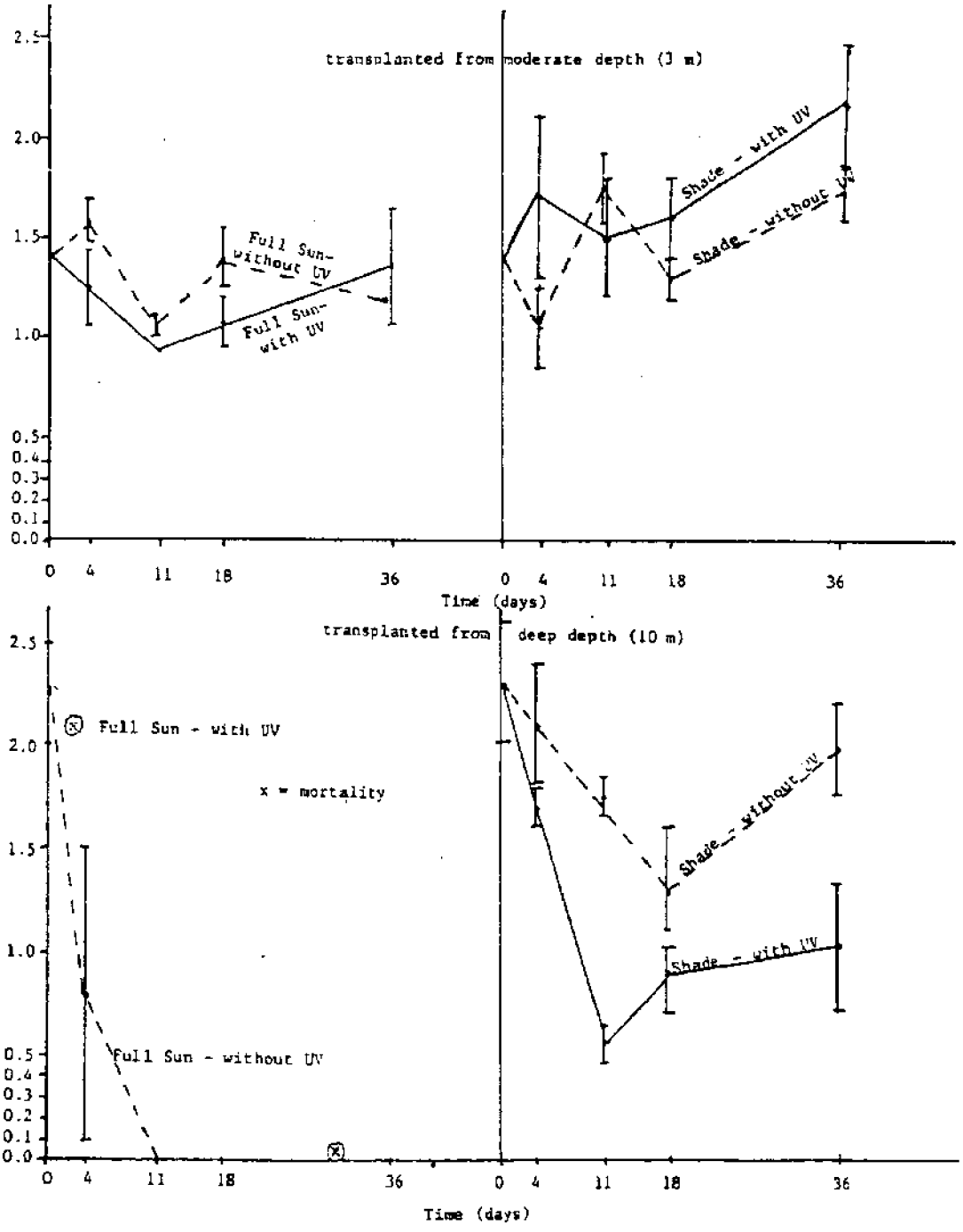

Fig. 5 a-d. Montipora verrucosa transplanted from moderate (3 m) and deep (10 m) depth to shallow aquaria. Change in chlorophyll a concentration under different light treatments.

Table 4. Relative increase in S320 concentration for Montipora verrucosa (<S320>final/<S320>initial) (and % mortality).

	Colonies from 10 m		Colonies from 3 m	
	With UV	Without UV	With UV	Without UV
Full sunlight	100% mortality -*	100% mortality (24x)**	16x	7x
Reduced sunlight	63x	15x	12x	6x

*100% mortality occurred before 2nd sampling.
**This value was determined via the initial and 18th day absorbance values.

Table 5. Result of two level ANOVA applied to change in chlorophyll a concentration for moderate depth colony relative to light intensity and UV.

Source of Variation	SS	DF	MS	F	Significance
Light Intensity	1.34440	1	0.5171	32.73	p<0.0001
UV treatment	0.19536	1		4.76	0.0498
Intensity*UV treatment	0.01145	1		0.28	0.6072
Error	0.49299	12	0.0411	--	--
TOTAL	2.04425	15	--	--	-

Table 6. Chlorophyll a ($\mu g/cm^2$) for the corals transplanted from moderate (3 m) and deep (10 m) into the shallow aquaria (Mean ±SD) (n=4).

	Colonies from 3 m				Colonies from 10 m			
	Full Sun		50% Sun		Full Sun		50% Sun	
Time (days)	With UV	Without UV	With UV	Without UV	With UV	Without UV	With UV	Without UV
0	1.422±0.041				2.293±0.293			
4	1.264 ±0.275	1.591 ±0.137	1.732 ±0.465	1.059 ±0.190	--	0.799 ±0.726	1.687 ±0.088	2.094 ±0.313
11	0.943 ±0.197	1.061 ±0.054	1.489 ±0.283	1.762 ±0.173	--	0.038 ±0.039	0.566 ±0.085	1.745 ±0.101
18	1.071 ±0.136	1.387 ±0.152	1.606 ±0.191	1.290 ±0.121	--	--	0.894 ±0.223	1.290 ±0.340
36	1.368 ±0.273	1.200 ±0.143	2.150 ±0.332	1.726 ±0.172	--	--	1.029 ±0.301	1.968 ±0.243

Table 7. Results of two level ANOVA applied to change in chlorophyll a concentration in *M. verrucosa* colonies in shaded treatments relative to colony type (from moderate vs. deep habitat depth) and UV.

Source of Variation	SS	DF	MS	F	Significance
Original Depth of Coral	6.11326	1		111.86	p<0.0001
UV	0.43957	1	2.6739	8.04	0.0150
Depth*UV	1.46894	1		26.88	0.0002
Error	0.65583	12	0.0547	--	--
TOTAL	8.67760	15	--	--	-1 6760

(Goreau and Wells, 1967; Dustan, 1982). Chong et al. (1983) report that the strain of S. microadriaticum from M. verrucosa may photoadapt by changes in the activities of CO_2-fixing enzymes or electron transport systems. They also observed light induced changes in pigmentation. Algal photoadaptation was evident in the present study and was assessed by changes in chlorophyll a concentration. Colonies collected from an environment receiving ~1.3% surface PAR (10 m) had approximately double the chlorophyll a concentration per unit area as another colony receiving ~44% (3 m). When transplanted into an experimental treatment (~38% PAR), a change in pigment concentration was observed for both colonies. The colony from 3 m showed a net increase in chlorophyll a, having a relative increase of 97% PAR. The highest concentration of chlorophyll a at lower light levels most likely increases the efficiency of light capture.

Solar Ultraviolet radiation is an important physical fctor affecting shallow coral reef inhabitants. These wavelengths damage chloroplasts and chlorophyll, resulting in zooxanthellae mortality, and if severe enough, will lead to coral death. This study demonstrates that M. verrucosa colonies adapt to UV by producing S320, a UV absorbing pigment and suggests that this pigment may be essential to survival in a shallow reef environment.

The concentration of S320 is significantly higher in colonies from 3 m than the concentration observed at 10 m, having a ratio of 9:1. Assuming that UV is required to stimulate pigment production, the negative correlation of S320 with depth indicates that the corals are responding to attenuated levels of UV. Dunlap and Chalker (1984) reports similar findings for Acropora on the Great Barrier Reef.

The moderate depth colony was relatively well adapted to a high light intensity - high UV environment, whereas the deep colony was shade adapted with low UV exposure. The shade adapted colony had virtually no protective screening pigment. Consequently, a sudden increase in light intensity and UV resulted in coral death. However, the same colony, in the treatment not receiving UV also suffered 100% mortality, suggesting that strong intensity visible light (PAR) may be a factor. Yet, UV may still be a relevant factor because the cutoff point for the polycarbonate filter does not occur at exactly 400 nm. Radiation in the 380-400 nm range is transmitted and may be at a sufficient level to damage an unprotected coral. This may also explain the increase in S320 observed for all of the UV-blocked treatments. Alternately, S320 production may be stress-related. The results show a trend of higher pigment concentration with increased UV intensity: corals in the full intensity sunlight with a UV transparent filter had the highest S320 concentration, while the shaded treatment with the UV blocking filter had the lowest.

The decrease in chlorophyll a content following transplantation indicates UV incurred damage. After approximately 10 days, the chlorophyll a concentration increased and seemed to equilibrate. S320 increased immediately, providing a UV screen. The UV absorbancy pigment reached maximum level and equilibrium by the 18th day. Except for the extreme case (the deep colony transplanted to full sun), M. verrucosa was able to photoadapt to high light intensity and increased UV radiation within 2-3 weeks.

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Evaluation of some methods for quantitatively assessing the toxicity of heavy metals to corals

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Abstract

The effects of dissolved copper on respiration, nutrient uptake and release, pigments, and zooxanthellae expulsion were investigated in Montipora verrucosa. The LC50 was determined to be 0.048 mg/L Cu (II). No significant change was detected in any other function after exposure to Cu (II) between 0.01 and 1.0 mg/L, except that polyps were visibly bleached and zooxanthellae expelled in proportion to copper concentration and to LC50. Bleaching in response to short-term exposure was slowly reversible in subdued light but was reinstated upon exposure to full sunlight in proportion to loss of the pigment S320. It is proposed that both zooxanthellae and S320 may hold an important place in the self-protection of corals against toxic chemicals.

Introduction

Heavy metals in the tropical marine environment have received little attention with respect to their potential toxic effect on reef-building corals (Mitchell and Chet, 1975; Evans, 1977; Brown and Holley, 1982). Evans (1977) found that continued exposure of Montipora verrucosa and Pocillopora damicornis to a dissolved copper concentration of 0.01 mg/L (as cupric sulphate) killed both species of coral within six days. This concentration was quoted as being slightly above ambient for coastal waters off Oahu, Hawaii (Evans, 1977).

In quantifying toxicity of metals to an organism, one would normally establish a 48 h or 96 h LC50, i.e., those concentrations of a chemical which kill 50% of the test individuals in 48 or 96 h. Herein lies an immediate difficulty in using this approach for corals, as the "individual" may not be easily identifiable or defined: the degree of coloniality which exists between polyps within a coral head will affect the decision as to what may be regarded as an individual (Hubbard, 1973; Shelton, 1979). This relationship may also vary between colonies. Additionally, determining the point of death of a polyp is not straightforward.

There are two approaches to assessing toxicity: 1) acute exposure to relatively high concentrations of toxicant, and 2) chronic exposure to low concentrations. While acute LC50 values are useful for comparing the relative toxicity of various agents to a species or between species, the assay has two major limitations. Firstly, LC50 values do not necessarily imply that 50% of the test individuals survive exposure at that concentration over time; it is possible to have 100% mortality of the organisms some time later, even if they have been removed from exposure to the pollutant. Secondly, the acute LC50 values give no indication as to the lower limit of chronic exposure to a pollutant which would deleteriously affect the growth and reproduction of organisms constituting a population.

There is a need, therefore, to establish methods for quantitatively assessing both the acute and chronic toxic influence of pollutants on coral physiology. Aspects of physiology which might be used are respiration, uptake and excretion of nutrients, loss of symbiotic algal pigment, and inhibition of reproduction and growth. The latter two parameters require long term studies, and, as a more

rapid means of evaluating toxicity would be desirable, the objectives of the investigations described in this paper were: 1) to obtain a 96 h LC50 and 2) to evaluate the use of respirometry, nutrient uptake and excretion, and loss of zooxanthellar pigment as quantitative estimates of the toxic response of Montipora verrucosa to dissolved copper (II).

Materials and Methods

As time for conducting the investigation was limited, it was decided to confine the experimental corals to acute exposure to total copper. A master standard of pure cupric chloride, $CuCl2 \cdot 2 H2O$ was made up in deionized water, equivalent to 100 mg/L as copper (II) (1.57mM Cu^{++}). Test solutions were prepared by appropriate dilution of the master standard with sand-filtered sea water; Cu background was not measured but was assumed to be close to that reported for other coastal waters (about 0.001 mg/L) (Burton, 1976). The proportion of cupric ion at each dilution also was not determined although unionized $Cu(OH)2$ and $CuCO3$ would be expected as significant Cu species (Zirino and Yamamoto, 1972) at the lower Cu concentrations.

Corals

Montipora verrucosa branches were collected from the reef flat on Coconut Island, Kaneohe Bay, Oahu, Hawaii, from a depth of 2-3 m and transferred to holding tanks at the Hawaii Institute of Marine Biology. The corals were maintained in running sea water for 24 h prior to use in experiments and shaded from strong sunlight to prevent possible loss of zooxanthellae. All coral branches used in any given experiment were obtained from the same colony.

Respirometry

Dark respiration of corals was measured using a YSI Dissolved Oxygen Probe Model 57 inserted in a closed volume of filtered sea water (600 mL). A schematic diagram of the experimental system is shown in Fig. 1.

The respiration chamber was placed in a bath of running sea water to maintain constant temperature (about 26 °C). The experimental system was kept in a dark room supplied with red lighting to minimize photosynthetic activity of symbiotic algae. Corals were placed in the respiration chamber and allowed to recover from handling for 30 min. During this period, filtered sea water saturated externally with air was allowed to run through the respiration chamber. The water flow was then shut off and the dissolved oxygen concentration in the chamber monitored for a period of 60 min. The system was then flushed with aerated, filtered sea water for a further 30 min. and either (a) respiration of the coral remeasured over 60 min. (control), or (b) copper (II) solution run through the system for one hour after which time the flow was shut off and the respiration measured over 60 min (tests). Background respiration of the system without corals was measured for both the sea water and copper solutions.

Nutrients

The same experimental system was used as for respirometry. Duplicate water samples were taken before and after incubation for 60 min in the chamber and immediately frozen for subsequent analysis. To test whether the presence of copper in the water samples affected the nutrient analyses, a separate experiment was conducted wherein corals were pre-exposed to copper for 60 min in a separate vessel before being transferred to the respirometry chamber. Water samples were taken from the chamber at the beginning and end of a 60 min period, having first allowed 30 min acclimation. A total of three runs was carried out.

Phosphate, nitrate/nitrite, and ammonium were determined using a Technicon AutoAnalyzer II. Two replicate analyses of each water sample were conducted.

Loss of Zooxanthellae

Quantification of loss of zooxanthellae was attempted using a chlorophyll extraction procedure. Montipora branch tips were exposed to copper (II) concentrations of 0.05, 0.04, 0.03, 0.02 and 0.01 mg/L for 1 h. Controls were maintained in filtered sea water. After exposure, all corals were placed in clean sea water and kept under reduced light for 24 h. The corals were then rinsed in sea water to remove extruded zooxanthellae, ground with a mortar and pestle to a

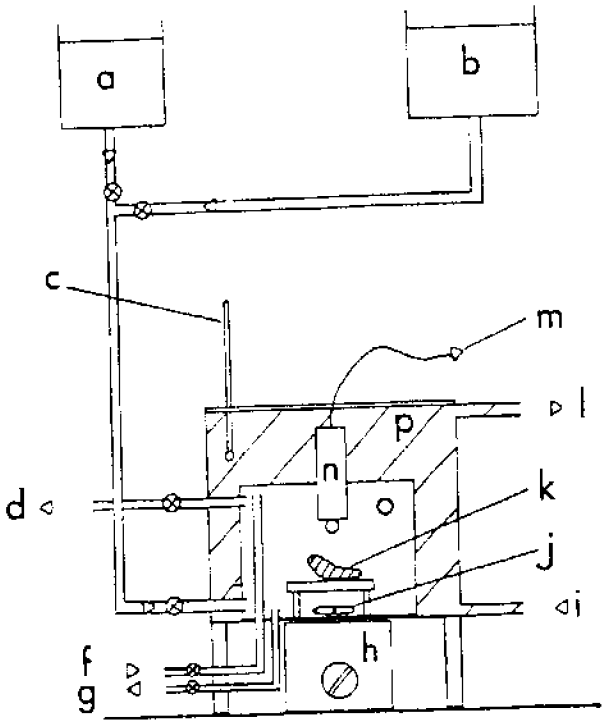

Figure 1
A=Aerated sea water.
B=Aerated copper solution.
C=Thermometer.
D=Respirometry chamber overflow.
E=Respirometry chamber inlet.
F=Air bleed.
G=Nutrient sample port.
H=Magnetic stirrer.
I=Water bath inlet.
J=Stirrer bar.
K=Coral.
L=Water bath outlet.
M=To dissolved oxygen meter.
N=Oxygen electrode.
O=Respirometry chamber.
P=Water bath.

homogeneous paste, and an aliquot removed for chlorophyll analysis. Protein analyses were performed on the same aliquots after extraction of chlorophyll in order to standardize comparisons between coral branches in the form of micrograms chlorophyll-a/mg protein.

Chlorophyll extraction was carried out by adding 4 mL of acetone to the crushed coral sample in a test tube and holding in a refrigerator for 24 h. Each extract as mixed thoroughly before centrifuging and then decanting the supernatent. All samples awaiting processing were kept in the dark, on ice. The supernatents were allowed to warm to room temperature (approximately 30 min) before measuring absorbences at 630 nm and 663 nm (Jeffrey and Humphrey, 1975). Residues from centrifugation were frozen until ready for protein assay. Coral tissues were removed from the skeletal element by digestion in 1 M aqueous sodium hydroxide for 10 min at 50 °C followed by a rinse with deionized water until the skeletal fragments appeared clean. The sodium hydroxide extract was made up to a known volume and aliquots subjected to a modified Lowry protein assay as described by Bartree (1972).

A second series of solutions were prepared with copper concentrations of 1.0, 0.5, 0.1, 0.05 and 0.01 mg/L. Montipora branches were exposed to the copper solutions for 1 h and then kept in 600 mL glass jars containing filtered sea water for 24 h. After this period, zooxanthellae which had been expelled by the corals in response to copper exposure were centrifuged from the sea water and examined under a Zeiss Fluorescence microscope for pigment content. Samples of zooxanthellae which were not expelled from the corals were also inspected after isolation from the crushed tissues. This was achieved by repeated agitation of the crushed coral with chilled sea water and filtering the washings through a 70 micron nylon mesh. Zooxanthellae were centrifuged out, rinsed with filtered sea water, centrifuged again, resuspended in 1 mL of sea water, and an aliquot placed onto a microscope slide for inspection. Counts of fluorescent and non-fluorescent cells were made under both ultraviolet and white light illumination.

96 Hour LC50 Assay

Groups of ten small Montipora branch tips were exposed to copper (II) concentrations in sea water of: 0.10, 0.05, 0.03, 0.02 and 0.01 mg/L. Control corals were kept in filtered sea water. Each branch tip was held in a glass jar containing 100 mL of solution which was changed every 12 h. The corals were inspected regularly and their condition recorded. Corals were deemed dead when polyp tissue could no longer be seen within the calices. The corals were observed for a total period of 164 h.

Histology

Effects of copper at the cellular level were observed simultaneously with toxicity assays. Histological studies were made on corals which had been exposed for one hour to copper concentrations of 0.0, 1.0, 0.5, 0.05, and 0.01 mg/L and kept for 24 h in filtered sea water. A second series of corals was exposed to 1.0 mg/L of copper (II) for one hr before transfer to sea water. Coral samples were removed and fixed every hour thereafter for a period of 6 h in an attempt to observe the process of zooxanthellae expulsion. Corals were fixed in 2% formalin in sea water for 24 h and decalcified with 2% formic acid with several changes over 4 d. Decalcified tissues were processed to wax using an Autotechnicon Model 2A Automatic Tissue Processor. Embedded tissues were sectioned at 6 microns using an American Optical Model 820 Microtome and stained with haematoxylin and eosin for inspection under the light microscope.

Recovery from Exposure to Copper

Branch tips of Montipora were exposed to copper concentrations of 1.0, 0.5, 0.1, 0.05 and 0.01 mg/L for 1 h, placed into tanks provided with running sea water, and inspected regularly to record any recovery which occurred following bleaching.

Small heads of Montipora (approximately 10 cm diameter), exposed to copper concentrations of 0.1, 0.05 and 0.01 mg/L for 1 h, were transplanted onto the reef at a depth of 1-2 m, to compare recovery in holding tanks with that in the field.

Results

Respirometry

Dissolved oxygen readings were found to fluctuate during the first 10 min after closing off the water supply to the respirometry chamber. The reasons for this are unclear but may be related to pressure changes as a result of closing valves or a response to reduced water flow through the system affecting diffusion rates across the electrode membrane. For this reason, oxygen consumption was taken as that drop in dissolved oxygen which occurred between 20 and 60 min. after closing off the water flow. Table 1 compares the decrease in oxygen concentration of sea water containing Montipora branches before and after exposure to 1.0 mg/L of copper (II). It can be seen that there was no consistent effect of copper (II) on respiration rate: there was a tendency for oxygen uptake to decrease after exposure to copper (II), although it actually increased in several samples. Measurements on corals without exposure to copper (II) also showed slight decreases in oxygen uptake. Overall, the mean rate of oxygen uptake for corals before copper (II) exposure was not significantly different from that after copper exposure. Measurements on corals after a period of 24 h also failed to show any consistant effect of exposure even to 1 mg/L Cu II on respiration, although at this point the coral already was bleached. However, respiration in all cases was significantly greater than in seawater alone.

Table 1. Montipora verrucosa: Decrease in oxygen concentration (mg/L/40 min) before and after exposure to copper (II) (1 mg/L).

Before exposure to copper (II)	After exposure to copper (II) 4 h	24 h copper	Background respiration (no coral)
-0.20	-0.15	-0.20	-0.05
-0.30	-0.25	-0.15	-0.20
-0.45	-0.30	-0.35	-0.20
-0.25	-0.20	-0.20	-0.05
-0.45	-0.35*	-0.40*	-0.10
-0.55	-0.50*	-	+0.15
-0.35	-0.40	-	0.00
-0.30	+0.45	-	-0.05
-0.10	-0.15	-	-0.05
-0.20	-0.15	-	-0.05
Mean -0.32**	-0.26		-0.06
S.D. 0.138	0.131		

*Control, not exposed to copper

**Variance ratio of means Before/After: F=1.11(D.f. 9,9), not significant: t=0.42 (D.f. 18), not significant.

Nutrients

Changes in nutrient concentration of sea water containing Montipora branch tips before and after exposure to 1.0 mg/L of copper (II) are given in Table 2. There was no consistent effect of copper (II) on any of the nutrients monitored. Differences between "before" and "after" exposure varied from +0.12 to -0.09 micromole/L for nitrate plus nitrite, 0.07 to -0.14 micromole/L phosphate, and +0.12 to -0.04 micromole/L ammonium. Thus each of the nutrients was taken up in some experiments and excreted in others, with each acting independently of the other two. Control corals exhibited a short term variation in nutrient uptake of a magnitude similar to that observed in copper-exposed corals.

Table 2. Montipora verrucosa: Net change in dissolved nutrient concentration during incubation (umoles/L)*.

Sample	Phosphate			Nitrate/Nitrite			Ammonium		
	B**	A	B-A	B	A	B-A	B	A	B-A
Background (no corals)	-0.01	0	-0.01	-0.03	0	-0.03	0	-0.04	+0.04
Controls (no copper)	-0.04	-0.01	-0.03	-0.17	-0.06	-0.09	-0.12	-0.18	+0.06
	0	-0.03	+0.03	-0.07	-0.19	+0.12	-0.28	-0.40	+0.12
Test (copper exposed)	+0.05	-0.02	+0.07	+0.03	-0.09	+0.12	-0.14	-0.17	+0.03
	+0.02	0	+0.02	-0.12	-0.03	-0.09	-0.16	-0.14	-0.02
	0	+0.12	-0.12	-0.06	-0.10	+0.04	-0.17	-0.13	-0.04
	-0.02	+0.12	-0.14	-0.06	-0.15	+0.09	-0.13	-0.09	-0.04

*Mean of 4 replicates.

**B=Before exposure to copper, A=After exposure to copper.

Loss of Zooxanthellae

Table 3 summarizes the results of chlorophyll assays. Visually, there was a gradation of bleaching proportional to the concentration of copper (II): higher concentrations of copper elicited a greater degree of bleaching. This trend was not supported by chlorophyll per unit protein assays, where an analysis of variance indicated no significant variation between treatments (Table 4).

Table 3. Montipora verrucosa: Mean chlorophyll content of branch tips exposed to a range of copper concentrations (g chlorophyll/mg protein).

Copper (mg/L)	Mean	S.D.	n	Coefficient of Variation(%)
0.00	4.35	0.97	4	22.3
0.01	3.36	0.52	5	15.5
0.02	3.27	0.55	5	16.8
0.03	3.84	1.20	4	31.3
0.04	4.32	0.52	5	12.0
0.05	3.37	0.53	5	15.7

Table 4. Montipora verrucosa: Analysis of variance of mean chlorophyll content of branch tips exposed to a range of copper (II) concentrations.

Source of Variation	Degrees of Freedom	Sums of Squares	Mean Squares
Between treatments	5	6.00	1.20
Within treatments	22	11.70	0.50
Total	27	17.70	

F=2.40 (D.f. 5,22)
F 0.05(5,22)=2.66, i.e., there is no significant difference in variance between treatments.

A further chlorophyll assay was carried out on corals exposed to 1.0 mg/L of copper (II) for 1 h followed by 24 h in sea water. The results (Table 5) indicate a significant difference ($p<0.01$) in mean chlorophyll content between test and control corals.

Table 6 gives the results of microscopical inspection of expelled zooxanthellae. Corals from 1.0 and 0.5 mg/L Cu II exposure appeared equally bleached, with very little color remaining in the polyp. At concentrations of 0.1 mg/L Cu II and less, bleaching visually appeared proportional to copper concentration. Controls retained their normal color. Table 6 indicates that the number of zooxanthellae expelled appeared to be proportional to copper (II) concentration up to 0.5 mg/L. The number of zooxanthellae expelled at 1.0 mg/L Cu II was similar to that for 0.5 mg/L. Corals in control and 0.01 mg/L Cu II did not appear to expel zooxanthellae. The proportion of expelled algal cells which had lost their pigment was also proportional to copper concentration. Zooxanthellae remaining in the coral tissues after exposure to copper (II) appeared healthy in all test concentrations of the metal. Thus, zooxanthellae expelled from Montipora showed a degree of pigment loss proportional to exposure concentration, whereas zooxanthellae retained in the tissues appeared normal. No attempt was made to quantify the number of zooxanthellae expelled as a proportion of the total number present in the coral tissues.

Table 5. Montipora verrucosa: Mean chlorophyll content of branch tips exposed to 1.0 mg/L copper (II) (ug chlorophyll/mg protein).

Sample	Mean	Standard Deviation	n	Coefficient of Variation(%)
Control	4.50	0.64	4	14.2
Test	2.60	0.30	4	11.5

$F=4.55$ D.f. (4,3)
$F_{0.05(4,4)}=6.39$, therefore variances not significantly different.
$t=4.68$ D.f. 6
$t_{0.01(6)}=3.01$, therefore the means are significantly different $p<0.01$)

Table 6. Montipora verrucosa: Proportions of normal and bleached zooxanthellae expelled from branch tips after exposure to a range of copper (II) concentrations.

Copper Conc. (mg/L)	Total Cells Counted	Total Normal	% Normal
1.00	810	19	2.3
0.50	969	118	12.2
0.10	518	74	14.3
0.05	134	76	56.7
0.01	4	4	(100.0)
Control	1	1	(100.0)

96 Hour LC50

Fifty percent mortality figures were obtained for Montipora branch tips at copper concentrations of 0.0, 0.10, 0.05, and 0.03 mg/L. Even after 164 h of exposure, e, /e, only 1 out of 10 Montipora branch tips was dead in 0.02 mg/L Cu II and none were dead at 0.01 mg/L. All corals were bleached by these concentrations and exhibited variable degrees of skeletal exposure, while controls appeared normal. Fig. 2 plots the time taken for 50% of the branch tips to die at each experimental copper (II) concentration and yields a 96 h LC50 of 0.048 mg/L.

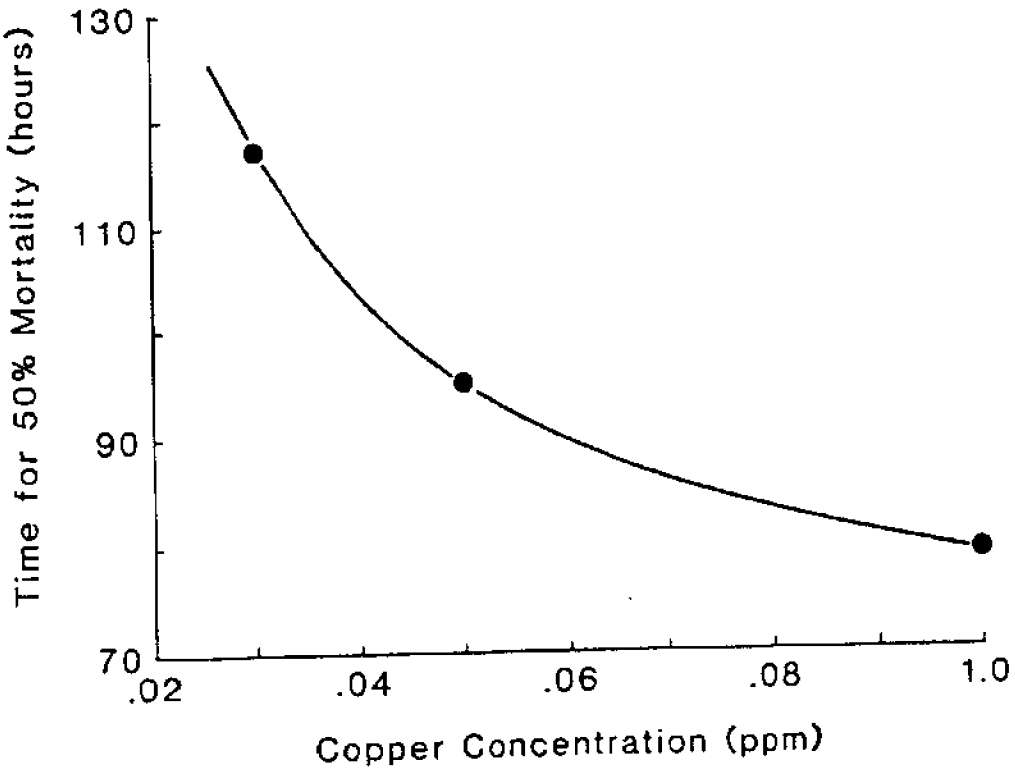

Fig. 2. Time for 50% mortality of Montipora verrucosa at various copper concentrations.

Histology

Inspection of histological sections of Montipora following exposure to copper (II) concentrations of 1.0 and 0.5 mg/L confirmed extensive zooxanthellae loss observed in the experiments described previously. Additionally, columnar ectodermal tissues showed extensive disruption at 1.0 mg/L but not at 0.5 mg/L Cu II. At concentrations lower than 0.5 mg/L, no obvious histological differences from control tissues could be discerned.

The mechanism of expulsion of zooxanthellae was not easily evaluated, as interpretation of the histological sections was difficult. However, zooxanthellae

were observed to lie outside endodermal tissues within the enteron of corals exposed to 1.0 and 0.5 mg/L Cu II but no so in controls nor in corals exposed to concentrations lower than 0.5 mg/L. It is assumed that the zooxanthellae were extruded via the pharynx, although this was not actually observed in the sections. Extruded zooanthellae were invariably bound in thick mucus in all experiments.

Recovery from Exposure to Copper (II).

Laboratory Study

All test corals showed bleaching proportional to copper (II) concentration within 24 h following a 1 h exposure. At concentrations of 1.0 and 0.5 mg/L, large areas of skeleton were exposed due to tissue withdrawal, and there appeared to be some tissue degeneration. After 53 h, extensive diatom growth was recorded on areas of exposed skeleton; polyps were fully retracted but responded to mechanical stimulation and retained some zooxanthellae, especially in the tentacles. Diatom growth was reduced after 77 h, and polyps responded to mechanical stimulation. Between 77 and 197 h (8 d) after exposure, there was no further change in the corals. Change in condition thereafter was slow but gradually improved until by the 22nd d after exposure, although the corals were still bleached at all concentrations of copper, tissue had again covered the skeleton. By the 35th day after exposure, corals at 1.0, 0.5 and 0.1 mg/L Cu II were slightly pale in color compared with controls, although zooxanthellae were distributed throughout the tissues. Corals from 0.05 and 0.01 mg/L Cu II appeared similar to controls. On the 40th day after exposure, all treated corals appeared similar to controls.

During the period of recovery, corals were kept under subdued light. After regaining normal coloration, the corals were placed in full ambient sunlight. Within 48 h, corals had bleached in proportion to the initial copper concentration exposures. Control corals did not bleach.

Field Study

Corals exposed to Cu II for 1 h in the laboratory and then returned to the reef flat showed an early response similar to that of corals maintained in tanks. Montipora branches from 0.10 and 0.05 mg/L Cu II exposure exhibited bleaching, whereas those from 0.01 mg/L showed no difference from controls. However, during the second week after exposure, control corals also developed extensive bleaching on their upper surface coinciding with very low tides, and after 45 days, no apparent recovery had occurred in either test or control corals.

Discussion

The 96 h LC50 of 0.048 mg/L for total Cu is in the range of that reported for many other aquatic species (Black et al., 1976), although no similar data are available for other corals with which it may be compared. This copper concentration is approximately 50 times greater than that of coastal sea water (Burton, 1976) but within the range of concentrations found in highly polluted inshore waters (Zeitoun et al., 1969). The LC50 data also coincided with the observed bleaching and the expulsion of zooxanthellae. Because of this, the outcome of the LC50 experiment must be viewed with concern, as it may be inferred from the other experiments that lower concentrations of copper (II) over a prolonged period of time would have a detrimental impact on coral communities.

The apparent lack of effect of 1.0 mg/L of copper (II) (which may be considered a high concentration) on respiration, is unusual. Copper (II) is well documented as affecting respiration in a number of organisms (Scott and Major, 1972), and respiratory impairment is a primary manifestation of the toxicity of this element. That this was not observed in Montipora suggests that initially, the Cu II may be sequestered by zooxanthellae before the coral itself is affected to any large degree. At low concentrations of copper, relatively few zooxanthellae were lost, but polyps remained withdrawn for several days. Higher concentrations of copper resulted in coral tissue degeneration (initially confined to surface epithelia but ultimately resulting in massive tissue loss and polyp death), and zooxanthellae which were ejected showed varying degrees of pigment loss according to exposure concentration. The effect of copper (II) on the zooxanthellae seem likely to have occurred in the endodermal tissues, but as no

bleached zooxanthellae were observed *in situ* in histological sections, pigment loss may have occurred after ejection as a defensive detoxication mechanism of the polyp.

Experimentation was hampered by great variability in the data. Buddemeier and Kinzie (1976), in their review of methods for assessing coral growth, commented on the variability of data in that "even when systematic variations are allowed for..., a substantial amount of 'noise' remains." Highly variable data also were reported by Barnes and Crossland (1982), where coefficients of variation for calcification in *Acropora acuminata* ranged from 20 to 39% and occurred over time, within and between coral colonies, and within any group of experimental replicates. Similar coefficients of variation in calcification rates and protein assays can be found in data published by Kendall et al. (1983) on the effects of drilling muds on growth and metabolic state of *Acropora cervicornis*.

This latter study made some relevant observations concerning the use of protein assay as a basis for normalization of experimental results. It was found that protein varied significantly over a 24 h period and, furthermore, controls were very different from each other on different days, depending upon the mode of normalization chosen (protein, polyp number, skeletal weight). This may explain why protein-based normalization of the data presented in Table 3 failed to yield statistical support to visual observations of graded bleaching in *Montipora* exposed to a range of copper concentrations; reflectance colorimetry may prove to be a more useful technique for quantifying the bleaching. The graded response also could be due to varying degrees of tissue withdrawal in response to the copper; "bleaching" could be an artifact induced by increased transparency of the tissues as they retracted into the fenestrate skeletal matrix, allowing the skeleton to become more visible. Histological inspection of copper exposed corals support this alternative, inasmuch as zooxanthellae were abundant in the endoderm of corals exposed to 0.05 mg/L Cu II and less. The data presented in Table 6, however, also suggest that few zooxanthellae are expelled from the coral at copper (II) concentrations less than 0.05 mg/L. As protein assays may be influenced by loss of zooxanthellae from the corals, the problems associated with protein as a basis for data normalization are compounded: the evaluation of respiration rates and nutrient uptake must also be normalized in order to make comparisons between experimental groups.

Data variability may be a major obstacle in attempting to establish a truly quantitative sublethal bioassay for coral polyps; any attempt to develop sensitive, quantitative estimates of the sublethal toxicity of metals (or any other chemical) to corals, must deal with the inherent "noise". Evans (personal communication) has suggested establishment of a large data base on natural variation in a range of physiological parameters in corals against which the effect of specific materials could be measured, but financially justifying the large time commitment required to establish it may prove difficult. The use of short term procedures in addition to those described in this paper, e.g., ^{45}Ca growth rates and ^{14}C photosynthetic activity of zooxanthellae, probably would also involve the use of unrealistically high concentrations of metal to be able to statistically separate metal effects from background noise. If it proved impossible to develop satisfactory short term sublethal bioassays for coral intoxication, then the immediate alternative is for the much more restricted long term monitoring of low level exposures of the type described by Evans (1977).

Despite the limiting influence of noisy data in quantifying the effect of dissolved copper on *Montipora*, the observed sensitivity of this coral to very short exposures at low concentrations is remarkable. Branch tips exposed for as little as 1 h to 0.03 mg/L of copper (II) showed initial signs of bleaching within 3 to 4 h after return to clean sea water and were extensively bleached after 24 h. Polyps typically were withdrawn after exposure and remained closed for several days. In the absence of major respiratory or nutrient effect, the action of copper (II) remains unknown but would appear to be prolonged. The copper appears to influence both the coral and zooxanthellae, but attempts to apportion the contribution by either to the overall toxic response is difficult. The results suggest that there is input from the coral and zooxanthellae on an individual basis and that the proportion may depend upon the particular exposure concentration.

The process of expulsion could be stimulated by metabolites from degenerating zooxanthellae and may also initiate coral tissue death. The pathway of expulsion appeared to agree in general with observations of Yonge and Nicholls (1931) insofar as zooxanthellae seemed to be ejected by way of the enteron and pharynx.

One major difference, however, was that zooxanthellae were discharged directly into the enteron from the endoderm, and no evidence was found to suggest transport of zooxanthellae in amoebocytes to mesenterial filaments as described by Yonge and Nicholls. These authors found the mechanism of expulsion to be consistent when elicited by increased temperature, prolonged periods in the dark, starvation or oxygen deprivation. The action of copper on Montipora zooxanthellae thus appears to be different from what may be considered as normal environmental perturbations.

The long term bleaching effect is probably due to the length of time required to regenerate zooxanthellae. The period of five weeks for complete regeneration in Montipora compares with six weeks in Acropora palmata and Montastrea annularis (Jaap, 1979) and eight to twelve weeks in Pocillopora damicornis, Porillopora danae and Porites lobata (Egana and DiSalvo, 1982). An interesting observation in the regeneration of zooxanthellae was the apparent sensitization of the coral to ambient light after recovery under reduced light intensities; the amount of bleaching coincided with the proportion of zooxanthellae which had been regenerated during the five week recovery period. A possible cause is that the regenerated zooxanthellae were not light-adapted and lacked the ultraviolet-absorbing pigment "S320" (Jokiel and York, 1982): subsequent exposure to full ambient light caused the UV destruction of these zooxanthellae.

Measurements of S320 in corals after copper-induced loss of zooxanthellae showed that they contained less S320 than controls (Table 7). Their ratio of chlorophyll-a to S320 suggested that the S320 was associated with the zooxanthellae. Furthermore, incubation of S320 extract with copper (II) did not result in a decrease, which suggests that the action of the copper is on the zooxanthellae and not on the S320. This would support the contention that reduction of S320 in copper-exposed corals is associated with zooxanthellae expulsion and could be verified by measuring S320 in corals before and after recovery of zooxanthellae under both reduced and full light conditions. In the field, a major part of pollution damage to corals may be due to reduced self-protection from UV radiation.

Table 7. Montipora verrucosa: Changes in S320 (absorbance/9mm diameter core) and chlorophyll-a (µg/9mm diameter core) following exposure to 1.0 mg/L copper (II).

Sample	Mean	Standard Deviation	Ratio of S320 to Chlorophyll-a
S320 Test	0.107	0.013	0.104
S320 Control	0.161	0.011	0.093
Chl.-a Test	1.033	0.120	
Chl.-a Control	1.729	0.300	

The longer period required for corals to recover in the field when compared with laboratory studies suggests a synergistic effect of environmental variables on the response of Montipora to copper (II). In view of the sensitivity of Montipora to very short exposures at low concentrations of copper (II), synergism with other perturbants becomes important. Synergistic effects were highlighted by Antonius (1981) when describing the alarming "shut-down reaction" of stressed corals; rapid death of corals can result from exposure to a relatively harmless additional impact which would not normally damage a healthy coral. Synergistic interactions may also underly the recent mass coral mortalities reported on the Pacific coast of Panama (Glynn, 1983).

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Short term copper bioassay on the planula of the reef coral Pocillopora damicornis.

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Abstract

A short term (96 h) copper bioassay was done on the planulae of the reef coral Pocillopora damicornis and the 24 h, 48 h and 96 h median lethal concentrations (LC50) were determined graphically and by formal probit analysis. Concentrations of copper (added as CuCl) ranged from 10-1000 $\mu g\ l^{-1}$ (ppb). A toxicity curve was plotted as the experiment proceeded. Planula under stress showed signs of contraction, mucus-secretion, zooxanthellae-expulsion and breakdown of the body wall. Comparisons with previous studies show the planula of P. damicornis to be the more resistant life stage to heavy metal toxicity, surviving in higher concentrations for longer periods of time than the adult coral colony. In spite of the difficulty in determining death in colonial organisms, the adult coral colony of P. damicornis is recommended for future use in toxicity studies being the more sensitive stage of the coral life cycle.

Introduction

Research into the effects of heavy metal pollution in coral reef systems has increased in recent years (Bryan, 1980 and Howard and Brown, in press). Studies of heavy metal toxicity on hermatypic corals, however, have been limited to qualitative laboratory observations made at various exposure times across a range of concentrations.

The relative sensitivity of larvae and adults of the same species to the heavy metal copper has been investigated in several invertebrate. These include: barnacles (Pyefinch and Mott, 1948), bryozoans, tubeworms, molluscs and brine shrimp (Wisely and Blick, 1967), crabs and lobsters (Conner, 1972), and bivalves (Calabrese et al., 1973, 1974, 1977). In the case of hermatypic corals, however, research has been confined in all instances to the adult stage in the life cycle (Livingston and Thompson, 1971; Sreekumaran and Gogate, 1972; Mitchell and Chet, 1975; Evans, 1977).

The purpose of this study was to establish the range of copper concentrations in seawater that induce lethal and sublethal effects on the planula larvae of Pocillopora damicornis, and to arrive at an approximation of the 24 h, 48 h and 96 h median lethal concentrations (LC50).

P. damicornis is a cosmopolitan Indo-Pacific reef coral. The planula larvae of P. damicornis are 1.5 mm in average length and highly contractile, varying in shape from a sphere to an ellipsoid with the aboral end broader and rounder than the oral end (Edmondson, 1946). They are non-feeding or lecithotrophic, non-calcifying, solitary, planktonic organisms (Harrigan, 1972). The planula is covered by uniform short cilia which function directly after release from adult. Harrigan (1972) observed and classified the movements of planula into 11 classes. For the purpose of this study, these classes have been regrouped into three basic types of behavior. These are: 1. change of body shape, 2. stationary rotation about an oral-aboral axis and 3. active swimming. The total immobilization of the planula can be considered an indication of death (Rand et al., 1975), allowing the measurement and calculation of the LC50.

Materials and Methods

A colony of P. damicornis (approximately 10 cm diameter) was collected and placed in a 3 l container maintained at a flow of 0.5 to 1.0 l m^{-1} of seawater. Water flowing through the containers was channeled into collectors made from plastic beaker bases with walls constructed from 180 micron plankton netting. Collection of newly released was done on 26 June 1983. Release of planulae has been stimulated by warming the water to 35°C for a few minutes (Edmondson,

1946). However, this was not done as this method tends to produce damaged and immature specimens. Three hundred "actively swimming" planulae (i.e., exhibiting all the three modes of movement previously described) were separated and put in Millipore-filtered (0.45 micron) natural, seawater for a 48 h acclimation period. Throughout the acclimation period, temperature of the water was kept constant at 27°C. The seawater was aerated continuously but not changed. Mortality was observed at the end of the accumulation period, prior to the start of the bioassay. It has been suggested that organisms should not be used if at least 1% mortality is exhibited during the 48 h period immediately before the beginning of a bioassay (Rand et al., 1975). This was not observed.

Round, widemouth, clear-glassed jars (472 ml volume) were used in the bioassay. All containers and glasswares were washed twice with detergent, rinsed twice with 50% nitric acid, distilled water and finally with Millipore-filtered seawater. All concentrataions of copper were made using CuCl. The copper ion has been recognized as the toxic form of copper in seawater (Steeman-Nielsen and Wium-Anderson, 1970). A 100 mg l^{-1} stock solution in distilled water was made, from which measured quantities were taken and diluted in Millipore-filtered seawater for the required concentrations of the bioassay. It must be noted that the concentrations in the study are that of added copper. The initial concentration of copper in the water used to make the solutions was not determined.

The selection of test concentrations was made based on the progressive bisection of intervals on a logarithmic scale suggested by Rand et al., (1975). Use of log concentrations where each is 55 to 57% of the next highest concentration assures reasonable accuracy when plotting the toxicity curve.

Ten actively swimming planulae were then placed in each jar previously filled with 100 ml of the test solution (resultant depth of the solution in the jar was 2.2 cm). Two replicates were made for each concentration including two controls which were Millepore-filtered natural seawater. The bioassay was conducted in a shallow holding tank in the shade of an awning. The larvae received indirect natural sunlight. Temperature of the solutions varied from 26.8°C to 27.4°C, being kept relatively constant by submerging the jars halfway in the holding tank which had natural seawater continuously flowing through it. The jars were aerated constantly throughout the 96 h bioassay period by a stream of air from a glass tube. Only glass came into contact with the test solutions and planulae. This was a short term static bioassay. It was not necessary to renew test solutions during the duration of the study. The bottles were covered with parafilm to insure cleanliness.

At the designated time intervals, the planula were observed. Any planulae which remained completely immobile even after gentle prodding with a glass pipette, were recorded as deaths, they were removed and put in fresh Millepore-filtered natural seawater and continuously observed for signs of recovery (i.e., resumption of any form of movement).

The data were analyzed in the manner described by Rand et al., (1975). The median lethal concentrations were determined graphically and through probit analysis and these were then plotted on the toxicity curve. The probit analyses function of the computer language SAS (Statistical Analysis System) was used to obtain the 95% confidence limits and the slopes of the individual determinations of lethal concentrations for different time lengths. The chi-square analysis of the same system was used to test for homogeneity.

Results

The chi-square analyses of the data sets done at each time interval revealed homogeneity of the organisms ($p>0.10$). This was expected as all the test organisms were collected from a single planulating colony of P. damicornis.

Planulae were observed against a bright background. Prior to the start of the bioassay, they were oblong in shape and exhibited dark brown lines of zooxanthellae in their interseptal regions. They were swimming actively, changing in shape at the moment of contact and returning to their original tubular shape after several seconds. The planulae were observed to contract into spherical shapes and remain contracted, however, upon exposure to the copper solutions. This was not observed in the control jars.

As the bioassay proceeded, the planulae in the higher concentrations (i.e., >100 ppb added copper), extruded "filaments" and "nodules," similar to those ob-

served by Rinkevich and Loya (1979) in planulae of the Red Sea coral Stylophora pistillata. The filaments were curled into ring-like shapes and were found mostly near the oral end. The globular nodules containing dark zooxanthellae were found along the body wall of the planula in areas near both the oral and aboral poles. The planula appeared bleached in the later stages (after 6-8 h into the bioassay). Mucus was also observed in the surrounding copper solution. Rinkevitch and Loya (1979) have also observed such mucus-secretion and zooxanthellae-expulsion in planulae under stress. Rotational movement about an oral-aboral axis was still observed at this point. The planulae, however, were highly contracted into flattened, shortened forms. Contraction of this kind has been noted by Edmondson (1946) in planula of P. damicornis exposed to fresh water.

In the later stages of the bioassay, the planulae showed destruction of the body wall. The epithelial layers at the oral end appeared torn. The nodules eventually became disconnected from the body wall but with parts of the wall still attached to them. This was followed by the lysis of the entire planula, i.e., disintegration of the body wall and loss of body form. The planulae now had totally irregular shapes, appearing as masses of mucus and tissue at the bottom of the jars. At this point there was cessation of all modes of movement.

The planulae in the lower concentrations, (i.e., <100 ppb added copper) did not exhibit this destruction of body form. The first effect observed was contraction into spherical shapes, then into more shortened, flattened forms. When prodded, the planula usually contracted more and/or began to rotate on their oral-aboral axis. They appeared "bleached" towards the end of the bioassay and minute amounts of mucus were evident in the surrounding solution. Nodules and filaments were also noted, mostly near the oral end. The nodules did not become detached, however, at any time during the bioassay.

Upon cessation of all modes of movement (even after gentle prodding) the planulae were removed from the copper solutions and placed in natural Millepore-filtered seawater. None of the planulae were observed to revive, (i.e., no resumption of movement was evident). All of them eventually exhibited sloughing off of the epidermal layer, and disintegration of body form after 24 h.

All the planulae in the control jars retained their oblong or responded to prodding by changing shape or by moving. All three modes of movement were exhibited throughout the duration of the experiment. Bleaching was not observed in the controls but minute amounts of mucus were evident in the surrounding solutions. None of the controls settled at the bottom of the jars. The planulae were usually observed at the surface to a depth of about 1 cm. Nodules and filaments were not observed at any time.

The data and median lethal concentrations are shown in Table 1. The graphical estimates for the 24 h, 48 h and 96 h LC50's are shown in Fig. 1. To construct these graphs, percentage mortality was plotted on the vertical axis versus concentration on the horizontal axis. Mortality is on a probability or probit scale and concentration on a logarithmic scale. Because the probit scale never reaches 0 or 100%, such points were plotted with an arrow indicating their true position. Only one successive 0% and one 100% mortality value was used in each calculation, these being the ones nearest the center of range of concentrations. The line was fitted to the points by eye, giving most consideration to points between 16% and 84% mortality (Rand et al., 1975). The graphical estimates are very close to those obtained by formal probit analysis with the computer.

The toxicity curve (Fig. 2) showing the progress of the bioassay was plotted using LC50's determined previously. The curve closely approaches an asymptote with time, but may not quite have reached it. Therefore, no threshhold LC50's were determined in the present study. The 95% confidence limits of each LC50 is reported in Table 1 and is indicated as horizontal bars on the toxicity curve (Fig. 2).

Discussion

All previous work with copper toxicity has been confined to the adult stage of the coral animal. It is now possible to compare the effects of the metal at two different life stages. Evans (1977) exposed adult colonies of P. damicornis to solutions of copper sulfate at concentrations of 10 to 0.01 mg l^{-1} (ppm). At

Table 1. Experimental data. Estimates of median lethal concentration (LC-50) values using graphical and probit analysis at 27°C ± 0.4°C in natural millipore-filtered seawater using chloride solutions.

Concentration of Added Cu (ppb)	Number Dead																	
	2 h		4 h		6 h		8 h		12 h		24 h		48 h		72 h		96 h	
	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56	0	0	0	0	0	0	0	0	1	1	1	1	6	4	7	7	8	8
100	0	0	0	0	0	0	2	0	6	5	6	5	6	5	6	7	8	9
180	0	1	0	1	2	3	7	6	7	8	8	9	10	9	10	10	10	10
320	3	4	5	4	8	8	8	9	10	10	10	10	10	10	10	10	10	10
560	6	7	7	9	8	10	10	10	10	10	10	10	10	10	10	10	10	10
1000	8	9	10	9	10	10	10	10	10	10	10	10	10	10	10	10	10	10
LC-50 graph	556		440		290		190		120		115		90		70		63	
LC-50 probit	552		438		286		195		123		114		87		69		57	
95% Conf. Limits	418 740.21		333 580.84		209 375.33		150 252.56		95 164.88		89 148.58		60 120.03		47 121.39		40 96.32	
Slope-probit	.004		.008		.006		.010		.016		.020		.018		.016		.025	

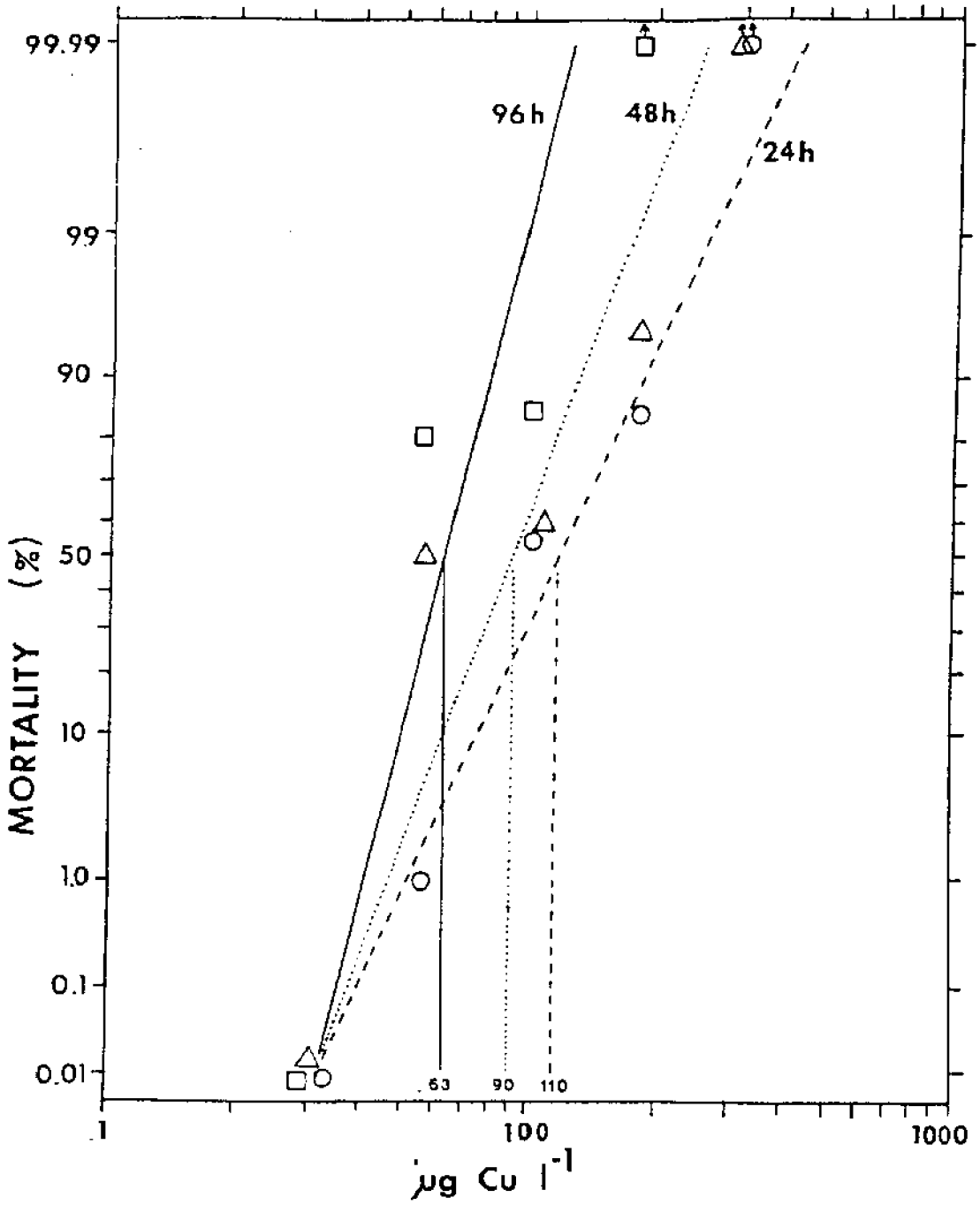

Fig. 1. Median lethal concentration (LC50) as determined by graphical analysis. Legend: 24 Hour LC50 = 115 ppb is represented by circles and dashed line; 48 hour LC50 = 90 ppb is represented by triangles and dotted line; 96 hour LC50 = 63 ppb is represented by squares and solid line.

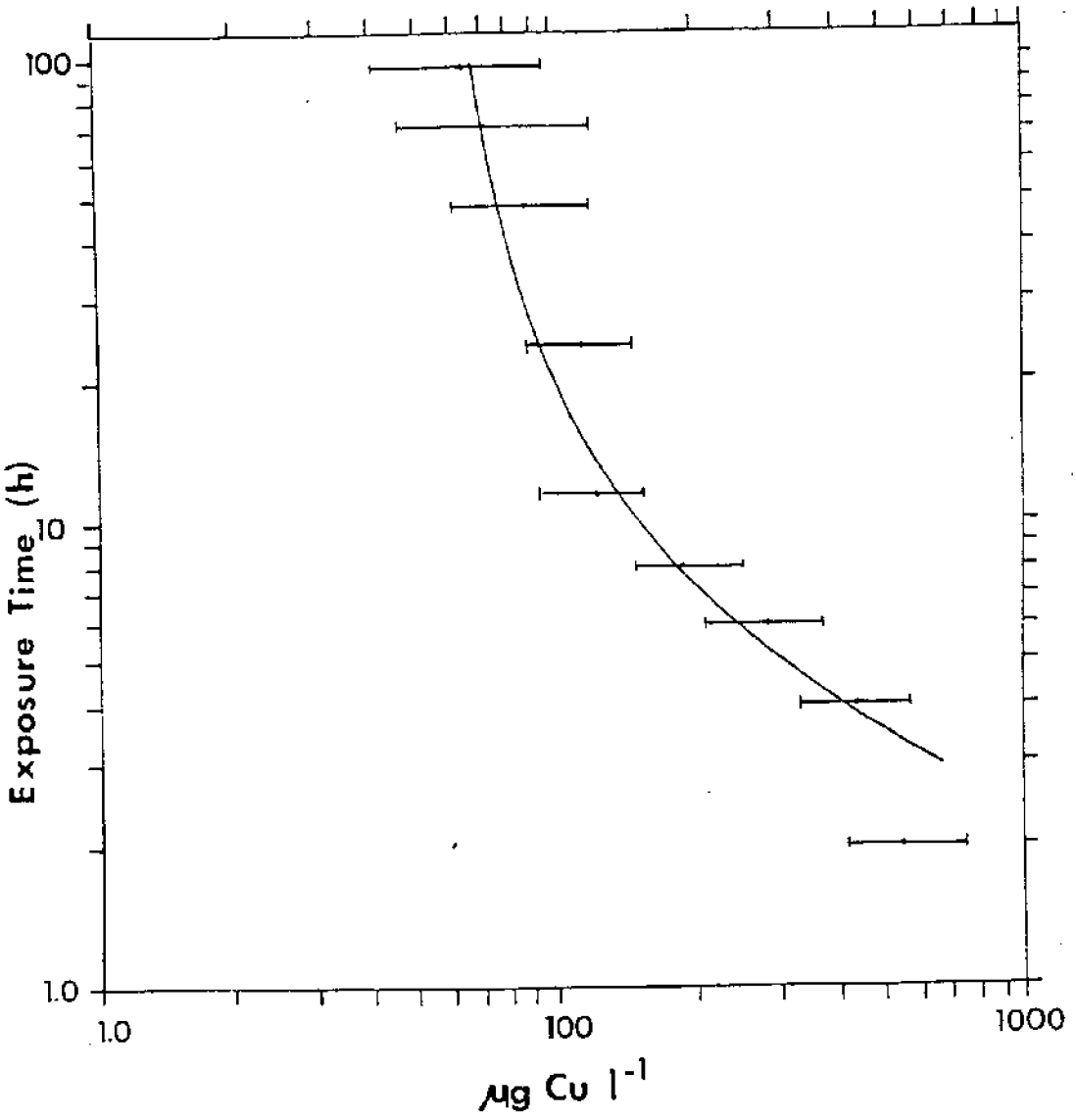

Fig. 2. Graph of the toxicity curve drawn as the experiment proceeded, from LC-50's determined graphically. Curve has become almost asymptotic with the time axis. The 95% confidence limits determined by formal probit analysis are shown for each LC50.

exposures of 0.1 mg l^{-1} Cu (100 ppb) or greater, all coral colonies died within 24 h. Planula used in the present study showed 50% to 90% survival at 24 h exposures of 100 and 180 ppb added Cu. Evans also noted that the coral colonies showed symptoms of "severe stress" with polyps withdrawn and whitened after 48 h exposure to 0.01 mg l^{-1} Cu (=10 ppb). All the planulae in the present bioassay were alive and showing no evidence of stress, i.e., the planula were moving in the three modes of movement previously mentioned and retained their dark brown healthy coloration even after 48 h exposure to 10, 18 and 32 ppb added Cu.

Edmondson (1946) observed the effects of altered saline and thermal conditions in the planulae of P. damicornis and suggested that the planula may be the more resistant life stage of the coral animal. The results of this study support that theory. The planula of P. damicornis appear to be more resistant to heavy metal toxicity than the adult, surviving in higher concentrations for longer periods of time. The causes of these differences in resistance between stages are not clear at the present time. There are marked differences in morphology and physiology between the various stages in the life history of the coral animal.

Various means by which copper is assimilated into the adult coral animal have been proposed by Howard and Brown (in press). In the planula, the copper may be incorporated as soluble metal in food material; it may be directly incorporated by the zooxanthellae; and it may be associated with osmoregulatory or respiratory functions. As the planula is considered a lecithotrophic planktonic organism (Harrigan, 1972), the feeding activities of the planula, (if any) may not represent a significant input of metals. The possible incorporation of heavy metals by symbiotic zooxanthellae and their potential toxic effects on the host coral in terms of possible growth inhibition is discussed in detail by Howard et al. (in press). In both of these pathways, the heavy metals penetrate the tissue where they act intracellularly on metabolic processes. Heavy metal ions might not penetrate the tissues. They could exert their effect by absorbing onto the surface membrane of the organism. This could interfere with such vital processes as respiratory exchange or osmoregulation. Any of these mechanisms could be possible explanations for the contraction, bleaching, mucus-secretion by and lysis of planulae observed in the present study.

In any case, it is evident that further research is necessary in order to ascertain the exact manner by which the copper affects the coral to be able to fully interpret the observations in this paper. In spite of the difficulty in determining death in colonial organisms, the adult colony of Pocillopora damicornis, being the more sensitive life stages, (i.e. less resistant to heavy metals), appears to have a greater potential as a test organism for research in toxicity experiments, pollution control and water quality determinations.

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Preliminary investigations into the occurrence and toxicity of commercial herbicide formulations in reef building corals

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Abstract

Pesticides were detected in several species of reef-building corals inhabiting the Pacific coastal waters of Panamá, an area subject to intense agriculture. Relatively high levels of herbicide residues, notably phenoxy acids (2,4-D and 2,4,5-T), were found in the tissues of stressed corals that had lost symbiotic zooxanthellae and were often in a morbid state. Highest phenoxy acid concentratins reached 8-20 ppb (2,4-D) and 8-19 ppb (2,4,5-T); a combined concentration of 39 ppb phenoxy acids was found in one coral colony. Controlled tolerance experiments testing 2,4-D, MCPP and Tergitol (a dispersant) were performed on Pocillopora damicornis in Hawaii, the same species affected in Panamá. Short duration (24 h) laboratory tests demonstrated drasatic effects (tissue sloughing and death) on corals at 2,4-D concentrations near those found in affected field specimens (0.02 ppm). Although present results demonstrated that herbicides can kill corals at low concentrations and for brief exposures, the natural mortality event observed in Panamá in 1983 was associated with a period of prolonged sea water warming (El Niño Southern Oscillation) that probably also affected corals adversely.

Introduction

This study on the effects of herbicides on reef-building corals was motivated by the detection of herbicide residues, most notably phenoxy acids (2,4-D and 2,4,5-T), in the tissues of stressed and dying corals on the Pacific coast of Panamá. The reef areas initially affected in Panamá border continental shores which are subject to intense agricultural activities (crops and cattle) and high herbicide inputs. Chiriquí Province has a dominantly humid tropical climate with an annual precipitation slightly in excess of 2,500 mm (Anonymous, 1975). Coral mortality in the Gulf of Chiriquí, Panamá, which encompasses a sector of about 10,000 km² (Fig. 1), typically occurred 5-6 weeks after affected corals lost their zooxanthellae (Glynn, 1983). From 50% to 80% of the total live coral cover died on many of the Chiriquí reefs during January-April 1983.

We report here 1) the concentrations of herbicides and the presence of other pollutants in the tissues of affected Chiriquí corals, and 2) controlled tolerance experiments testing 2,4-D, MCPP and Tergitol (a dispersant) on corals in Hawaii. The test species, Pocillopora damicornis (Linnaeus), is present in similar habitats in Hawaii and Panamá, and is the most abundant coral that suffered heaviest mortality in Panamá. While these observations and experiments are limited in scope, their publication seems justified in view of the scant information available on pesticide effects to coral reefs.

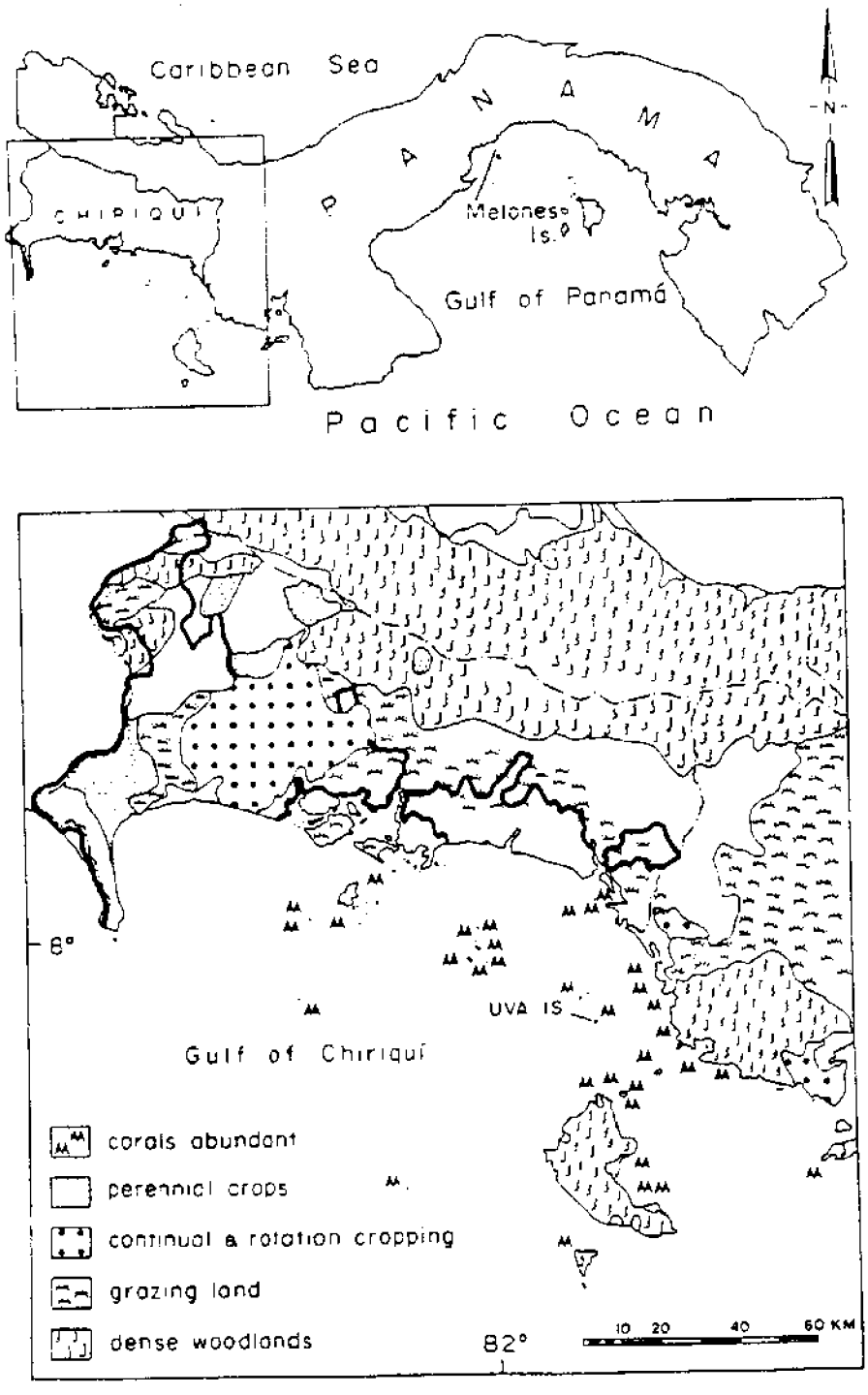

Fig. 1. Gulf of Chiriquí and Chiriquí Province, Panamá.

Materials and Methods

Coral tissue extraction

Pieces of coral, 12-25 g wet wt., were broken from eight species (Table 1) of field specimens in Panamá (Uva Island, Gulf of Chiriquí), wrapped immediately in aluminum foil and frozen in preparation for herbicide analysis. Corals wrapped in aluminum foil were broken into small pieces and transferred to pre-weighed 250 ml round-bottom flasks. Coral and flask were weighed and 150 ml 1:1 acetone-ether was added. Each sample was spiked with 20 µl of Silvex in acetone. The aluminum foil was rinsed with an additional 10 ml of ethyl-ether, added to the round-bottom flask. The tissue was digested by refluxing gently in a soxhlet flask for 12 h. The digest was added to a 500 ml separatory funnel. The digestion flask was rinsed with an aliquot of ethyl-ether which was added to the funnel. The ethyl-ether digest was washed with acid water to remove the acetone and decanted. The ether extract was poured into a 300 ml round-bottom flask containing 15 ml distilled water, 2 ml of 37% KOH solution and two to three teflon boiling chips. A three ball Snyder column was fitted. The ether was evaporated in a steam bath for 30 minutes. The basic aqueous solution was transferred to a 125 ml separatory funnel, washed twice with 20 ml portions of ethyl-ether and the ether was discarded. The aqueous layer was acidified with 2 ml of 25% sulfuric acid and extracted with 20 ml, and then twice with 10 ml of ethyl-ether. The ether extracts were combined and dried over 1 g of acidified anhydrous sodium sulfate. Then the extracts were transferred to a 25 ml evaporator tube and 0.5 ml of benzene was added. A Snyder column was fitted and the contents were concentrated in a water bath. The concentrated extracts were removed from the water bath and allowed to cool before adding 0.5 ml of 14% boron-trifluoride-methanol esterification reagent. They were again placed in the water bath for 30 minutes at 50 °C. After removing them from the water bath, 8.5 ml of 5% sodium sulfate solution were added and they were mixed on a vortex mixer.

Florisil chromatography separation

A glass Pasteur disposable pipet was packed with a small wad of pre-extracted glasswool, one inch of florisil, one-half inch of anhydrous sodium sulfate and a thin layer of Nuchar-Attaclay by tapping the pipet to ensure uniform packing. The contents in the evaporator tube were added to a 5 ml volumetric flask and the benzene layer was pipetted from the flask and placed on the florisil pipet column until all the benzene in the volumetric flask was removed. More benzene was added to the volumetric flask and the operation was repeated until 5 ml of sample was collected in an 8 ml vial and covered with aluminum foil and a screw top. The samples were then analyzed by gas chromatography.

Water extraction

The method used for the extraction of water samples is similar to the coral tissue extraction except that one l of water sample, acidified with sulfuric acid, was transferred to a two-liter separatory funnel and 100 ml of diethyl ether was added. The sample was shaken vigorously for two minutes and sufficient time was allowed for complete phase separation. The lower aqueous layer was drained and the upper ether layer was poured into a 500 ml Erlenmeyer flask containing two grams of acidified anhydrous sodium sulfate. The above procedure was repeated with another 100 ml of diethyl ether. The ether extracts were combined and dried over one gram of acidified anhydrous sodium sulfate for approximately two hours. The extract was then transferred to a Kuderna-Danish assembly consisting of a 250 ml K-D flask attached to an evaporative concentrator tube containing two teflon boiling chips. The extract was concentrated to 5 ml in a water bath and the same esterification and chromatographic procedure was carried out as for the corals.

Gas chromatography

A tracor gas chromatograph Model 222 equipped with 2 nickel-63 electron capture detectors was employed and nitrogen was used as the carrier gas. A 6 ft glass column (2 mm ID) packed with 4% SE30 and 6% OV210 on 100.120 mesh Supelcon was used. Gasflow at 45 ml min^{-1}, column temperature at 180 °C, detector temperature at 250 °C and the inlet temperature at 210 °C were maintained.

Energy dispersive X-ray analysis

Oven-dried (60 °C) corals were examined for the presence of heavy metals using energy-dispersive X-ray (EDX) analysis. All analyses were done within one week of coral collection. The oven-dried samples were chipped further. Small, flat-surfaced specimens of less than 1 cm square were selected for EDX analysis. Each sample was mounted on a carbon stub with an isopropyl alcohol-based glue. They were sputter-coated first with a gold film of about 500 Å thickness followed by a graphite coating. An empty stub was coated identically to serve as the control sample and its EDX spectrum served as the background spectrum. The sample was placed in a scanning electron microscope and examined with an electron beam of 15kV. A Si-Li (drifted) detector was used to collect the emitted X-rays and a Kevex 7045 EDX System was used for data analysis and element identification. The data analysis included the normalization of the EDX spectrum of the sample with the background spectrum followed by its subtraction. The gold M-series X-ray peak at 2.14 KeV was used as the normalization peak. Scanning time was about 200 seconds.

Few data are available on detection limits for EDX analysis. The reported value for Na is 0.195 wt %, while it is 0.085 wt % for Ca (Goldstein et al., 1981). EDX sensitivity to heavier elements is much higher than that for Na and Ca. The detection limits for these elements using atomic absorption spectrometry are 0.0003 and 0.0005 µg/ml respectively. For an elemental analysis by atomic absorption using a 100 mg sample dissolved in 10 ml of solvent, and assuming that the coral organisms make up less than 0.01% of the total weight sample on a dry weight basis, the atomic absorption detection limit would be 0.03 and 0.05 wt % for Na and Ca in the coral tissue. The observed differences in detection limit for the two methods only applies if one is interested in elemental composition of the entire sample. In the case of corals our interest was in elemental composition of the coral tissues and the outer layer of coral skeleton. Because the EDX method is able to examine only those specific areas of interest, the effective sensitivity of the method is much higher than it appears. Two additional advantages of using the EDX technique are 1) it can determine if an element is localized in one spot (as a contaminant) or if it is evenly distributed in the sample. This separation is not possible with techniques that require sample dissolution; 2) the EDX results are affected by whether an element is organic or inorganic bound. Frequently the solubility behavior of an element organic bound is different from that observed when it is inorganic. EDX is independent of solvent extraction efficiency or limits of compound solubility.

Tolerance tests

A commercial herbicide sold under the trade name of "Weed-B-Gon" (marketed by Chevron, EPA Registration No. 239-2499-AA) was obtained from a local gardening supply center in Kaneohe, Hawaii. The manufacturer's description of ingredients was given as: "Dimethylamine salt of 2,4 dichlorophenoxyacetic acid (0.20%). Dimethylamine salt of 2-(2 methyl 4 chlorophenoxy) propionic acid (0.20%). Inert ingredients 99.60%." The latter compound is also an herbicide and in the acid form is known as MCPP. Although not used as commonly as 2,4-D it is similar in structure and has almost as great a toxicity with an LD-50 of 650 as compared to 500 for 2,4-D. This herbicide was selected for study because one of its active ingredients, 2,4-D, was found in relatively high concentrations in affected field corals, and because many of the herbicides in use in Panamá contain 2,4-D.

The reef-building coral Pocillopora damicornis served as the test species in the tolerance experiments. Specimens were collected from 1-2 m depth on the fringing reef at Coconut Island, Kaneohe Bay. An initial range-finding experiment (A) was set up to assess the possible toxicity of the herbicide to Pocillopora: Dilutions of the herbicide were prepared with filtered sea water to give final concentrations of the 2,4-D amine salt of 100.00, 10.0, 1.0, and 0.1 ppm. MCPP was also present in equal concentrations. Three small colonies of Pocillopora, 4-6 cm in diameter, were placed in 600 ml of each of the solutions for 24 h. The solutions were renewed after 12 h. All test solutions and controls were aerated throughout the experimental period.

Based on the results obtained in A above, a second series of exposures at identical concentrations (B) were conducted. For this experiment, pure 2,4 dichlorophenoxyacetic acid was used. Since the solubility of the acid in sea wa-

ter was very low it was necessary to convert the acid to the sodium salt. This was accomplished using a minimum volume of N 1. NaOH to dissolve the acid followed by dilution with sea water. No precipitation of the sodium salt was observed.

Five liters of each of a series of solutions were prepared equivalent to 2,4-D concentrations of 1.00, 0.10 and 0.05 ppm. In order to determine the 'start' and 'finish' concentrations of 2,4-D in the test solutions, one liter samples of each solution, plus control, were preserved in cleaned 'Nalgene' plastic bottles to which 5 ml of concentrated H SO had been added. Three small colonies of Pocillopora (4-6 cm) were placed in each of the test solutions for 12 h and provided with aeration.

At the end of 12 h one coral colony from each test solution, plus control, was wrapped in aluminum foil and frozen for later analysis of tissue concentrations of 2,4-D. The remaining two colonies from each solution were placed in clean running sea water for observation over 7 d.

Based on the results obtained in B, a re-run of A was conducted, but using "Weed-B-Gon" 2,4-D amine salt concentrations of 10.0, 1.0, 0.5 and 0.1 ppm (C). Corals were exposed to herbicide for 24 h then placed in clean running sea water for observation.

As for C above, corals were exposed to "Weed-B-Gon" 2,4-D amine salt concentrations of 10.0, 1.0 and 0.1 ppm plus controls (D). Water samples were taken for before and after exposure. One coral colony per treatment was wrapped in aluminum foil and frozen for later analysis.

Many herbicides contain wetting agents. It is not known whether "Weed-B-Gon" contains a wetting agent but it certainly possesses detergent properties. One chemical often used as a wetting agent is "Tergitol NPX" marketed by Union Carbide. This agent is normally used at a concentration of 0.25 to 0.50% by volume in the herbicide. A 0.50% solution was made up in sea water and a series of dilutions made with sea water to give concentrations of 25.0, 2.50 and 0.25 ppm Tergitol. These dilutions were the same as those used for "Weed-B-Gon" to give concentrations of 10.0, 1.0 and 0.1 ppm of the 2,4-D amine salt. Three colonies of Pocillopora were exposed to each solution, plus control, for 24 h, then transferred to clean sea water. All samples received aeration during exposure to the detergent.

Two tests were performed with "Tergitol NPX" at low concentration (0.025 ppm) and elevated sea water temperatures. Each group of coral (3 colonies) was held in 3 l of aerated sea water. The first test lasted 24 h and comprised the following treatments: 1) Tergitol and normal sea water temperature (25 - 27 °C), 2) high variable sea water temperature, elevated from 25.7 °C to 34.5 °C over a 4 h period, and then allowed to cool gradually to ambient temperature, 3) Tergitol and high variable sea water temperature (as in 2 above). The second test lasted 66 h and comprised the following treatment: 1) Tergitol and normal sea water temperature (26 - 27 °C), 2) high, relatively constant sea water temperature (28.2 - 31.8 °C), 3) Tergitol and high sea water temperature (as in 2 above). The corals were transferred to tanks with running sea water after each test and their condition observed for 1 week.

Results

Coral tissue analyses

Phenoxy acid concentrations ≥10 ppb were detected in four of the eight coral species analyzed (Table 1). All bleached corals contained relatively high concentrations of herbicide and 2,4-D was present generally in higher amounts than 2,4,5-T (2,4,5-trichlorophenoxyacetic acid), in 9 of 12 specimens. However, some species that appeared in normal condition, e.g. Pocillopora damicornis and Psammocora stellata (Verrill), had relatively high concentrations of phenoxy acids, whereas partially bleached or bleached conspecifics had lower amounts. No herbicides were found in an apparently normal coral (Pocillopora damicornis) sampled in the Gulf of Panamá (Fig. 1), but a partially bleached coral, (Pavona varians, Verrill) sampled in Chiriquí was also herbicide free.

Insecticides found in Panamanian (Pacific) coral tissues included P, P' DDT; O,P' DDT; O,P' DDD; P,P' DDE; Lindane, Endrin ketone 153, Endrin, Dieldrin, Ethion, Endosulfan I, Chlordecone and Dimethoate. Two plasticizers were also identified, BBP (butyl benzyl phthalate) and DEHP (di-(2-ethylhexyl) phthalate).

Table 1. Phenoxy acid concentrations in coral tissues at Uva Island, Gulf of Chiriquí, 28 April 1983.

Coral species	Condition	ppb concentrations (ng/g dry wt.) 2,4 D	2,4,5 T
Millepora intricata Milne-Edwards	bleached	15.850	2.050
Pocillopora damicornis	normal	20.050	19.380
	partially bleached	1.330	2.140
	bleached	7.729	3.860
	normal[1]	ND[2]	ND
Pocillopora elegans Dana	partially bleached	1.290	0.376
Pavona clavus Dana	partially bleached	2.920	0.640
Pavona varians	normal	0.199	0.907
	partially bleached	ND	ND
	bleached	16.710	8.170
Gardineroseris planulata Dana	partially bleached	4.326	2.840
Porites panamensis Verrill	bleached	8.630	1.160
Psammocora stellata	normal	12.080	10.850
	partially bleached	2.690	3.973

[1]Collected at Melones Island, Gulf of Panamá, 5 May 1983

[2]None detected.

In the EDX analysis, Ca and Cl were the two most widely found elements in both sxeletons and tissues of eight coral species exaained (Table 2).

Herbicide tolerance tests

In the range-finding experiment with "Weed-B-Gon" (A), considerable mucus production by the corals was observed within three hours of exposure to herbicide concentrations of 1.0 ppm and greater. Corals in 0.10 ppm 2,4-D were producing mucus after 12 to 18 h of exposure. The process of tissue loss appeared to result in the release of polyps from the calices. The condition of the test corals after 24 h exposure is given in Table 3.

Exposure of Pocillopora to 'pure' 2,4-D (sodium salt) in concentrations ranging from 0.1 to 100.0 ppm (B), showed no apparent effects. After seven days all coral colonies were of 'normal' color with polyps fully open. Mucus production was not observed at any stage.

In light of the results from (B) a repeat of experiment (A) was conducted using concentrations of the "Weed-B-Gon" 2,4-D amine salt ranging from 0.1 to 10.0 ppm (C). All corals suffered complete tissue loss within 48 h (Table 4). The mechanism of tissue loss was similar to that observed in (A) with apparent polyp bail-out (Sammarco, 1982) although 48 h elapsed before coral death occurred compared with 24 h in (A). Considerable amounts of mucus were found in the water containing dead corals. Planulae released from corals were of normal appearance, were very mobile and possessed zooxanthellae. Settlement of the planulae was not observed.

Results from experiment (D) were similar to (C) in so far as planulae were released by corals in all test solutions but not by controls. Coral death, however, was recorded only at the highest concentration of "Weed-B-Gon" (10.0 ppm 2,4-D amine salt) although corals in 1.0 ppm 2,4-D amine salt appeared to be stressed and the 0.1 ppm 2,4-D amine salt solution was turbid (Table 5). The initial, before and after concentrations of 2,4-D and MCPP in the test solutions containing corals are given in Table 6. Initial concentrations of herbicide solutions and the actual concentrations found in the water at the beginning and termination of the experiment are shown. The differences in concentration between initial and before represent the loss to the glassware, and the differences in concentration before and after represent the loss primarily due to uptake by the coral. Although the MCPP also had initial concentrations from 0.1 to 10.0 ppm, the actual concentrations indicate that most of this herbicide was probably lost to the glassware.

The corals were exposed to different concentrations of 2,4-D Na^+ and 2,4-D ($CONH_2$) and the extent of accumulation of these herbicides is given in Table 7. The maximum concentration found in coral tissues was 0.137 ppm 2,4-D ($CONH_2$) at an initial concentration of 10.0 ppm. An increase in the initial concentration of herbicide, from 0.10 to 10.0 ppm, did not necessarily increase the uptake by the coral. MCPP was not detected in the corals but was detected in the test solutions. Since none was detected in the corals, this would also indicate that it was absorbed to the glassware.

The Tergitol NPX disperant showed an adverse effect on corals at a concentration of 0.25 ppm. All corals were dead after 2 d when exposed to this dispersant for 24 h (Table 8). Corals exposed to a low concentration of Tergitol (0.025 ppm) and high temperatures were still alive and appeared normal after 1 week. In the experiment with a high variable temperature, all corals planulated and the polyps remained expanded during the 24 h test period. In the 66 h experiment, a combined treatment with Tergitol and elevated temperature, one coral whitened slightly and retracted its polyps.

Discussion

It is significant that relatively high phenoxy acid concentrations, in the range of 10-20 ppb, were found in coral tissues in Panamá, especially in an area of high insolation, strong tidal flux and warm sea temperatures. Such environmental conditions tend to hasten the breakdown of phenoxy acid herbicides. The presence of these labile chemicals, as well as Ethion and Dimethoate, suggests a large and/or constant source of the material entering the reef areas.

A registry of pesticides consulted in the Health Ministry (Republic of Panamá) listed seven approved herbicides whose main active ingredients are phe-

Table 2. Elemental composition of corals collected at Uva Island, Gulf of Chiriqui, 28 April 1983, based on EDX analysis.

Coral species	Condition	Sample	Element
Millepora intricata	bleached	bulk[1]	Ca
		surface[2]	Ca
Millepora platyphylla Ehrenberg	dead	bulk	Ca
		surface	Ca
Pocillopora damicornis	normal	bulk	Ca,Sr(?) or Si
		surface	Ca,Cl,S,P,K,Mg
	dead	bulk	Ca,S,Sr(?) or Si
		surface	Ca,Cl,S,P,K,Mg,Na,Zn(?)
Pocillopora elegans	bleached	bulk	Ca
		surface	Ca,Cl,Mg,Na,Si,K
Pavona gigantea Verrill	normal	bulk	Ca
		surface	Ca,Cl,Mg,Fe,Si,Na,K (Ti,Mn,Rb,Zn,Cr,V)?
Pavona clavus	bleached	bulk	Ca,Cl
		surface	Ca,Mg
Pavona varians	partially bleached	bulk	Ca,Mg
		surface	Ca,Cl,Mg,Fe
Gardineroseris planulata	partially bleached	bulk	Ca
		surface	Ca,Cl,Si,Mg

[1]Broken skeletal face, 2-3 mm below colony surface.

[2]Colony surface, with adhering tissues except in two dead specimens.

Table 3. Results of range-finding tolerance of *Pocillopora damicornis* to "Weed-B-Gon" (A).

2,4-D amine salt concentration (ppm)	Condition of corals after 24 h
100.0	Dead; complete loss of tissues from skeleton.
10.0	Dead; tissues sloughing off; large areas of bare skeleton.
1.0	Dead; complete loss of tissues from skeleton.
0.1	Morbid; tissues sloughing off; small areas of bare skeleton.
control	Appeared normal; polyps open.

Table 4. Condition of Pocillopora damicornis after exposure to "Weed-B-Gon" (C).

2,4-D amine salt concentration (ppm)	Condition of corals after 24 h	after 48 h
10.0	Appeared normal; many planulae released.	Dead; complete loss of tissues from skeleton.
1.0	Appeared normal; 10-20 planulae released.	Dead; complete loss of tissues from skeleton.
0.5	Appeared normal; 1-2 planulae released.	Dead; complete loss of tissues from skeleton.
0.1	Appeared normal; no planulae released.	Dead; complete loss of tissues from skeleton.
control	Appeared normal; no planulae released.	Appeared normal.

Table 5. Condition of Pocillopora damicornis after exposure to "Weed-B-Gon" (D).

2,4-D amine salt concentration (ppm)	Condition of corals after 24 h.	after 48 h.
10.0	Appeared normal; many planulae released.	Dead; complete loss of tissues.
1.0	Appeared normal; many planulae released.	Appeared stressed; water very turbid.
0.1	Appeared normal; many planulae released.	Appeared normal; water slightly turbid.
control	Appeared normal; no planulae released.	Appeared normal; many planulae released.

Table 6. Herbicide concentrations in laboratory test solutions.

Initial concentration (ppm)	Compound identified	Concentrations (ppb) before	after
Control	-	-	-
0.1	2,4-D	3.29	2.52
	MCPP	ND[1]	ND
1.0	2,4-D	60.78	4.97
	MCPP	1.37	ND
10.0	2,4-D	309.53	95.67
	MCPP	13.61	11.33

[1]Not detected.

Table 7. Herbicide concentrations detected in laboratory test coral tissues.

Compound	Initial concentration (ppm)	Concentration (ppm) 2,4-D	MCPP
Control	0	ND[1]	ND
2,4-D Na+	0.05	0.050	ND
	0.10	0.010	ND
	1.00	0.119	ND
2,4-D (CONH2)	0.10	0.133	ND
	1.00	0.103	ND
	10.00	0.137	ND

[1]Not detected.

Table 8. Condition of Pocillopora damicornis after exposure to the wetting agent Tergitol NPX.

Tergitol NPX concentration (ppm)	Condition of corals after 24 h	after 48 h
25.0	Dead; extensive loss of tissues; water green	Discontinued
2.50	Polyps withdrawn; water turbid	Dead; extensive loss of tissue
0.25	Appeared normal.	Dead; extensive loss of tissue
control	Appeared normal	Appeared normal

noxy acids. The amine salt of 2,4-D is the chief component in six of the herbicides, and the seventh (D2T2) contains both 2,4-D and 2,4,5-T.

Chiriquí Province, which borders the Gulf of Chiriquí to the north and west, is a highly productive farming region in Panamá. In absolute terms, Chiriquí and Veraguas (immediately east of Chiriquí) Provinces have the largest land areas under exploitation (Anonymous, 1975.) Five of the principal crops in Chiriquí in 1983, and the respective areas under cultivation, were corn, 2,000 ha.; sugar cane, 5,000 ha.; sorghum, 5,500 ha.; banana, 7,000 ha.; and rice 22,360 ha. (Gisela de Rangel, Departamento de Sanidad Vegetal, personal communication). Herbicides are applied regularly to these crops by aerial spraying. The recommended doses are slightly below 1 l ha^{-1}. However, it is highly probable that the recommended doses have been exceeded in some areas. Claims have been made by local farmers that crop dusters dump excess herbicides directly into the Gulf of Chiriquí before landing.

The universal presence of Ca in the elemental analysis of surface and bulk samples is probably due to the high calcium carbonate content of the coral skeleton. Chlorine was also commonly present, mainly in surface tissues. This could be due to natural salts and/or chlorinated pesticides in coral tissues. There was no evidence of heavy metal contamination based on EDX examination.

Some of the laboratory tolerance tests demonstrated dramatic effects on corals at 2,4-D concentrations near those found in the tissues of affected field specimens (0.02 ppm). Coral tissue sloughing and death occurred after exposure to the herbicide "Weed-B-Gon" (in 2 of 3 experiments) at a concentration of 0.1 ppm 2,4-D amine salt. Since these laboratory exposures were of short duration, not exceeding 24 h, it is possible that longer exposure at lower concentrations would also cause morbidity and death in corals.

The variable response of Pocillopora to similar concentrations of "Weed-B-Gon" in different experiments may be attributable to the changing physiological state of the corals. Pocillopora has a monthly planulation cycle and as experimentation spanned a period of two weeks, release of planulae from test corals but not controls in the latter two experiments, and the progressively longer time required to result in coral death at 0.1 ppm 2,4-D amine salt, suggests that changes associated with reproductive cycle may have influenced coral response to the herbicide. This may prove to be an important consideration in future toxicological studies on corals.

Two herbicides tested on Hawaiian Pocillopora damicornis by Lamberts (1983), at low concentrations (0.01-2.0 ppm) for 24 h, produced no evidence of injury. One of the herbicides tested was 2,4-D. Since concentrations were not reported in affected field corals, from an extensive kill of unknown cause in American Samoa, or in the test water and tissue in the laboratory studies, it is difficult to compare Lamberts' results with those reported here.

It should be noted that the toxic herbicide concentrations detected in the laboratory test coral tissues were notably lower than the initial concentrations. Also, since the MCPP herbicide tended to absorb to the glassware, it can be concluded that the killing effect was due largely to 2,4-D.

Because pure 2,4-D produced no apparent effect over a range of concentrations (0.1 to 10.0 ppm), it was reasoned that a wetting agent may also adversely affect corals. Tergitol NPX, a commonly used dispersant, did cause coral death at 0.25 ppm. Tergitol at a lower concentration (0.025 ppm), and in combination with high temperatures (32°-34.5 °C), produced no apparent damage to corals. This result was unexpected because previous studies in Hawaii have shown that elevated temperature alone, from 4 °C to 5 °C above ambient to 32°C, causes death in Pocillopora damicornis in 3 to 5 days (Jokiel and Coles, 1974; Coles et al., 1976; Jokiel and Coles, 1977).

While present experimental results demonstrate that herbicides can have a deleterious effect on corals, at relatively low concentrations and for brief exposures, the coral mortality that occurred recently in Panamá and elsewhere in the eastern Pacific (Glynn 1984; in preparation) can not be attributed to herbicide effects alone because of other confounding factors. The tropical eastern Pacific region was subjected to a very strong El Niño event during 1982-83, probably the strongest this century in terms of equatorial sea surface warming (Kerr, 1983). The warm water anomaly exceeded 4 °C over large areas of the eastern equatorial Pacific and even reached 6 °C in places (Rasmusson and Ball, 1983).

It can be reasoned that the high levels of herbicides in Chiriquí corals, in combination with an unusually prolonged warming spell, could act additively and thus lead to coral mortality. However, massive coral death also occurred in the Galápagos Islands, in coincidence with the 1982-83 El Niño, but in this area pesticide use is nil. In the light of these results, coral death and El Niño warming show the strongest correlation. Still, the high levels of phenoxy acids present in affected field corals, and the demonstrated laboratory effects, make it difficult to dismiss the possibility that herbicides also played a role in the Chiriquí coral death.

Acknowledgments

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Isolation and culture of symbiotic algae

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Abstract

Techniques for the isolation and culture of symbiotic algae are described. Freshly collected invertebrates are cleaned with sodium hypochlorite before removal of symbionts. The symbionts are suspended in clean seawater, passed through filters, and isolated with modified Pasteur-type pipets under stereo microscopes. Clone cultures have been the most successful and have been maintained for years.

Introduction

Several methods for isolating microscopic algae are described in chapters in The Handbook of Phycological Methods (Stein 1973). Other chapters in the same text discuss media, sterilization and culture. Using a modification of the Pasteur-type pipet technique, clones of symbiotic algae have been isolated from various marine invertebrates and added to the Algae Culture Collection of the University of Hawaii. After learning this technique during the 1983 Summer Program in Marine Science at the Hawaii Institute of Marine Biology, Laurie Read successfully isolated and cultured clones of Symbiodinium microdriaticum from the coral Pocillopora damicornis.

Preparation

Pasteur pipets (23 cm long) are stretched thin by melting the narrow section over an alcohol burner flame and pulling on the ends as they are removed from the flame. After cooling, they are bent until they break at the stretched part. The inside diameter should be about 100 microns at this point. The other end is plugged with cotton. The pipets are autoclaved in a cylinder that is also cotton plugged. All flasks, pipets, and test tubes are cleaned with laboratory detergent, thoroughly rinsed with distilled water, rinsed with 10% hydrochloric acid, rinsed again with distilled water, cotton plugged and autoclaved. The filtration apparatus and dissecting instruments are autoclaved. Seawater and nutrient stock solutions are filter-sterilized through 0.1-micron pore size polycarbonate membrane filters and stored in fluorocarbon (e.g. Teflon), polycarbonate or boro-silicate glass flasks. These can be stored at room temperature or refrigerated, except for the vitamin stock solutions which should be frozen. Sterilization by autoclaving may be more reliable but will alter the water chemistry, so in this case fluorocarbon flasks are preferred. The nutrients are added to a seawater flask to make "f" medium (Guillard and Ryther 1962). Ten milliliters of medium are dispensed to each 15-ml clear polycarbonate or boro-silicate glass test tube.

Isolation

Sodium hypochlorite is added to one of the sterile seawater flasks to make a 30 micromolar solution (e.g. approximately 1 drop Chlorox/250 mls). A few grams of animal tissue containing symbiotic algae are placed in the hypochlorite solution. After soaking for a few minutes, a small piece of tissue (e.g. branch tip, tentacle, etc.), is cut with a scalpel, and transferred by forceps to new hypochlorite solution. Small invertebrates, or reproductive products (e.g. planulae) are not cut. After two hours, the tissue is transferred by forceps to sterile seawater, agitated and transferred to a sterile petri dish (Falcon 1006) that is half filled with sterile seawater. The tissue is held with the forceps, while it is sliced and mashed with the scalpel. The cover is tightly placed on the petri dish which is then agitated. The suspension is poured into a test tube until it is about one-half full, sealed with a sterile silicon stopper, and shaken as vigorously as possible. This is poured through a sterile 20 micron mesh screen (e.g. Nitex) into a sterile petri dish and examined microscopically for the presence algal cells. A stereo microscope is used for isolation. At 100x magnification 10 micron size cells such as S. microadriaticum can be discerned.

If the algae are more concentrated than one to a few cells per field of view at low magnification (20-40x), the suspension is diluted with sterile seawater until this density is attained. After, a single cell is located with no other cells in the field of view at 100x magnification, the power is reduced to low magnification. While holding one finger against the large end of the Pasteur pipet, the small end of the pipet is placed next to the algae cell using one or both hands to hold the pipet. After the finger is removed from the end of the pipet, the flow of water should draw the cell into the pipet.

The tip of the pipet is then placed against the inside wall of one of the test tubes containing medium, and the cell is transferred by blowing into the other end of the pipet. The cotton plug is replaced, and the tube is swirled to wash the cell into the medium. A new pipet and test tube are used each time the procedure is repeated. In some cases, as many as 100 tubes may be necessary for a few successful clones.

Culture

The tubes are placed 20 cm from fluorescent light bulbs (e.g. Vita-lite, or Cool White). After blooming, the cultures can be maintained by transferring to new medium in test tubes, Erlenmeyer flasks, or other vessels monthly. Cultures of S. microadriaticum have survived years in the same flask when tightly capped to prevent evaporation.

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Time-Series analysis of biological data: a case study involving periodicity of coral spawning.

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Abstract

A time-series data set of solar radiation and planula production in two spawning types of the coral pocillopora damicornis was analyzed using adjustable, data-smoothing digital filters to separate the time-series into cyclic components. Annual and monthly cycles were described and separated from the noise component by a rigorous mathematical technique. This exemplary analysis demonstrates the usefulness of the method in biological applications on coral reefs.

Introduction

Investigations in the biological sciences frequently involve the measurement of one or more experimental variables at regular intervals. These measurements are often contaminated with random "noise" that obscures the behavior of the underlying phenomenon under study. Furthermore, if the true (i.e. noise-free) behavior is governed by several different influences that vary with time, the contribution of each driving force may be difficult to independently assess. In spite of these factors, patterns within and between data sets are often discernable. This article describes a set of data analysis tools and associated methodology for locating and measuring these patterns.

The data for each measurement is called a time-series and consists of a sequence of observed values of an experimental variable measured at equal intervals over a fixed period of time. The time-series analysis procedure described here (hereafter referred to as TSAP) has been designed to eliminate observation noise, resolve each time-series into a sum of component time-series, then compare the components using a lagged correlation technique. The TSAP can be installed on microcomputers for use in a laboratory environment. It provides working scientists with visual displays of their data, a procedure for modeling the data, and a means of measuring and displaying the correlation between any two time-series.

The TSAP uses an array of adjustable, data-smoothing digital filters to separate time-series into cyclic components whose frequencies, or periods, lie in specified ranges. (Note that frequence is the reciprocal of period length.) Each actual filtering computation is a running-weighted-average of the input time-series. That is, each computed output of the filter is a weighted average of input measurements during a short interval, or "data window", about the time of interest. Weights are calculated based on a prescribed data model so that the filter 'passes' model components fitting the window segment to a model by least-squares, then, based on the fit, calculating a filtered value for the midpoint of the data segment. The window then moves to the next time point and the process is repeated, thereby generating a filtered time-series of averaged segments. A slight modification of the process is used at the endpoints.

Each raw time-series is assumed to be the sum of one or more deterministic components, such as a trend or cycle, and a random or noise component. Analysis of this latter component is the subject of a vast literature (e.g. Koopmans, 1974: Chatfield, 1975: Anderson, 1976) and will not be discussed here. We are concerned instead with removing the noise (smoothing) and isolating each deterministic component for further analysis. The TSAP provides a setting in which trends, periodic components and noise are all modeled by a single family of functions. A trend, such as a linear trend, is interpreted as a slowly-varying or long period cyclic component while noise is interpreted as high frequency cycles. The digital filters may be thought of a "black boxes" which input a time-series, decompose it into cyclic components, discard selected components, combine the remaining components and output the resultant time-series.

In the next section, time-series models, filtering and correlation are discussed using several examples of real data to illustrate procedures. The last sections discuss the mathematics of filtering and correlation.

Example Data

Three time-series are used here as examples. The first is the average daily solar intensity (calories/cm) at Kaneohe Bay, Oahu, Hawaii between September 1981 and December 1982 (Fig. 1a); the second and third are planula release rates for two types of the coral pocillopora damicornis in the bay (Figs 1b and 1c). The data were transformed and plotted as the natural log of the quantity one plus the daily mean number of larvae released. Transformation of these data is useful because of the high variability encountered in the counts (three orders of magnitude) and the presence of zero values (log 0 is undefined). We are interested in what influences, if any, solar intensity has on the corals' reproduction rate. A complete description of methods and various results of these experiments can be found in Richmond and Jokiel (1984), Jokiel et al. (1985) and Jokiel (in press).

Clearly present in the solar data (Fig. 1a) is a cycle with a period of approximately 1 year corresponding to seasons of the northern hemisphere. This trend is not obvious in either of Figs. 1b or 1c. Similarly, Figs. 1b and 1c each contain an approximately monthly cycle thought to be related to the lunar cycle (Jokiel et al., 1985). If the light data contains an additional monthly

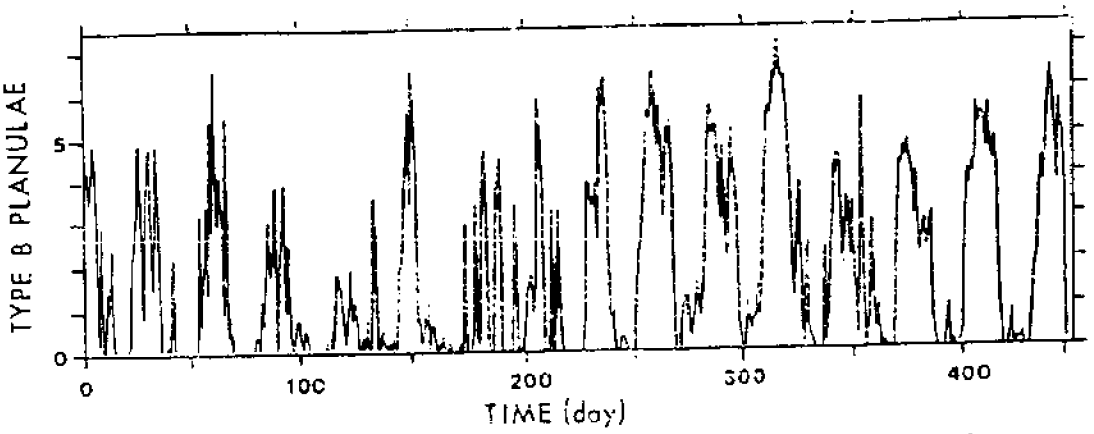


Fig. 1c. Logarithm of average daily production of Type B planula.

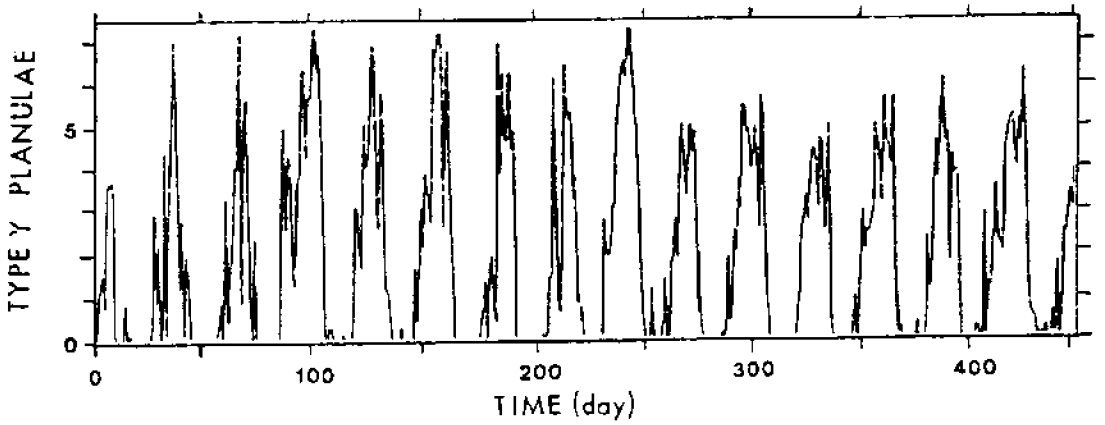


Fig. 1b. Logarithm of average daily production of Type Y planula.

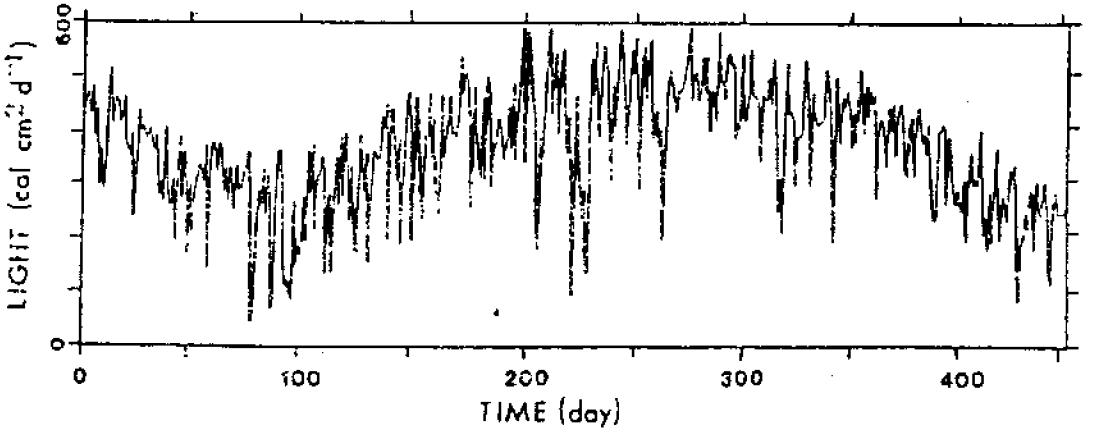


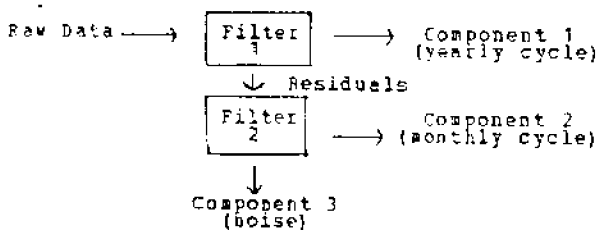
Fig. 1a. Average daily solar intensity in calories/cm².

Fig. 1. Raw Data

cycle, possibly due to sunspot activity, its presence has been obscured by the relatively high noise intensity, due for the most part to cloud cover. In the following section we will develop a general model assumed to hold for all three time-series that is based on the yearly cycle in Fig. 1a and the monthly cycles in Figs. 1b and 1c.

Data Modeling

From the above considerations, we are guided to separate each time-series into three components as indicated in the following diagram:



Residuals from Filter 1 are obtained by subtracting daily values of the yearly cycle from corresponding values of the raw data. Component 3 is obtained similarly. Notice that each filtering operation seperates its input time-series into exactly two components and that components 1 and 2 in the diagram are simply smoothed versions of their respective input time-series, with residuals in each case being regarded as noise with respect to the filter. Restricting filters to be smoothers simplifies the specification of filter parameters described below. Also, more components can be separated by simply adding more filtering operations.

We now have a general model of the input data, namely:

raw data = yearly cycle + monthly cycle + noise.

The next step is to match this to a mathematical model. TSAP's modeling procedure makes tacit use of a basic mathematical fact from linear algebra: any time-series of length, say, N measurements can be represented exactly (i.e. modeled exactly) by a linear combination of N other time-series, provided these latter time-series are independent of each other (Draper and Smith, 1966). Among the simplest classes of independent modeling functions are the polynomials and trigonometric functions. While the different classes allow the investigator greater modeling flexibility, our experience has been that final results are nearly the same, provided equivalent choices from each class are made. In the present case, the general model contains periodic components and so trigonometric functions are used as the modeling blocks. In other cases, such as stock market data that contains linear trends, polynomials may be more appropriate.

Let N represent the number of observations in the data window and let Φ represent a class of modeling functions defined by

$$C_k(n) = \text{cosine}(\pi(k-1)n/N) \qquad n=1,2,\ldots,N$$

for k = 1,2...,N. For each k, Ck is a discrete, periodic function having frequency (k-1)/2N cycles-per-day and period 2N/(k-1) days. When k=1, C1 = 1 for each n. This is a degenerate trigonometric function of infinite period, i.e., a horizontal line, and is required to model the overall mean of the data. Function C2 has a period of 2N days, C3 a period of N days and so on; finally CN has a period of 2 days. This is the minimum detectable period of a daily sampling rate.

For each component we must select a data window length N and then choose those members of Φ which best model the trend we are seeking to isolate. Since input time-series are always smoothed, only the first few functions in Φ are used to model the trend. If the first P functions are used we say the filter has order P. Filters are completely characterized by the window length N and the order P which are the only inputs required by the filtering algorithm, besides the input data. Selection of N and P may require a trial-and-error process. As a general guide, superimposed plots of raw and smoothed data should compare reasonably well with what the investigator might draw freehand. If P=1, that is if only the function C1 is used, the filtering process is identical with a simple moving average. As it contains very little model structure, this filter tends to oversmooth. Larger values of P mean the model is able to capture finer features in the data. However, care must be taken not to choose P too large, or portions of the noise may be included in the trend. Table 1 indicates appropriate choices for the present situation.

Fig. 2 shows the ouput from Filter 1 for each time-series. The similarity between 2a and 2c is now more apparent. Also, the lack of similarity between 2a and 2b is apparent. Residuals from this first filtering are shown in Fig. 3, where monthly cycles are still obvious in 3b and 3c, but not in 3a. Figs. 4 and 5 are the trend and noise, respectively, from Filter 2. Type Y planula exhibits a fairly regular cyclic pattern with a period of about 30 days, while Type B shows some irregularities during late winter and early spring. Also, maximum planula production for Type Y seems to occur later than Type B.

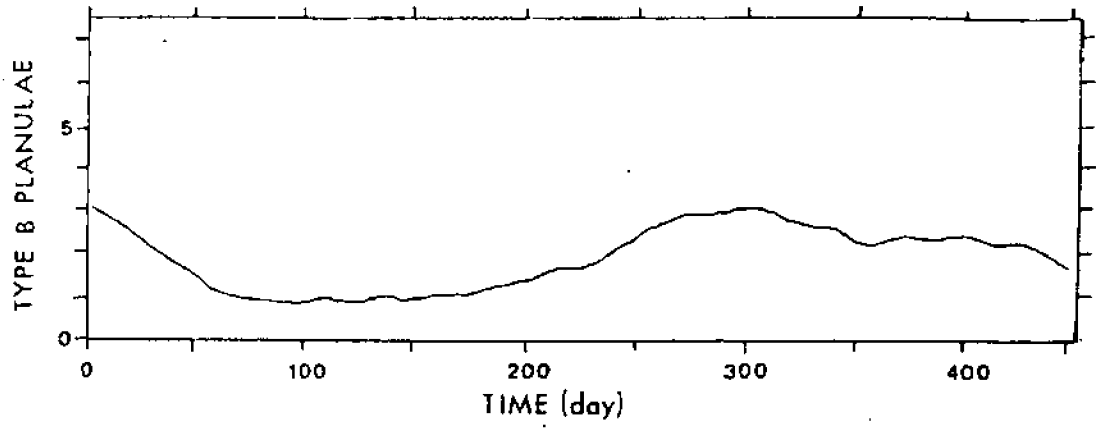


Fig. 2c. Type B planula yearly cycle.

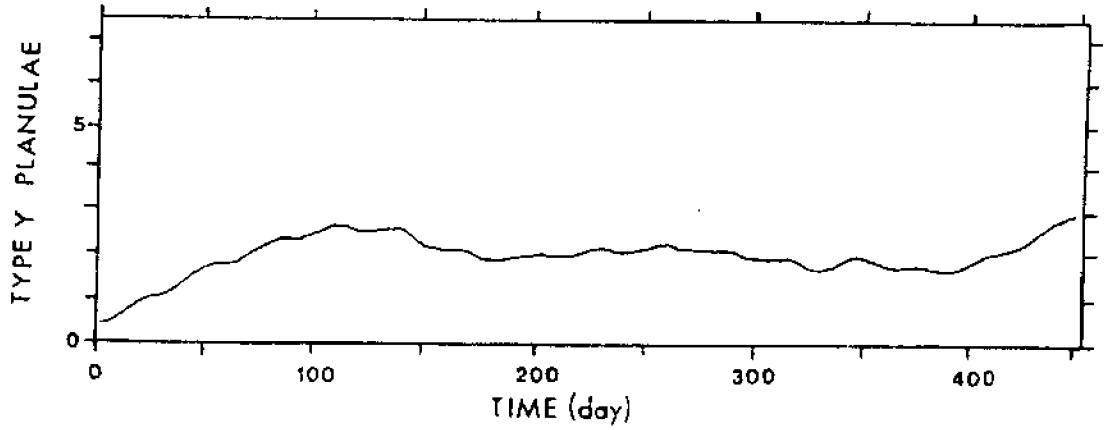


Fig. 2b. Type Y planula yearly cycle.

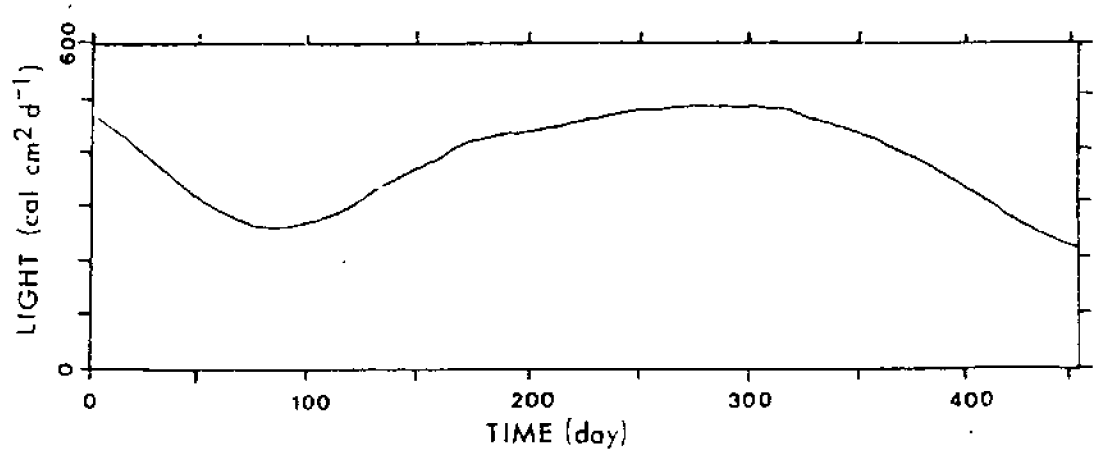


Fig. 2a. Solar yearly cycle.

Fig. 2. Component 1.

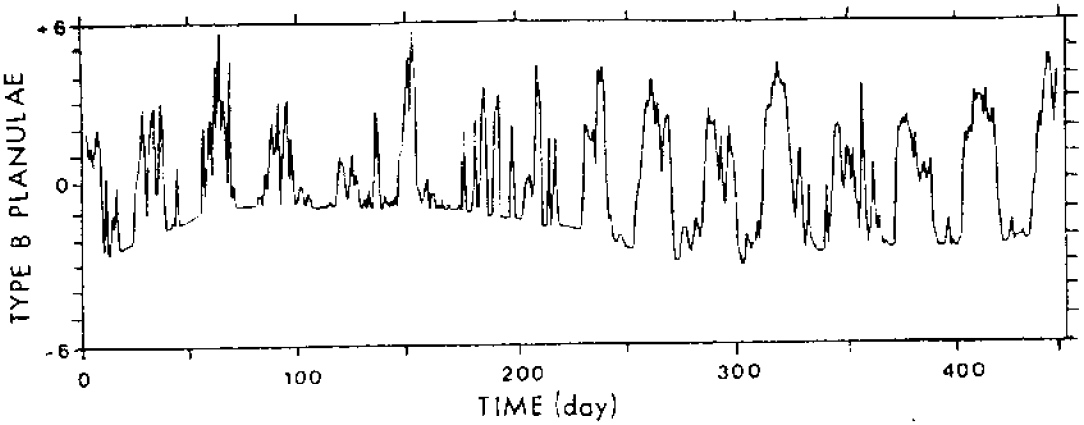


Fig. 3c. Type B planula residuals from Filter 1.

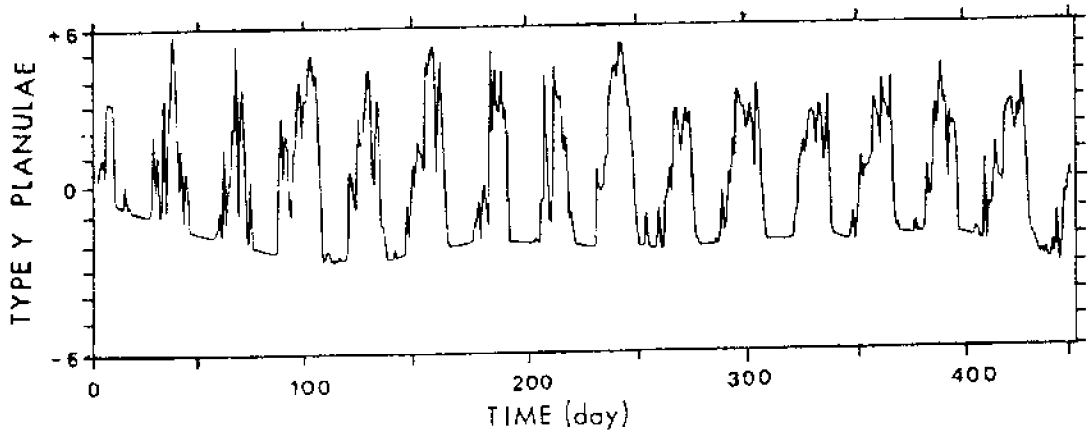


Fig. 3b. Type Y planula residuals from Filter 1.

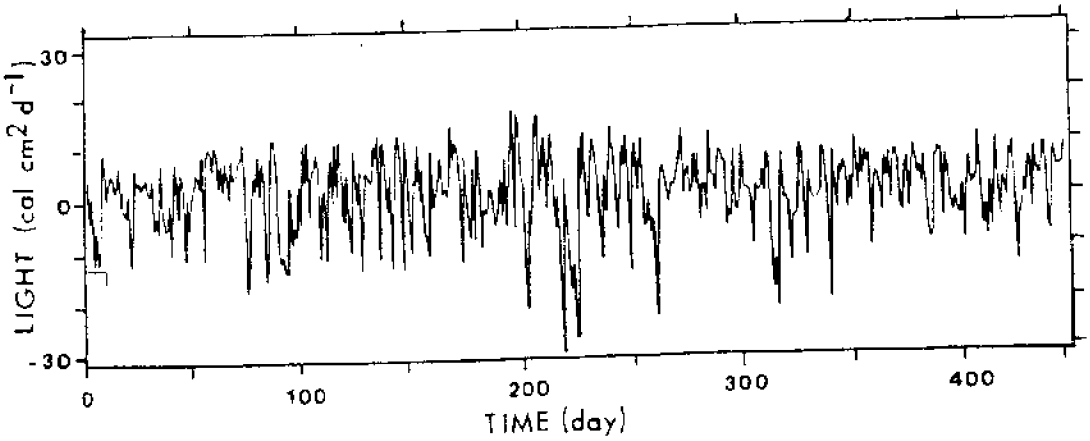


Fig. 3d. Solar residuals from Filter 1.

Fig. 3. Filter 1 Residuals

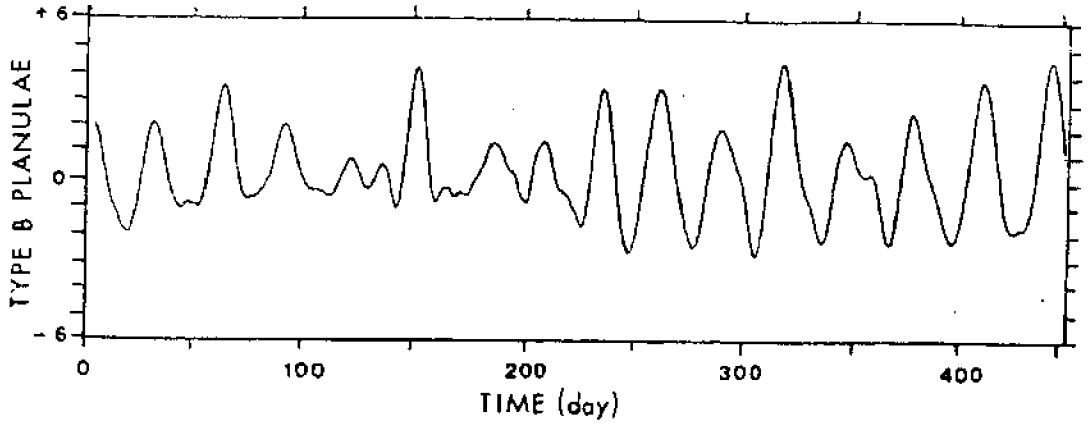


Fig. 4c. Type B planula monthly cycle.

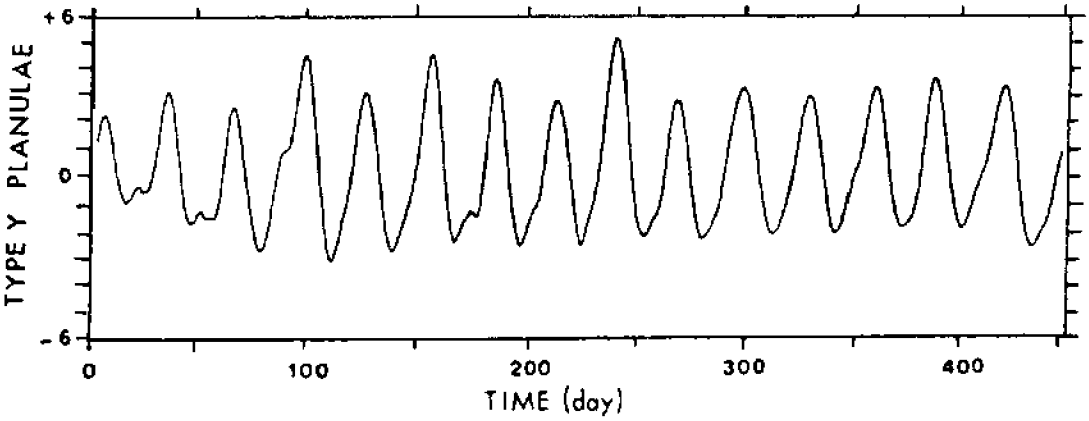


Fig. 4b. Type Y planula monthly cycle.

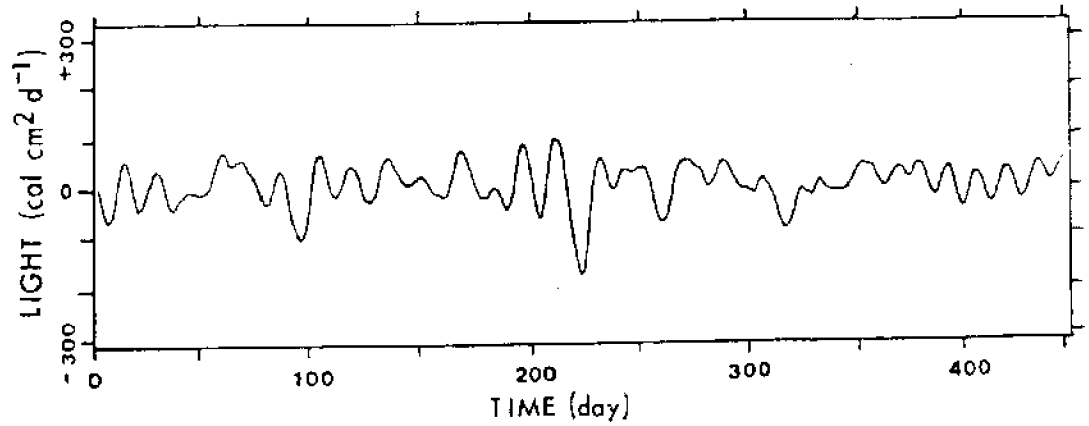


Fig. 4a. Solar monthly cycle.

Fig. 4. Component 2.

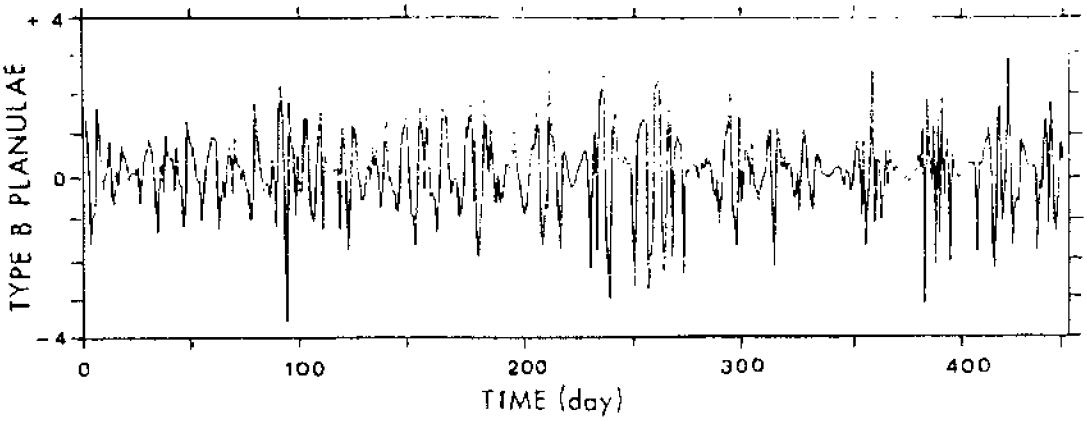


Fig. 5c. Type B planula data residuals from Filter 2.

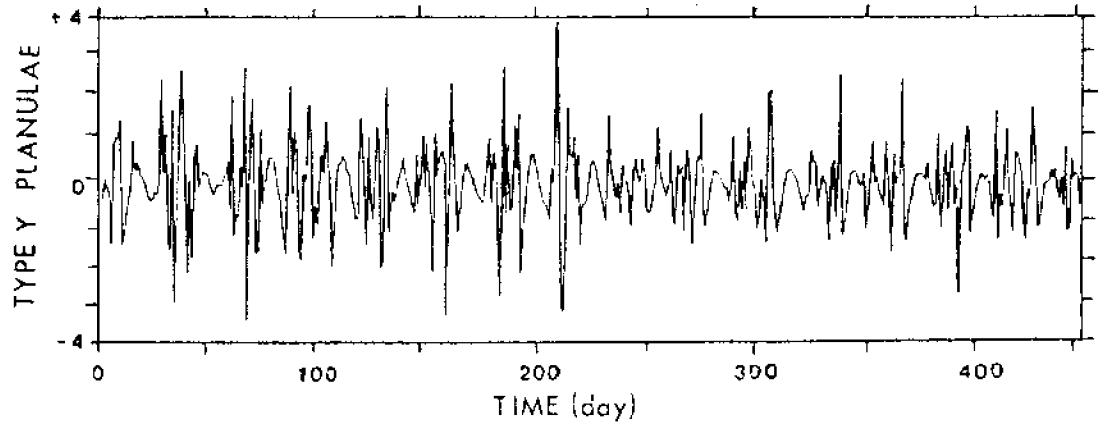


Fig. 5b. Type Y planula data residuals from Filter 2.

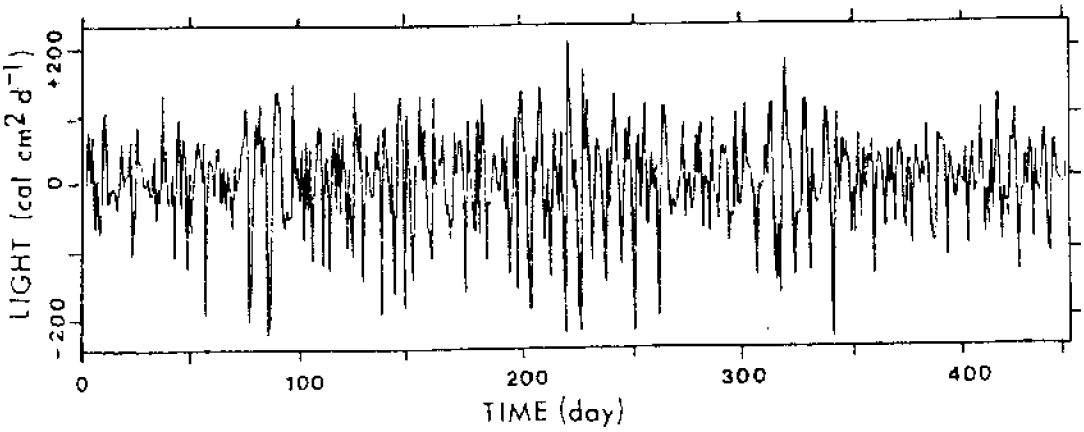


Fig. 5a. Solar residuals from Filter 2.

Fig. 5. Filter 2 residuals.

Table 1.

Component	Assumed Period	Window Length	k-values	Period of Ck	Filter Parameters
1	365 days	200 days	1	infinite	N=200
			2	400	P=3
			3	200	
2	30 days	30 days	1	infinite	N=30
			2	60	P=5
			3	30	
			4	20	
			5	15	

Some of these observations can be quantified using a statistic known as the (linear) correlation coefficient and denoted here by r. The correlation coefficient measures, in a sense, the similarity between two time-series. It can be regarded as a measure of how well one time-series can be be approximated by a linear function of the other. Values for r range between -1 and 1. If r=1 or r=-1 we say the time-series are completely correlated; if r is negative they are negatively correlated. If r=0 the time-series are uncorrelated or independent of each other. Another way to view r is that r^2 can be thought of as the fraction of the variance of one time-series that is "explained" by the other.

Correlation values for pairs of smoothed time-series are given in Table 2, column 3. Correlations for pairs 6a and 6b appear to agree fairly well with visual inspection. Small correlations for the pairs in Fig. 7 indicate they are essentially uncorrelated even though the monthly cycles for the corals (4b and 4c) appear quite similar. The reason is that they are slightly shifted: if Fig. 4b and 4c are superimposed and 4c is moved to the right 8 days relative to 4b, the curves line up much better. Fig. 4b is said to "lag" 4c by 8 days. A plot of correlation versus lag time may be made and the lag time at maximum correlation, the so-called phase-shift, read from the plot. Figs. 6, 7 and 8 are lagged correlation plots for the pairs in Table 2. The last column in Table 2 indicates the maximum correlation for non-zero lag times. Fig. 7a reveals a fairly high correlation between planula monthly cycles at 8 d lag time as expected. For pair 6a the large phase shift (200 days) relative to a period of about 365 days, and the low correlation indicate the two curves are unrelated, while 6b reveals a high correlation at a lag of 40 days. Apparently Type B corals are more respondent to gradual changes in solar intensity than Type Y. From Figs. 7b and 7c we conclude that planula monthly cycles are essentially uncorrelated with the somewhat irregular solar monthly cycle.

Table 2.

Figure	Time-series Pair	Zero-Lag Correlation	Phase Shift	Maximum Lagged Correlation
6a	2a-2b	-0.26	200	0.31
6b	2a-2c	0.61	40	0.86
7a	4b-4c	0.01	8	0.69
7b	4a-4b	-0.01	56	0.08
7c	4a-4c	-0.01	48	0.13
8a	4b-4b	1.00	30	0.92
8b	4c-4c	1.00	30	0.85

If a time-series is compared with a lagged version of itself, the resultant plot is called an auto-correlation. These have long been used to detect and measure the periods within a time-series. They have the property that zero-lag correlation is always one, as required by Equation 4, and that a phase shift equals the length of the period of a component. Auto-correlation plots for month cycles of both planula types are shown in Fig. 8a (Type Y) and 8b (Type B). Each reveals a phase shift of 30 days in agreement with the 29.5 day lunar cycle.

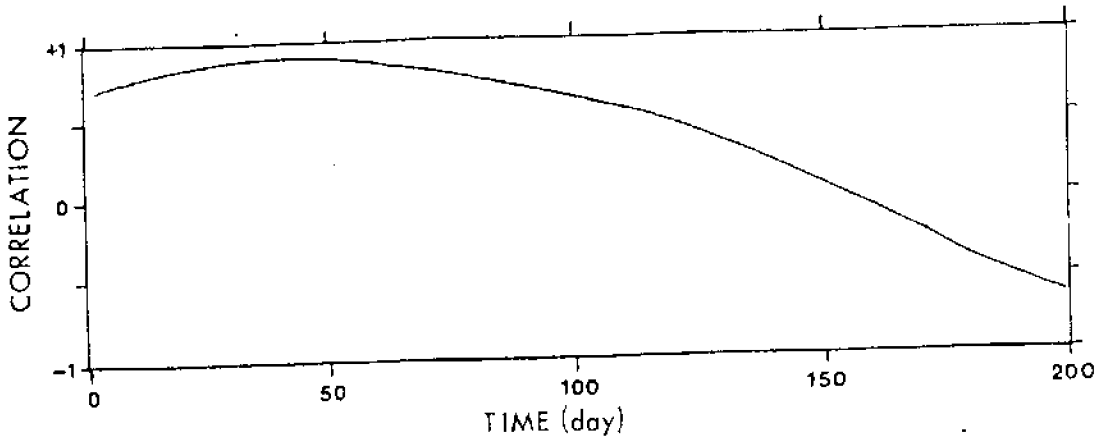


Fig. 6b. Correlation between yearly cycles of solar and Type B planula data.

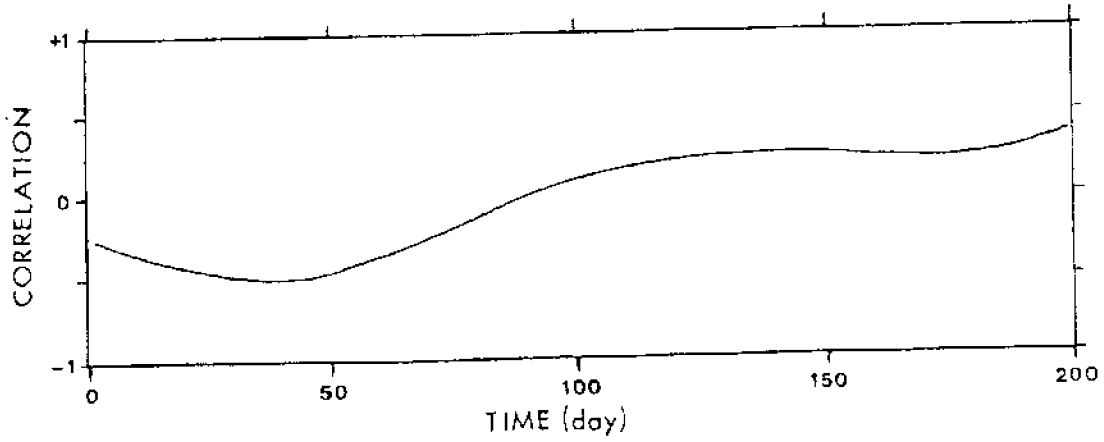


Fig. 6a. Correlation between yearly cycles of solar and Type Y planula data.

Fig. 6. Correlations for yearly cycles.

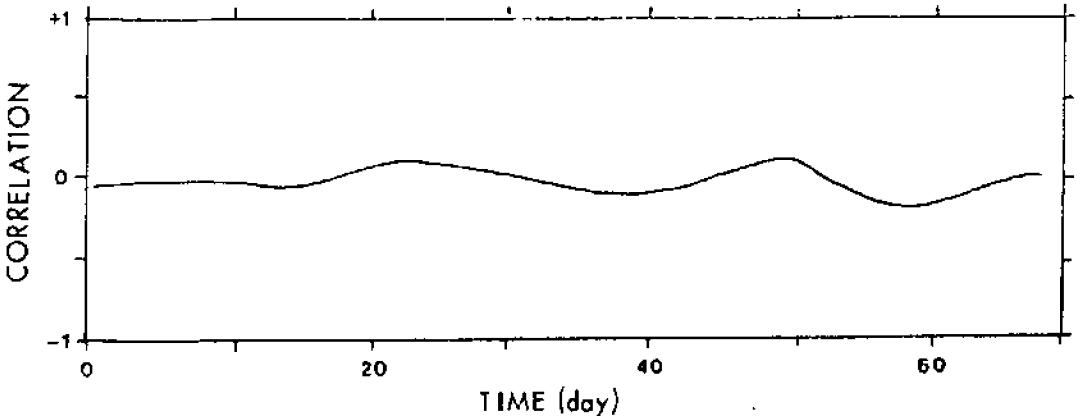


Fig. 7c. Correlation between monthly cycles of solar and Type B planula data.

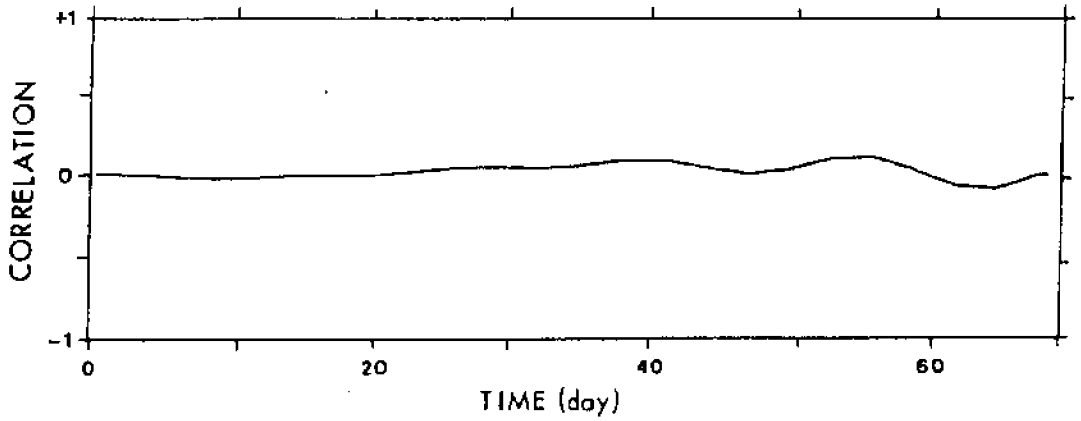


Fig. 7b. Correlation between monthly cycles of solar and Type Y planula data.

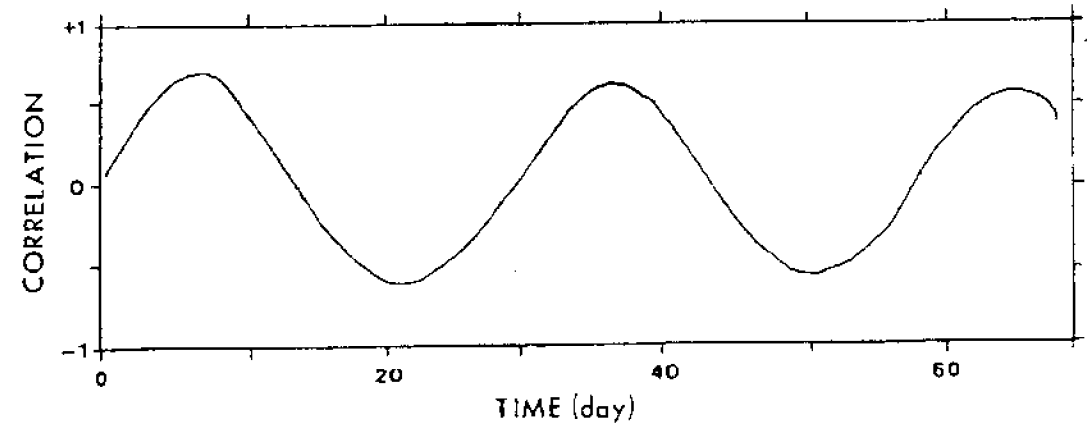


Fig. 7a. Correlation between monthly cycles of Type Y and Type B planula data.

Fig. 7. Correlations for monthly cycles.

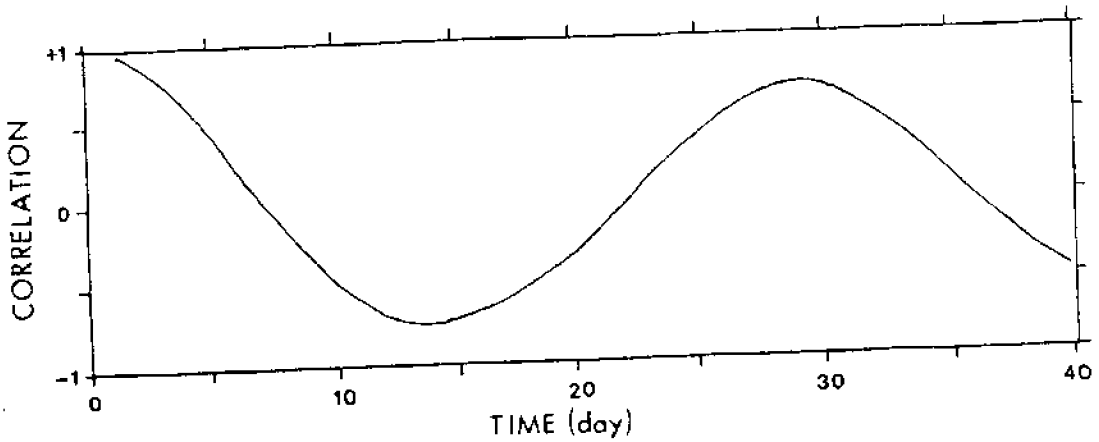


Fig. 8b. Auto-correlation for Type B planula data.

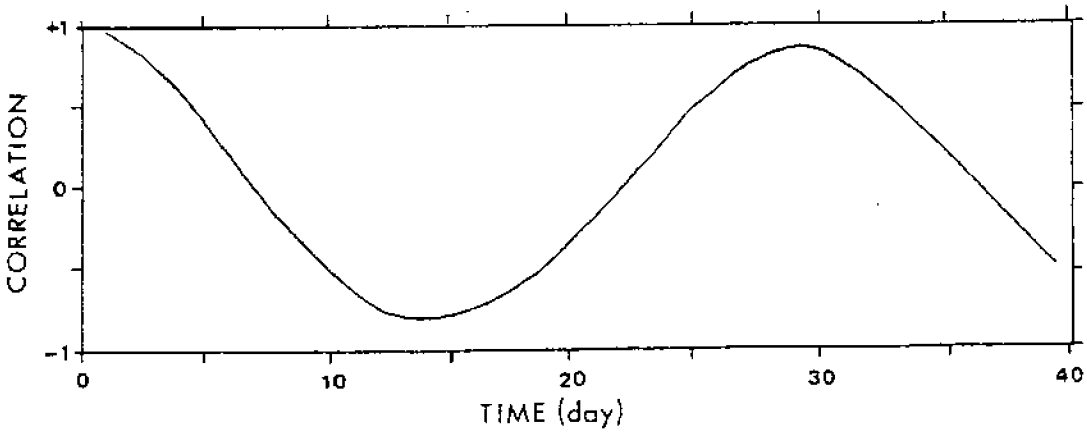


Fig. 8a. Auto-correlation for Type T planula data.

Fig. 8. Auto-correlations for planula monthly cycles.

The Filtering Algorithm

In this section we present the mathematics underlying the filtering algorithm. Let

$$X(1), X(2), X(3), \ldots, X(M)$$

represent time-series X of M observations, or measurements, and let X(n) represent the nth observation of X. For filtering purposes, X is assumed to have only two components:

$$X(n) = Y(n) + Z(n), \qquad n = 1, 2, \ldots, M$$

or, more simply: $X = Y + Z$. Here Y represents the trend in X and Z represents filter residuals. Since $Z = X - Y$, and X is known, we only need to estimate Y. Let N be the data window length where $1 \leq N \leq M$ and let $\Phi = (Ck, k=1,2,\ldots,N)$ represents a family of modeling functions for this window length. As described in Section 3, only the first few members of Φ are used to model a given data component. Let P be the number of required modeling functions. Then Y is estimated by a linear combination of the first P modeling functions:

$$\hat{Y} = A1\ C1 + A2\ C2 + \ldots + AP\ CP = \sum_{j=1}^{P} Aj\ Cj \tag{1}$$

where $\hat{Y}$ is the estimate of Y and the Aj's are regression coefficients. The Aj's are required to minimize the sum of squared differences between the estimate $\hat{Y}$ and the input data X. Using the method of least-squares, we find the Aj's that minimize

$$S = \sum_{n=1}^{N} (\hat{Y}(n) - X(n))^2 \tag{2}$$

Substituting for $\hat{Y}(n)$ in (2) gives

$$S = \sum_{n=1}^{N} \left(\sum_{j=1}^{P} Aj\ Cj(n) - X(n) \right)^2 \tag{3}$$

and the minimizing Aj's are found by differentiating S with respect to each Ak:

$$\frac{\partial S}{\partial Ak} = 2 \sum_{n=1}^{N} \left(\sum_{j=1}^{P} Aj\ Cj(n) - X(n) \right) Ck(n) = 0, \qquad k = 1, \ldots, P \tag{4}$$

Reversing the summation orders in (4) gives

$$\sum_{j=1}^{P} Aj\ Djk = \sum_{n=1}^{N} X(n)\ Ck(n) \qquad k = 1, \ldots, N \tag{5}$$

where

$$Djk = \sum_{n=1}^{N} Cj(n)\ Ck(n) \tag{6}$$

Equations (5) are know as the Normal Equations for this particular problem and are usually solved by inverting the matrix Djk. However, if P is larger than 2, matrix inversion at each data point requires too much computation time to be practical. Instead, using a technique known as the Gram-Schmidt orthogonalization procedure (Lancaster, 1969) the modeling functions Ck can be adjusted so that

$$Djk = \begin{cases} 0 & \text{if } j \neq k \\ 1 & \text{if } j = k \end{cases} \tag{7}$$

This adjustment has no effect on the modeling capabilities of the Ck's.

The Normal Equations (5) are now automatically solved for the Aj's:

$$Aj = \sum_{n=1}^{N} X(n)\ Cj(n) \qquad j = 1, \ldots, P \tag{8}$$

The actual filtering algorithm is now easily derived from equations (1) and (8). For any time m, $1 \leq m \leq N$, the estimate of Y is given by

$$\hat{Y}(m) = \sum_{k=1}^{P} Ak\ Ck(m),$$

$$= \sum_{k=1}^{P} \sum_{n=1}^{N} X(n)\ Ck(n)\ Ck(m),$$

$$= \sum_{n=1}^{N} \sum_{k=1}^{P} Ck(n)\ Ck(m)\ X(n),$$

and finally

$$\hat{Y}(m) = \sum_{n=1}^{N} Fm(n)\ X(n) \qquad m = 1,\ldots,N \tag{9}$$

where

$$Fm(n) = \sum_{k=1}^{p} Ck(n)\ Ck(m) \qquad m,n = 1,\ldots,N \tag{10}$$

Equation (9) is the filtering algorithm with filter coefficients (weights) Fm(n). If the window length is chosen equal to data length N, the algorithm is equivalent to a least-squares fit of the input data to the model. However, notice that, as it stands, the algorithm requires a different set of filter weights for each filtered point (each m), resulting in little, if any, computational savings over the matrix inversion procedure. To avoid this problem, and to provide a broader class of data models, the following approach is used. Assume N is odd and let u = (N + 1)/2; then $\hat{Y}(u)$ is the estimate of Y at the midpoint of the window. If the window moves forward in time by one unit, the midpoint filter weights do not change. Therefore, neglecting the first and last u points in the input time-series, estimates for Y can be written

$$\hat{Y}(k) = \sum_{j=-u}^{u} G(j)\ X(k+j) \qquad k = u,\ldots,N-u \tag{11}$$

where

$$G(j) = Fu(u+j) \qquad j = -u,\ldots,0,\ldots,u \tag{12}$$

Equation (11) is known as a convolution of the data X with filter weights G. This algorithm is easily programmed on micro computers and gives reasonably fast execution times. For large data sets, (i.e. long time-series), the algorithm is available "hard-coded" in devices known as array processors with extremely fast execution times.

The first and last u data points of the input time-series must be treated differently. The simplest and statistically most accurate approach is to use equation (10) to compute new filter weights for each of the endpoints. This, however, may significantly increase running times, especially if N is large. An alternative approach is to fit straight lines to the first and last u data points by least-squares and extrapolate these lines forward or backward as necessary to produce u additional points at each end of the input time-series. The moving window can then be used on the augmented input time-series. The fitting algorithm and resulting filtering algorithm are computationally very fast. This latter approach has been adopted here.

The Correlation Algorithm

As described in Section 3, the correlation coefficient r is a statistical measure of the degree of linear dependence between two time-series. We will first give a computational formula for r, then attempt to motivate its usage.

Let X and Y be two time-series of N observations each. The (sample) mean of X is defined by

$$\bar{X} = (1/N) \sum_{n=1}^{N} X(n) \tag{1}$$

and the (sample) variance of X by

$$V(X) = (1/N) \sum_{n=1}^{N} (X(n) - \bar{X})^2. \tag{2}$$

V(X) measures, in a sense, the size of X. Similarly, the (linear) covariance between X and Y is given by

$$Cov(X,Y) = (1/N) \sum_{n=1}^{N} (X(n) - \bar{X})\ (Y(n) - \bar{Y}) \tag{3}$$

which measures, in a sense, how closely Y resembles X. If the covariance is normalized by the variances of X and Y, we get the linear correlation coefficient between X and Y:

$$r = \frac{Cov(X,Y)}{\sqrt{V(X)}\ \sqrt{V(Y)}} \tag{4}$$

Motivation for this formula comes from the following considerations. Suppose we plot values of X versus Y on a Cartesian coordinate system, as in the diagram, and let

$$\hat{Y} = A + B\ X \tag{5}$$

represent the best linear fit of Y to X, i.e. the linear least-squares regression line. If all points fall on the line, that is, if Y = A + B X, then X and Y are completely (linearly) correlated and it is easily shown that r = 1 when B is positive and r = -1 when B is negative. On the other hand, if X and Y are completely independent of each other, then $\hat{Y}$ = A which implies Y = Y and from equations (3) and (4) we find r = 0. It should be pointed out that a high correlation between variables does not necessarily indicate a high degree of dependence. For example, the rainfall in Tokyo may be highly correlated with new home sales in San Francisco even though the two are obviously unrelated.

The notion of lagged correlation arises when one time-series is displaced in time relative to the other. Define a new time-series W by $W(n) = Y(n+k)$. Then W is said to lag X by k time units. If k takes values between zero and some maximum lag time, both Cov(X,W) and the associated correlation become functions of k. A plot of r versus k reveals the lag time at maximum correlation, or the so-called phase shift between X and W.

Discussion

The time-series analysis procedure described and demonstrated in this paper provides a useful tool to the coral reef biologist. Time-series data are notoriously difficult to analyze objectively. The TSAP procedure was designed to eliminate observation noise and resolve each time-series into a sum of component time-series. The components are compared using a lagged correlation technique. The TSAP is especially useful because it can be installed on microcomputers for use in a laboratory environment. The technique provides the coral reef biologist with a visual display of his data, a procedure for modelling the data, and a means of measuring and displaying the correlation between any two time series. The exempary data analysis demonstration shows the usefulness of this approach.

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