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ASPECTS OF THE ECOLOGY OF *PSEUDOPTEROGORGIA AMERICANA* AND *PSEUDOPTEROGORGIA ACEROSA**

by

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Abstract

Pseudopterogorgia americana and *P. acerosa* are among the most abundant gorgonian species on many western Atlantic reefs. *P. americana* can be distinguished from *P. acerosa* in the field by its sliminess. The two species are found together over a wide range of depths and habitats. Small scale dispersion patterns, densities, age frequencies, mortality, recruitment, growth, reproduction, and interactions with other organisms were studied.

Studies of small scale dispersion patterns revealed that substrate heterogeneity contributes to aggregated dispersion patterns of gorgonians. The number of gorgonians was inversely related to the amount of coral and other sessile organism cover which may also contribute to these aggregated dispersion patterns. The aggregated dispersion pattern of *P. americana* on even substrate may be due to a limited ability of the larvae to disperse.

The relative densities of the two species differed at different sites. Site (1) had the highest densities of both species with *P. americana* being far more abundant than *P. acerosa*, while *P. acerosa* was almost as or more abundant than *P. americana* at other sites which had lower absolute densities of both species. Age frequency percentages were usually not significantly different between the two species at different sites indicating that they respond similarly to a variety of factors which control age frequencies. Recruitment studies indicate that gorgonians compete with each other and other sessile organisms for space, and the extremely high recruitment of *P. americana* in cleared quadrats suggests that it is a colonizing species. Mortality was not significantly different from recruitment indicating that populations were stable over the study period.

Growth rates were measured by annual length increments in colonies and compared to growth estimates based on colony length per growth ring. Rings were found to be annual and were used to estimate growth rates at all sites. Linear growth rates were about 5 cm/yr for *P. americana* and 6 cm/yr for *P. acerosa*. Length-weight comparisons indicated that the growth form of the two species is similar. Growth rates are higher for colonies exposed to higher light levels, and this explains about 20% of the variability in growth rates.

Sexes are separate in colonies of the two species. *P. americana* had a slightly higher ratio of females than males, while *P. acerosa* had an even ratio between sexes. Gonadal volume was used as an index of reproductive periodicity, and synchrony within and between sexes for the two species are discussed. Small colonies usually lacked gonads indicating that reproduction is delayed for at least three to five years.

Damage by *Cyphoma gibbosum*, an ovulid gastropod which grazes on gorgonian tissue, is sometimes responsible for encrusting organisms settling on gorgonians and thus may contribute to mortality. Other commensal or parasitic organisms found on the two species did little obvious damage. *Thalassoma bifasciatum*, the bluehead wrasse, was often seen picking at gorgonians, but gut contents had few, if any, gorgonian remains.

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Introduction

Gorgonians are among the most conspicuous and abundant fauna on western Atlantic coral reefs. The familes Plexauridae and Gorgoniidae, in particular, are more abundant and diverse in the West Indies than anywhere else in the world (Bayer, 1961). Nevertheless, very little work has been done on the population dynamics of individual species, particularly in the western Atlantic.

Pseudopterogorgia americana (Gmelin) and *Pseudopterogorgia acerosa* (Pallas) are very similar congenerics which frequently cannot be distinguished by sight in the field. Both species are pinnately branched plumose gorgonians with slightly flattened branchlets. Polyps lie in single or biserial rows on the edges of the branchlets. Preliminary study revealed that *P. americana* and *P. acerosa* do not differ in the size of the polyps, the number of polyps per branchlet, or the number of branchlets. Branchlets are usually in one plane for both species, but tend to vary more in large specimens of *P. acerosa*. This, plus a tendency for large *P. acerosa* to be paler in color than large *P. americana* tends to make large colonies of the two species distinguishable by sight. The extreme sliminess of *P. americana* versus the "dry" or waxy texture of *P. acerosa* is a very reliable means of distinguishing the two species in the field. This copious mucus production of *P. americana* may be related to the very large number of symbiotic zooxanthellae found in this species compared to the number found in *P. acerosa* (Bayer, 1961).

Both *P. americana* and *P. acerosa* are reported throughout the Caribbean, the Gulf of Mexico, Florida, and Bermuda (Bayer, 1961). *P. americana* is reported to occur from the surface to 45 m deep, while *P. acerosa* is reported to occur from 4 to 33 m (Kinzie, 1970, 1973).

The order Gorgonacea is divided into the suborders of Scleraxonia and Holaxonia. Only two species of scleraxonians were found on the study sites, and both of these are encrusting or lobate forms. Due to their growth form, scleraxonians were included with encrusting organisms such as corals for the purpose of this study. The term "gorgonian" refers to holaxonian gorgonians only in this study.

The objectives of this study are to (1) compare patterns of distribution and abundances of *Pseudopterogorgia americana* and *Pseudopterogorgia acerosa* and (2) to compare factors which may influence their distributions and abundances, such as mortality, recruitment, growth, reproduction, and interactions with other organisms.

Literature Review

Bayer (1961) summarized the ecology and zoogeography of Caribbean gorgonians. Kinzie (1970, 1973) did the most complete work to date on gorgonian abundances and distributions for the Caribbean. He defined ten zones with characteristic gorgonian species assemblages in Jamaica. Although a "*Pseudopterogorgia* zone" was not present on the north coast of Jamaica, he noted its presence elsewhere. Other descriptive or quantitative studies on gorgonians in the Atlantic were done by Cary (1914, 1917, 1918), Goldberg (1973a), Opresko (1973) and Preston and Preston (1975). Grigg (1970, 1977) intensively examined the population dynamics of two species of *Muricea* in California.

Factors affecting gorgonian distributions include temperature, light, salinity, water motion, and sedimentation. Temperature and salinity tolerances were measured by Cary (1917, 1918) and Goldberg (1973a). In the latter study, optimal salinity ranges for *Pseudopterogorgia americana* ranged from 30 to 43°/oo, and temperatures ranged from 19.5 to 29.5°C. The relatively low upper temperature limits for *P. americana* may have been due to excessive mucus production under laboratory conditions. Temperature and salinity may have effects on gorgonian distributions (Weinberg, 1979).

The amount of light available is important for gorgonians containing symbiotic algae (Kinzie, 1970, 1973;

Weinberg, 1976, 1978). Shallow water symbiotic gorgonians appear to be more dependent upon their zooxanthellae than hard corals are (Goreau, 1964; Kinzie, 1970, 1973, 1974b), and should therefore be dependent upon light.

Both presence and absence of water movements are limiting for gorgonians (Barham and Davies, 1968; Kinzie, 1970, 1973; Birkeland, 1974). Heavy mortality and damage such as abrasion is most frequently caused by storm waves (Cary, 1914, 1918; Goreau, 1964; Stoddart, 1962; Glynn, *et al.*, 1964). Cary (1914) and Weinberg and Weinberg (1979) noted that large colonies are more vulnerable to wave stress than small ones. Birkeland (1974), however, in a study on storm effects on *Gorgonia* found that detachment due to storm waves may set an upper limit to colony size, but the greatest mortality was in the smaller than average size ranges. Although storm waves may be the immediate cause of mortalities, bioerosion of the substrate beneath the colony largely controls the strength of the attachment (Goreau and Hartman, 1963; Kinzie, 1970; Birkeland, 1974).

Small colonies, in particular, are vulnerable to heavy sedimentation (Weinberg, 1978). Preston and Preston (1975) concluded that gorgonians thrive even on a reef subject to high siltation and turbidity. Cary (1914) indicated that newly settled gorgonian polyps, due to their rapid growth perpendicular to the substratum, have an advantage over newly settled scleractinian polyps. He also notes that storm waves stripped the tissue off of the bases of colonies, and he attributed this to a "twisting" of the colonies by waves.

Biological factors affecting distributions have not been well studied. Kinzie (1970, 1973) found that the availability of hard substrate was the single most limiting factor to gorgonians. Although substrate space is a physical factor, Grigg (1970, 1977) indicated that suitable substrate may be limited by competition. He found no evidence for competition for space between the two species of *Muricea* but concluded that this was due to the heavy competition for space with other organisms. Kinzie (1970) found that *Muricea laxa* Verrill is capable of damaging other gorgonians with its large, spiny spicules. The heavy settlement of gorgonians in storm or artificially cleared areas (Cary, 1918; Opresko, 1974; Kinzie, 1970, 1977; Birkeland, 1974) is strong evidence for the existence of competition for space. Stoddart (1963) indicated that gorgonians in storm devastated areas recover more rapidly than hard corals.

Encrustation by other organisms, especially *Millepora* sp., is a common cause of mortality in gorgonians (Cary, 1914; Theodor, 1964; Kinzie, 1970; Grigg, 1970). Even apparently benign attached animals such as the bivalve, *Pteria* spp., may contribute to mortalities by their weight and water resistance (Weinberg and Weinberg, 1979). Randall (1967) found significant gorgonian remains (greater than 5%) only in the gut contents of the filefish, *Alutera scripta* (Osbeck). Known invertebrate grazers of gorgonians include the amphinomid polychaets (Kinzie, 1970; Birkeland, 1974), and gastropods of the genera *Cyphoma, Simnia,* and *Coraliophila* (Bayer, 1961; Ghiselin and Wilson, 1966). Birkeland and Gregory (1975) found *Cyphoma gibbosum* (Linnaeus) to be a "prudent predator" in the sense that it rarely overgrazes individual colonies. *Cyphoma gibbosum* is a major source of mortality to Jamaican octocorals (Kinzie, 1970). Denuded parts of the skeleton are potential sites for infestation by encrusting organisms (Cary, 1914; Kinzie, 1979; Birkeland, 1974). Weinberg and Weinberg (1979) found similar results for *Neosimnia spelta spelta* (Linnaeus) which feed on *Eunicella singularis* (Esper) in the Mediterranean. The effects of predation on small colonies have not been reported.

Many motile invertebrates such as *Astrophyton muricatum* (Lamarck), the basket star, and members of the genus *Ophiothrix* occur on gorgonians (Bayer, 1961; Clark, 1933). *Astrophyton muricatum* frequently utilizes *Pseudopterogorgia* spp. as a substrate from which to filter feed in the water column (Wolfe, 1978). The caridean shrimp, *Tozeuma carolinensis* Kingsley, is known to occur on *Pseudopterogoria* spp. (Bayer, 1961). Harpacticoid copepods and other organisms such as algae have been found in swellings on gorgonians (Theodor, 1964).

Growth rates of gorgonians were measured by Cary (1914), Grigg (1970, 1974, 1977), Kinzie (1970), and Weinberg and Weinberg (1979). Growth rates measured by the increase in branch length or colony height varied from 1 to 6 cm per year. Grigg (1974) also aged colonies by using growth rings. Strong currents or surge affect the growth forms of gorgonian colonies (Theodor, 1963). Gorgonians which are fanlike or branch in one plane tend to orient themselves normal to the direction of water motion (Barham and Davies, 1968; Theodor and Denizot, 1965; Wainright and Dillon, 1969; Rees, 1969; Grigg, 1972). Originally thought to be an adaptation for feeding (Laborel, 1960; Barham and Davies, 1968), orientation has been shown to be controlled by hydrodynamic factors (Theodor and Denizot, 1965; Wainright and Dillon, 1969; Rees, 1969; Grigg, 1972).

Roushdy and Hansen (1961) showed that gorgonians are capable of filtering phytoplankton. They believed, however, that zooxanthellae comprised a major part of the diet. Kanwisher and Wainright (1967) established the importance of zooxanthellae to coral nutrition. Attempts to observe polyps actively feeding have been largely unsuccessful (Rees, 1969, 1972; Wainright, 1967). Grigg (1970) observed active feeding on zooplankton by *Muricea* spp., a gorgonian which lacks zooxanthellae. Kinzie (1970) observed *Pseudopterogorgia bipinnata* and other gorgonians feeding on particulate matter but found them unable to capture live zooplankton. Bayer (1961) stated that some gorgonians with abundant zooxanthellae have few or no nematocysts. A comparison of day versus night polyp activity to zooplankton abundances indicated that most polyps were open during the day when zooplankton are scarce (Wainright, 1967). *Pseudopterogorgia* spp., however, were usually expanded at night.

Early reproductive work on octocorals in the Red Sea by Gohar (1940a, 1948) indicated that colonies have separate sexes and gonads are born on the six sulcal mesenteries. Sperm are formed in sacs called spermaries which are released from the polyp intact and open shortly after to release ripe sperm. Bayer (1974) implies that spermaries are not released, but are resorbed after releasing the sperm. Ova are often retained and fertilized internally, and octocorals may be viviparous or oviparous (Gohar, 1940a, 1940b, 1948; Gohar and Roshdy, 1961). Bayer (1974) and Goldberg and Hamilton (1974) found no sign of developing larvae or dividing eggs in *Plexaura homomalla* (Esper). Kinzie (1970) found *Pseudopterogorgia bipinnata* (Verrill) and *Pseudopterogorgia elisabethae* (Bayer) to be viviparous. Grigg (1970, 1977) found an even sex ratio of colonies, and colonies as old as ten years had no reproductive activity. He discovered that *Muricea fructicosa* (Verrill) contained gonads at about four years and *M. californica* (Aurivillius) at six years. He pointed out, however, that it might be another four to six years before gonads achieved the size found in older colonies. Goldberg and Hamilton (1974) studied reproductive periodicity in *Plexaura homomalla*.

Larval development and metamorphosis have been studied by Gohar (1940a, 1940b, 1948), Gohar and Roushdy (1961), Theodor (1967b) estimated the survival rate of *Eunicella stricta* (Rossi) larvae as one in 60,000 for the first year. Kinzie (1970, 1974b) reported that planulae may swim for some time or fall quickly to the bottom where they crawl. Larvae of *Eunicella singularis* (Esper) crawl over 2 to 40 m of bottom and attach about 30 hours after emission (Weinberg and Weinberg, 1979). *Eunicella singularis* larvae exhibited photopositive behavior in laboratory studies, but this was difficult to confirm in the field (Weinberg, 1979b). Preference for rugose bottoms was noted by Cary (1914), Gohar (1940b), Bayer (1961), and Theodor (1967b). Kinzie (1970) found no significant preference for light versus dark or smooth versus rugose substrate. The survival of very small colonies (under 1 cm) has not been reported, though Weinberg (1979a) believed it to be important.

Gorgonians were found to exhibit some antimicrobial action in bioassays (Burkholder and Burkholder, 1958). The discovery of large amounts of prostaglandins in *Plexaura homomalla* (Weinheimer and Spraggins, 1969) encouraged extensive examination of gorgonians for chemical compounds. Since then a number of organic compounds in gorgonians have been found to have weak antimicrobial activity which possibly inhibits overgrowth and predation by other organisms (Ciereszko, *et al.*, 1960; Ciereszko, *et al.*, 1960; Weinheimer, *et al.*, 1968a). Weinheimer, *et al.*, (1968b) found sesquiterpene hydrocarbons in *Pseudopterogorgia americana*.

Bayer (1951, 1953, 1959) published a number of works on gorgonian systematics, zoogeography, and evolution followed by the most comprehensive taxonomic study on West Indian gorgonians to date (Bayer, 1961). The first study which included West Indian gorgonians was by Duchassaing and Michelotti (1860, 1864). Kukenthal (1916a, 1916b, 1919) did a comprehensive account of West Indian gorgonians. Deichman (1936) published a monograph on the alcyonarians of the Blake expedition. A number of other papers include species lists of gorgonians found in particular areas of the western Atlantic (Hargitt and Rogers, 1900; González-Brito, 1970a, 1970b; Rees, 1973; Voss and Voss, 1955).

According to Bayer (1961) spicule characteristics are the most distinguishing features between these two species of *Pseudopterogorgia*. Spicule sizes are in the same range, but *P. americana* has strongly curved scaphoids with spiny convex sides while *P. acerosa* has slightly curved scaphoids with smooth convex sides. He also mentions the extreme sliminess of *P. americana* versus the "dry" or waxy texture of *P. acerosa*.

Materials and Methods

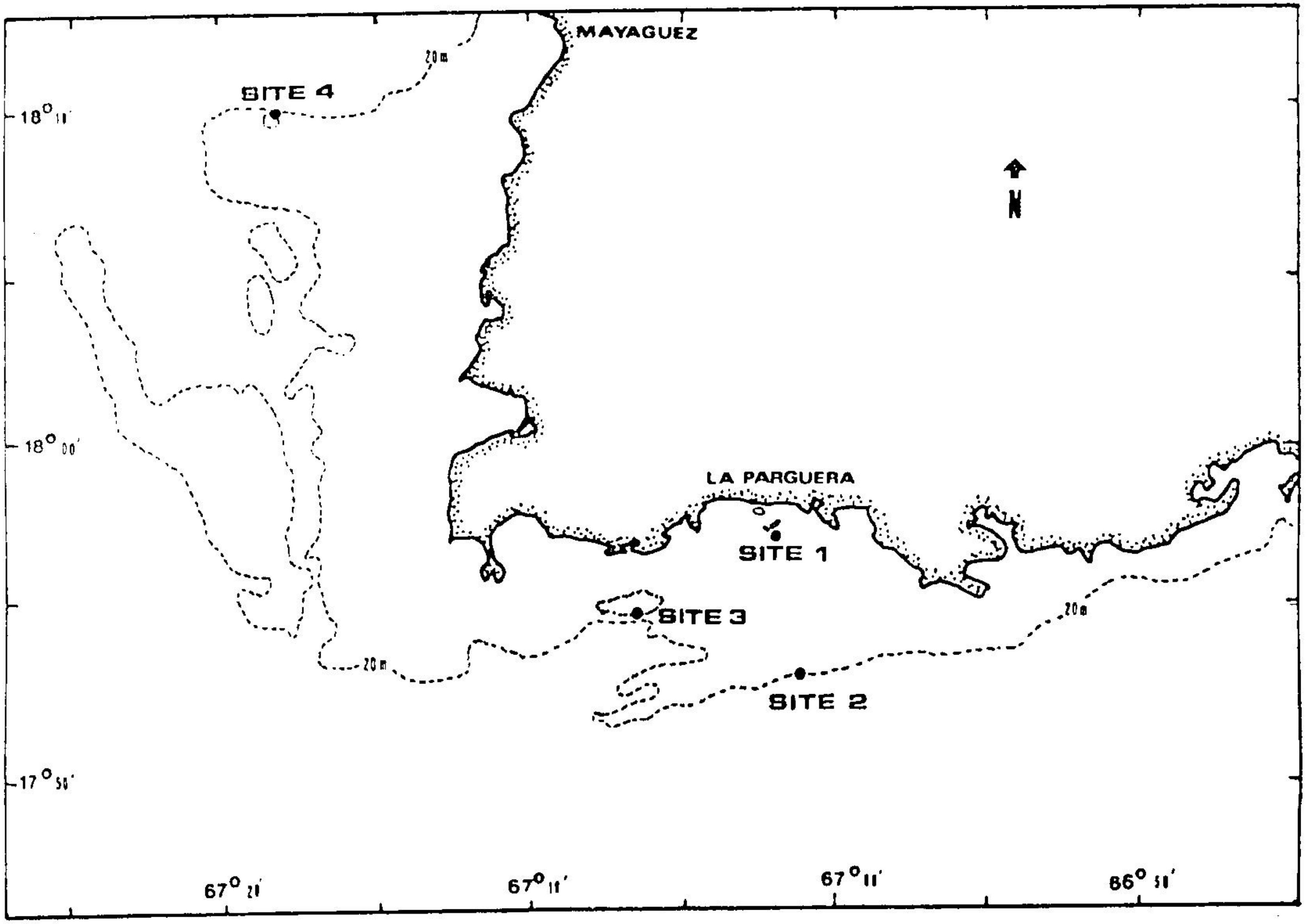
Physical Measurements

All field work was performed using SCUBA gear. Field data were recorded on plastic slates or underwater paper. Depth was measured either with a capillary or oil filled depth gauge. Temperatures were measured with an ordinary laboratory centigrade thermometer. Slope angles were measured to within 5° with a plastic protractor equipped with a plumb line. Visibility, surge, and currents were visually estimated whenever sites were visited and are relative between sites.

Study Sites

Site (1), near Magueyes Island, was chosen for intensive and temporal measurements. It is a patch reef located approximately 300 m SE of the channel between Cayo La Gata and Cayo Caracoles, almost in a direct line between the channel and Cayo Turromote (Figure 1). The reef is approximately 250 m long and 200 m wide, and depths vary from 3 to 15 m. The top of the reef is a gently sloping plateau which slopes sharply downward at a depth of 4 to 6 m, where it may be perpendicular or undercut to the reef base (about 15 m deep). The shallowest depths are on the northwestern side of the reef which is dominated by living and dead *Acropora palmata.* Gorgonians are very abundant to the east with occasional large heads of stony corals such as *Dendrogyra cylindricus* or *Montastrea annularis.* *Acropora cervicornis* stands occur

Figure 1. Map of south west Puerto Rico showing the study site locations.


MAYAGUEZ
SITE 4
20m
N
18° 11'
18° 00'
17° 50'
LA PARGUERA
SITE 1
SITE 3
SITE 2
20m
20m
67° 21'
67° 11'
67° 11'
86° 51'

randomly on the reef plateau. The substrate on the plateau area is uneven rock with frequent small patches of sand.

In addition to the abundance of gorgonians, this reef was chosen as the major study site because of its proximity to the laboratory and easy access in most weather. Disadvantages of this area included poor visibility and strong surge action. Visibility ranged from about 2 to 15 m with an average of 6 m. Surge was often strong on the plateau due to shallowness and exposure of the reef to the prevalent southeast winds and waves, while surge on the slopes (even on the fore reef) was much less. Temperatures were uniform from the top to the bottom of the reef on the two times measured, and a thermocline was rarely noticed. Current velocities were weak and did not exceed 13 cm/sec. When apparent, currents were from the southeast which is the direction of the prevailing winds. Orientations of the plane of branching of gorgonians have been suggested as indicators of the presence and direction of strong surge or currents (Barham and Davies, 1969); and on this reef are strongly oriented with the plane of branching perpendicular to the surge. Accumulated sediments and poor visibility indicate a high siltation rate on this reef. The reef base, especially, receives a great deal of sediments which are moved there by surge action from the plateau.

Site (2) is located approximately 10 km SSE of La Parguera on the shelf edge reef and approximately 150 m E of the "buoy" site (Figure 1). The shelf edge reef runs in an east-west direction, roughly parallel to the coast. The north side is bounded by a sandy area about 50 m wide and 22 m deep known as the "moat". From the moat, the reef rises to the south approximately at a 20° angle and gently levels out to a platform 16 to 18 m deep and about 150 m wide. The platform slopes gently to the south until reaching the shelf edge break at about 26 m in depth. The region near the shelf edge slope is often cut by sediment chutes, sand channels, which run perpendicular to the fore reef slope. Unlike site (1), the rock substrate is mostly even with few patches of sediment.

Visibility is between 13 and 50 m (averages 20-25 m). Siltation is probably less than on site (1). Surge is not as common as at site (1), but may be very strong when present. Currents are sporadic, mostly westerly, the direction of the wind, and often strong. Gorgonian orientation is normal to the surge rather than to the current. Strong thermoclines are infrequent, and temperatures are only a few °C cooler or the same as on site (1).

Site (3) lies seaward of the fore reef slope of Cayo Margarita which is located about 9.4 km WSW of La Parguera (Figure 1). Margarita, a long, exposed reef, runs in an east-west direction parallel to the coast. The area examined was on a very gentle slope from about 7 to 15 m deep. The study area was located about mid-distance along the length of the fore reef where there is a moderately even rock substrate with infrequent sandy areas. Although located some distance from the shelf edge, this reef is exposed to the prevailing winds and seas. Both currents and surge are probably often strong in this area, though very little current was present during four visits. Temperatures were not recorded. Visibility ranged from 6 to 24 m and seems to be intermediate between the first two sites. Sedimentation also appears to be intermediate.

Site (4), located approximately 10 km W of Punta Guanajibo on the west coast of Puerto Rico, is a part of Tourmaline reef (Figure 1). The area sampled was a moderately level platform from 11 to 15 m deep from where it sloped steeply downward. Only the platform area 11 to 13 m deep was sampled, and the site was visited once.

Physically this site resembled site (3) in surge, visibility, sedimentation, and depth. It is far enough offshore to receive little influence from the rivers which empty into Mayaguez Bay. There was no current or surge during the sampling, though the presence of sudden strong currents in this area is common knowledge. The substrate was very similar to sites (2) and (3).

Sessile fauna on the different sites were roughly compared. Gorgonians were abundant and diverse at all four sites, but they appear to be most abundant at site (1) and least abundant at site (4). Between 20 and 28 species occurred at site (1), and many of these were present at the other sites as well. All four sites also had abundant and diverse coral growth. It was estimated that 15 to 20 coral species occur at site (1) with coverage decreasing from the top to the bottom of the reef. Zoanthids, actiniarians, and corallimorpharians were more abundant at site (1) than at any of the other sites. Sponges were most abundant at sites (1) and (2), but many of the species differed at the two locations. Sites (3) and (4) appeared to have more similarities in the sessile fauna to site (2) than to site (1) which may indicate a stronger effect of substrate type and exposure than other physical conditions such as turbidity or sedimentation.

Distributional Studies

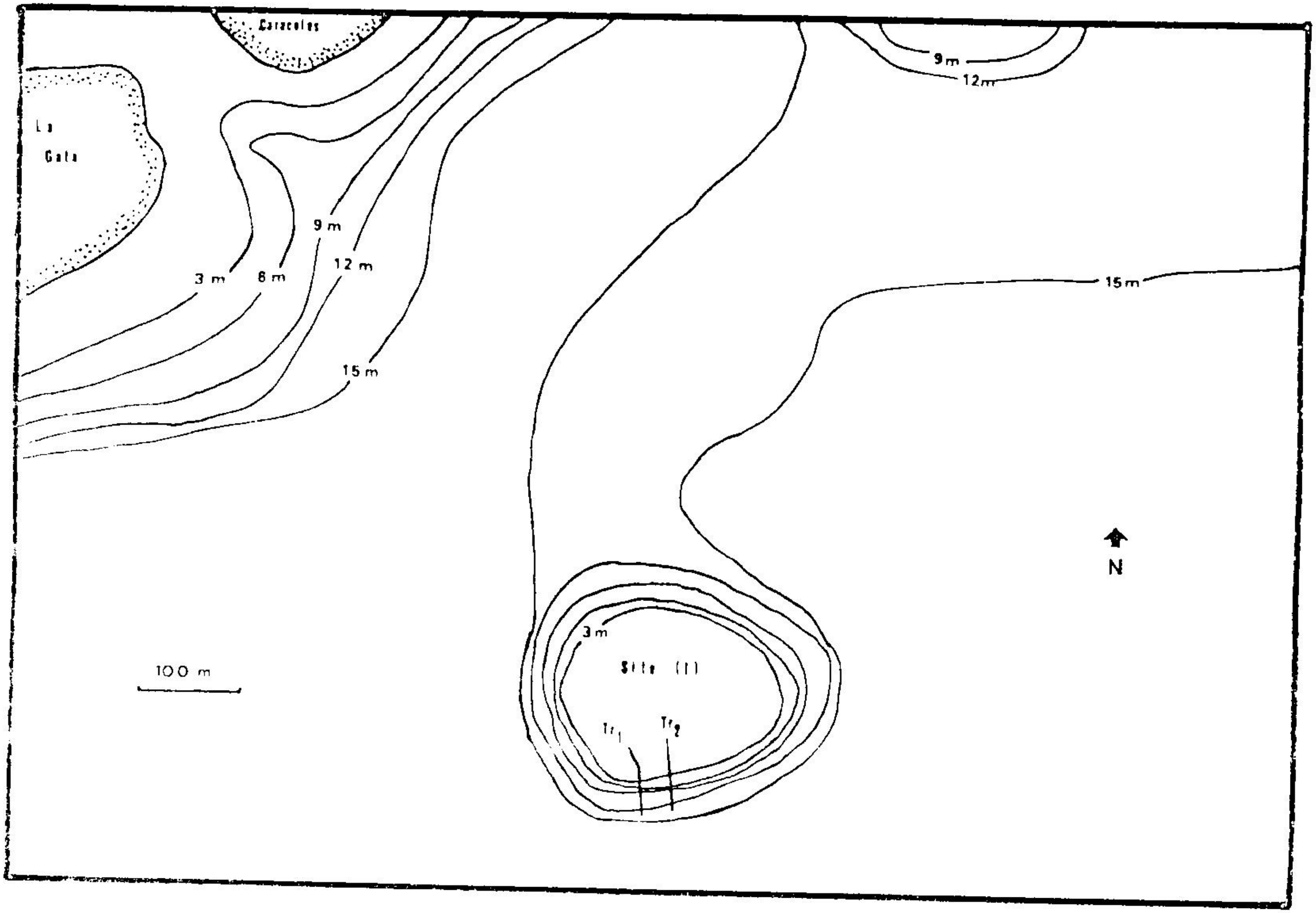
Pseudopterogorgia americana and *P. acerosa* were usually identified in the field by feel. *Pseudopterogorgia americana* feels very slimy, while *P. acerosa* feels "dry". This method is very accurate for *P. americana*, but may contain a small amount of error for *P. acerosa* due to the infrequent presence of similar species. Identifications were sometimes confirmed by spicule examination. The spicules were examined under a compound microscope after the organic material was removed with sodium hypochlorite.

Quadrat Studies

On study site (1), two 50 m long plastic transect lines were placed parallel to each other about 25 m apart. Both ran from the base of the fore reef slope, up the face of the reef, and well onto the plateau (Figure 2). These lines aided orientation and placement of permanent quadrats on the reef. A random stratified sampling pattern, which allowed all of the depth strata to be sampled while randomizing the samples within each stratum, was used to select positions for the permanent quadrats. The reef was arbitrarily divided into three 3.3 m depth strata from depths of 3.3 m to 13.3 m. Four depths were selected randomly within each stratum. These depths were used to position twelve 1 m^2 quadrats with six on each transect line. Quadrats were marked by thin nylon lines secured tightly to the bottom either by nails or strings tied to bottom features. *Pseudopterogorgia americana, P. acerosa,* other gorgonians, and other sessile fauna (corals, zoanthids, corallimorpharians, sponges, scleraxonian gorgonians, etc.) were mapped in all of the permanent quadrats.

Twelve other 1 m^2 quadrats at the same depths were first mapped and then cleared. Corners were marked by nails so that a metal 1 m^2 quadrat could be placed repeatedly in the same position. All sessile organisms were removed from the six quadrats along transect 1 with a hammer, chisels, and wire brushes. Hard corals which could not be chipped out were scoured with a wire brush until all visible tissue was removed and the septa heavily damaged. Six quadrats along transect 2 were cleared only of gorgonians using a

Figure 2. Map of site (1) located south east of La Parguera illustrating transect locations and depth contours.


Caracoles
La
Gata
3 m
6 m
9 m
12 m
15 m
9m
12m
15m
N
3m
Site (1)
Tr_1
Tr_2
100 m

hammer and chisel to remove the tough holdfasts.

A large 4 by 4 m quadrat, divided into 1 m^2 units by nylon lines, was tied on the plateau between transects 1 and 2. *P. americana*, *P. acerosa*, and other gorgonians were mapped and lengths measured. Lengths were measured with a flexible 1.5 m long measuring tape. Mapping was accurate enough to divide the quadrat down to 1/16 m^2 units.

Density and Size Frequency Studies

Density and size frequency data for *P. americana* and *P. acerosa* were taken concurrently. Six depths were sampled at site (1), five at site (2), two at site (3), one at site (4), and one shallow depth only for *P. americana* on El Negro reef near site (4). At site (1) two depths were selected randomly within each of three depth strata. At site (2) one transect was placed near the reef sand interface on the moat (19.8 m) while the four other transects were placed at randomly chosen depths over the reef. Transect depths at sites (3) and (4) were selected haphazardly for convenience. A nylon transect line was temporarily placed along each depth contour. Colonies of each species within a meter of either side of the line were counted for the first ten meters to estimate densities. Colony lengths and the number of major branches for *P. americana* and *P. acerosa* were measured for all colonies within a meter of either side of the line until 50 colonies of each species were recorded. Any colony over 3 cm could be easily spotted. Because slopes along different contours varied, actual depth variations on a line ranged from less than 0.3 m to 1.5 m. Relative abundances of the species were estimated from the size frequency data by noting the ratio of *P. acerosa* to *P. americana* when 50 of the more abundant species had been counted.

Mortality and Recruitment Studies

Since larvae of different species of octocorals cannot be easily distinguished, and are difficult to collect, no attempt was made to quantify larvae or to determine their rates of mortality. Therefore, newly settled polyps were regarded as recruits for the purposes of this study.

The permanent quadrats were monitored for mortality and recruitment. *P. americana* and *P. acerosa* colonies were mapped bimonthly; and the other gorgonians were mapped at six month intervals for a year. Any mortalities or recruitments were noted and causes of mortality determined when possible. Cleared quadrats were checked bimonthly for recruitment.

Additional recruitment studies were carried out at an area on the shelf edge near site (2) known as the buoy. The buoy was secured to concrete blocks on the bottom by a chain. While it was in place, the chain completely scoured an area nearly 100 m^2 removing virtually all of the corals, gorgonians, and sponges. The buoy was removed in February of 1977, and the area was examined in August of 1979. Density and sizes of all gorgonian colonies were measured over an area of

20 m^2 in the center of the scoured area.

Growth Studies

Length of all colonies in the 12 permanent quadrats were measured periodically. *P. americana* and *P. acerosa* were measured bimonthly while other gorgonians were measured at 6 month intervals. Five colonies of *P. americana* and seven of *P. acerosa* were tagged and measured bimonthly at site (2). Colonies were tagged by attaching Dymo tape tags by surgical steel or insulated electrical wire to the base of the colonies. No damage other than localized chafing ever appeared with either wire; in fact, gorgonian tissue or encrusting organisms grew over the wire and tags and were periodically scraped off. Light readings were taken with a Gossen Luna-Pro light meter in a waterproof case on a cloudless day with about 10 m of visibility under water. Individual readings were taken for all *Pseudopterogorgia* in the permanent quadrats.

Growth rings were also examined. All colonies of *P. americana* and *P. acerosa* from the cleared quadrats at site (1) were collected, measured, air dried, and weighed. A number of colonies of each species were collected at the other sites, and treated in the same manner. Colonies on sites other than (1) were either collected haphazardly or for a wide size range. The colonies were sawed in cross section as close to the base as possible, and then ground and polished on a bench grinder equipped with a buffing wheel. Rings were counted under a dissecting microscope, counting whichever branch had the greatest number of rings in both the base and main stem. Where difficult to distinguish, rings were also counted by making a cellulose acetate peel.

Reproduction

Nine colonies of each species were tagged near the north end of transect 1 on site (1). Large colonies (greater than 40 cm) were selected to minimize sampling effect. A small branchlet (about 4 cm) was clipped monthly from each colony with pruning shears, bagged individually, and returned to the laboratory. The clippings were examined alive under dissecting and compound microscopes equipped with ocular micrometers. Sizes of the five largest eggs or spermaries were measured, and approximate numbers of eggs or spermaries per polyp recorded. Several spermaries from each colony were broken open and examined microscopically. Ripeness of the sperm was determined by head size, head shape, and activity. Clippings from throughout two colonies (a male and a female) were examined to determine if there was any pattern in maturity of the gonads within the colony. Four colonies, two male and two female, were sampled every four or five days for a month to determine if there was any short-term periodicity in gonadal maturity. Whenever necessary, histological sections were made to determine sex and position of the gonads. Polyps were fixed in paraformaldehyde and stained with hematoxylin and eosin.

Originally, five colonies of each species were tagged at site (2). Three of these were not relocated apparently due to loss of the tags. Hence, clippings were examined monthly for only three colonies of *P. americana* and four colonies of *P. acerosa*.

All *Pseudopterogorgia* in the large 4 by 4 m quadrat were examined for gonads. Over 80% of the large colonies were sexed to determine how the sexes were dispersed relative to each other.

Grigg (1970) indicated that small colonies of *Muricea* as old as ten years did not contain gonads. For this reason, small colonies (under 30 cm) were collected at both sites (1) and (2) and examined under dissecting and compound microscopes for gonads. Ten of those which showed no evidence of gonads with these methods were examined histologically. At the same time, medium to large colonies were collected and examined to provide an expected ratio of colonies with gonads absent to gonads present at that time.

Ecological Interactions

Coverage of sessile fauna other than gorgonians (corals, zoanthids, sponges, scleraxonians, etc.) was estimated on the 12 permanent quadrat maps. A plastic overlay divided into small squares was used to make the estimates. Gorgonian recruits in the totally and partially cleared quadrats were counted.

Gorgonians growing with the bases touching were examined for any sign of damage. Any damage such as abrasion, grazing, or encrustation from other organisms was recorded. Encrustations on gorgonians within the permanent quadrats were measured bimonthly. Other organisms found on either species of *Pseudopterogorgia* were examined and the apparent relationship established.

Colonies of *P. acerosa* or *P. americana* being grazed by *Cyphoma gibbosum* were marked with small subsurface buoys placed near them and observed for several months. The scars were measured after the *C. gibbosum* left and subsequent healing or encrustation by other organisms noted. The ratio of *C. gibbosum* to gorgonian colonies on site (1) was estimated.

As *Thalassoma bifasciatum* (Bloch), the bluehead wrasse, was observed to be picking at gorgonians frequently; seven specimens were speared and the gut contents examined. A small portion of the gut contents was examined for spicules after first removing the organic matter with sodium hypochlorite.

Selective caging was attempted twice during the study. Four cages 1/4 m^2 by 1/4 m high were constructed of 1/2 inch hardware cloth. Two were open on top and two were closed. One of each was nailed onto two cleared quadrats. All four cages were destroyed by surge and deterioration within a month. A large number of *Diadema antillarum* (Philippi) were seen on one quadrat where many recruits had disappeared within one month. Two of the 1 m^2 cleared quadrats with abundant recruits were then fenced with chicken wire fastened tightly to the bottom with nails. All *D. antillarum* were removed from one and ten placed in the other. These cages were intact for 22 days until they were removed by storm waves caused by Hurricane David.

Diurnal activity of the two species was briefly examined. Counts of colonies divided into expanded, partially expanded, or retracted polyps were made during different times of the day.

Results

Distributional Studies

Small Scale Dispersion Patterns

Small scale dispersion patterns were examined to determine if gorgonians were evenly, randomly, or patchily dispersed over various quadrat sizes. These patterns have been used to study the results of recruitment, mortality, and behavior of species. Stimson (1974), for instance, found that colonies of *Pocillopora* sp. were evenly distributed due to the avoidance of existing colonies by settling larvae.

Fisher's index of dispersion (1958) was used to determine spatial pattern. This index is based on the Poisson distribution where variance equals the mean for randomly dispersed populations. Average densities of *P. americana*, *P. acerosa*, and total gorgonians were not significantly different between transects using a t-test. This justified combining quadrats between transects since the assumption of the Poisson of variance equals mean is not violated (Dana, 1976).

The highest variance to mean ratios occurred at 1 m^2 indicating that 1 m^2 approaches patch size (Table 1). The random dispersion patterns for *P. acerosa* may be an artifact of low densities because in such instances it is difficult to distinguish statistically even and aggregated from random patterns. Quadrat studies were done only on site (1). The

TABLE 1. Variance to mean ratios ($\frac{S^2}{\bar{x}}$) for abundances of *Pseudopterogorgia americana*, *Pseudopterogorgia acerosa*, and total gorgonians for different depths and quadrat sizes at site (1).

	DEPTHS														
	P. americana					*P. acerosa*					Total Gorgonians				
Quadrat Size	3.3 m to 6.1 m	6.1 m to 9.2 m	9.7 m to 12.2 m	C	Q 4 m	3.3 m to 6.1 m	6.1 m to 9.2 m	9.2 m to 12.2 m	C	Q 4 m	3.3 m to 6.1 m	6.1 m to 9.2 m	9.2 m to 12.2 m	C	Q 4 m
4 m^2 N				a 3.50 3	0.57 4				0.64 3	1.24 4				a* 3.55 3	1.17 4
1 m^2 N	a** 4.86 4	a*** 4.53 4	1.19 4	a** 3.73 12	1.61 16	0.67 4	a* 2.86 4	0.66 4	1.48 12	1.34 16	2.53 4	a*** 10.22 4	a*** 11.22 4	a*** 7.04 12	a*** 3.47 16
1/4 m^2 N	a** 2.06 16	a*** 3.46 16	1.09 16	a*** 2.22 43	a*** 1.53 56	0.80 16	a** 2.03 16	0.94 16	1.34 48	a** 1.50 56	a*** 2.61 16	a*** 2.61 16	a*** 2.46 16	a*** 3.50 48	a*** 2.43 56
1/16 m^2 N	a*** 1.90 64	e* 0.54 64	1.17 64	a*** 1.63 192	a* 1.15 256	1.00 64	1.00 64	1.00 64	0.95 192	a*** 1.66 256	a*** 1.78 64	a*** 2.79 64	a** 1.48 64	a*** 1.94 192	e*** 0.74 256

C = first three sets of quadrats combined, Q = large 16 m^2 quadrat at 4 m deep, N = number of quadrats, a = aggregated, e = even, $p<.05$*, $p<.01$**, $p<.005$***

Formula for determining significance:

$$X^2_{(n-1)} = (n-1)\frac{S^2}{\bar{X}}$$

heterogeneous substrate in this area may be a major factor causing the patchy distribution of gorgonians.

Densities and Size Frequencies

Densities of *Pseudopterogorgia americana* and *Pseudopterogorgia acerosa* at various depths within a site and at different sites are shown in Table 2. Ratios were obtained by dividing the number of *P. acerosa* by the number of *P. americana* when 50 of the more abundant species had been counted. A two way analysis of variance (ANOVA) was used to compare abundances between depths and species at site (1). Abundances were log transformed to normalize data and equalize variances. No significant difference between depths was found for *P. americana* or *P. acerosa* (Table 3, F-test). *P. americana* was significantly more abundant than *P. acerosa* (p<.001, F-test). On site (2) a two way analysis of variance (ANOVA) showed no significant differences between depths or species (Table 4). Site (3) had only two depths taken and they were very similar.

A two way analysis of variance (ANOVA) for densities showed significant differences between the two species and between the first three sites (Table 5). Site (4) was not included as only one density measure was taken. The significant interaction (p<.005, F-test) is an indication that relative species abundances differ between sites. This interaction can also be inferred from the ratio of abundances in Table 2 where *P. americana* is more abundant than *P. acerosa*

TABLE 2. Density of colonies per 20 m^2 for *Pseudopterogorgia americana*, *Pseudopterogorgia acerosa* for different depths at different sites, and ratios of *Pseudopterogorgia acerosa* to *Pseudopterogorgia americana* when 50 of the most abundant species were counted.

	SITE (1)						SITE (2)					SITE (3)		SITE(4)
Depth (m)	4.2	5	7	7.8	9.5	11	Moat 19.8	18.9	18.3	16.8	Edge 21.4	7.3	9.8	11.9
P. americana	66	90	39	75	63	45	6	9	6	4	3	18	36	8
P. acerosa	21	14	8	18	8	4	13	3	9	8	2	7	12	18
Ratio	.20	.38	.32	.24	.14	.18	2.27	1.43	1.32	2.08	.96	.18	.24	.92

TABLE 3. A two way analysis of variance (ANOVA) for densities between depths and *Pseudopterogorgia americana* and *Pseudopterogorgia acerosa* for Site (1).

	SS	df	MS	F ratio	Significance
Between species	1.73	1	1.73	$F_{1,5}=96.1$	$p<.001$
Between depths	0.37	5	0.074	$F_{5,5}= 4.1$	NS
Error	0.09	5	0.018		
Total	2.19	11			

SS=sum of squares, df=degrees of freedom, MS=mean square, F=F-test

TABLE 4. A two way analysis of variance (ANOVA) for densities between depths and *Pseudopterogorgia americana* and *Pseudopterogorgia acerosa* for Site (2).

	SS	df	MS	F ratio	Significance
Between species	0.01	1	0.01	$F_{1,4}=0.17$	NS
Between depths	0.38	4	0.095	$F_{4,4}=1.64$	NS
Error	0.23	4	0.058		
Total	0.62	9			

SS=sum of squares, df=degrees of freedom, MS=mean square, F=F-test

TABLE 5. A two way analysis of variance (ANOVA) for densities between *Pseudopterogorgia americana* and *Pseudopterogorgia acerosa* and sites.

	SS	df	MS	F ratio	Significance
Between species	1.08	1	1.08	$F_{1,20}=20$	$p<.001$
Between sites	2.49	2	1.245	$F_{2,20}=23.06$	$p<.005$
Interaction	0.83	2	0.415	$F_{2,20}=7.69$	$p<.005$
Error	1.07	20	0.054		
Total	5.47	25			

SS=sum of squares, df=degrees of freedom, MS=mean square, F=F-test

TABLE 6. Comparisons of age frequency percentages between *Pseudopterogorgia americana* and *Pseudopterogorgia acerosa* at the study sites. Probabilities calculated from the Kolmogorov-Smirnov test.

Depths Site(1)	p	Depths Site(2)	p	Depths Site(3)	p	Depths Site(4)	p	Combined Sites	p
4.2 m	NS	19.8 m	NS	7.3 m	NS	11.9 m	NS	Site(1)	NS
5 m	NS	18.9 m	.05[2]	9.8 m	NS			Site(2)	NS
7 m	.05[1]	18.3 m	NS					Site(3)	NS
7.8 m	NS	16.8 m						Site(4)	NS
9.5 m	NS	21.4 m							
11 m	NS								

1. By age 5, *P. acerosa* has a higher percentage
2. By age 4, *P. acerosa* has a higher percentage

TABLE 7. Comparisons of age frequency percentages between depths for *Pseudopterogorgia americana* and *Pseudopterogorgia acerosa* at Site (1). Probabilities calculated from the Kolmogorov-Smirnov test.

	P. americana						*P. acerosa*					
Depths (m)	4.2	5.0	7.0	7.8	9.5	11.0	4.2	5.0	7.0	7.8	9.5	11.0
4.2		NS	NS	$.05_1$	NS	NS		NS	NS	NS	NS	NS
5.0			NS	NS	NS	NS			NS	NS	NS	NS
7.0				$.05_2$	$.05_3$	NS				NS	NS	NS
7.8					NS	NS					$.05_4$	NS
9.5						NS						NS
11.0												

1. By age 3, 7.8 m has a higher percentage
2. By age 5, 7.8 m has a higher percentage
3. By age 7, 9.5 m has a higher percentage
4. By age 2, 7.8 m has a higher percentage

TABLE 8. Comparisons of age frequency percentages between depths for *Pseudopterogorgia americana* and *Pseudopterogorgia acerosa* at Site (2). Probabilities calculated from the Kolmogorov-Smirnov test.

	P. americana					*P. acerosa*				
Depths (m)	Moat 19.8	18.9	18.3	16.8	Edge 21.4	Moat 19.8	18.9	18.3	16.8	Edge 21.4
19.8		NS	$.01_1$	$.01_2$	$.01_3$		NS	NS	NS	NS
18.9			NS	$.02_4$	NS			NS	NS	NS
18.3				NS	NS				NS	NS
16.8					NS					NS
21.4										

1. By age 7, 18.3 m has a higher percentage
2. By age 6, 16.8 m has a higher percentage
3. By age 5, 21.4 m has a higher percentage
4. By age 6, 16.8 m has a higher percentage

TABLE 9. Comparisons of age frequency percentages between depths for *Pseudopterogorgia americana* and *Pseudopterogorgia acerosa* at Site (3). Probabilities calculated from the Kolmogorov-Smirnov test.

	P. americana		*P. acerosa*	
Depths (m)	7.3	9.8	7.3	9.8
7.3		NS		NS

TABLE 10. Comparisons of age frequency percentages between sites for *Pseudopterogorgia americana*. Site (2) does not include data for 18.9 m and 19.8 m as these are treated separately. Probabilities calculated from the Kolmogorov-Smirnov test.

SITES	Site (1)	Site (2)	Site(2) 18.9 m	Site(2) 19.8 m	Site(3)	Site(4)
Site (1)		$.01_1$	NS	NS	NS	$.01_2$
Site (2)			NS	$.01_3$	$.01_3$	NS
18.9 m				NS	NS	$.01_4$
19.8 m					NS	$.01_4$
Site (3)						$.01_5$
Site (4)						

1. By age 2, Site (2) has a higher percentage
2. By age 7, Site (4) has a higher percentage
3. By age 5, Site (2) has a higher percentage
4. By age 3, Site (4) has a higher percentage
5. By age 4, Site (4) has a higher percentage

TABLE 11. Comparisons of age frequency percentages between sites for *Pseudopterogorgia acerosa*. Probabilities calculated from the Kolmogorov-Smirnov test.

SITES	Site (1)	Site (2)	Site (3)	Site (4)
Site (1)		NS	$.01_1$	$.02_2$
Site (2)			$.01_3$	NS
Site (3)				$.01_4$
Site (4)				

1. By age 4, Site (1) has a higher percentage
2. By age 4, Site (4) has a higher percentage
3. By age 3, Site (2) has a higher percentage
4. By age 4, Site (4) has a higher percentage

Table 12. Comparisons of age frequency percentages between study sites and El Negro reef for *Pseudopterogoria americana*. Probabilities calculated from the Kolmogorov-Smirnov test.

	Site (1)	Site (2)	Site(2) 18.9 m	Site(2) 19.8 m	Site (3)	Site (4)
El Negro	$.01_1$	$.01_2$	$.01_3$	$.05_4$	$.01_5$	$.01_6$

1. By age 5, Site (1) has a higher percentage
2. By age 4, Site (1) has a higher percentage
3. By age 8, Site (2) has a higher percentage
4. By age 18, Site (2) 19.8 m has a higher percentage
5. By age 9, Site (3) has a higher percentage
6. By age 3, Site (4) has a higher percentage

at sites (1) and (3) and less abundant or equal at sites (2) and (4).

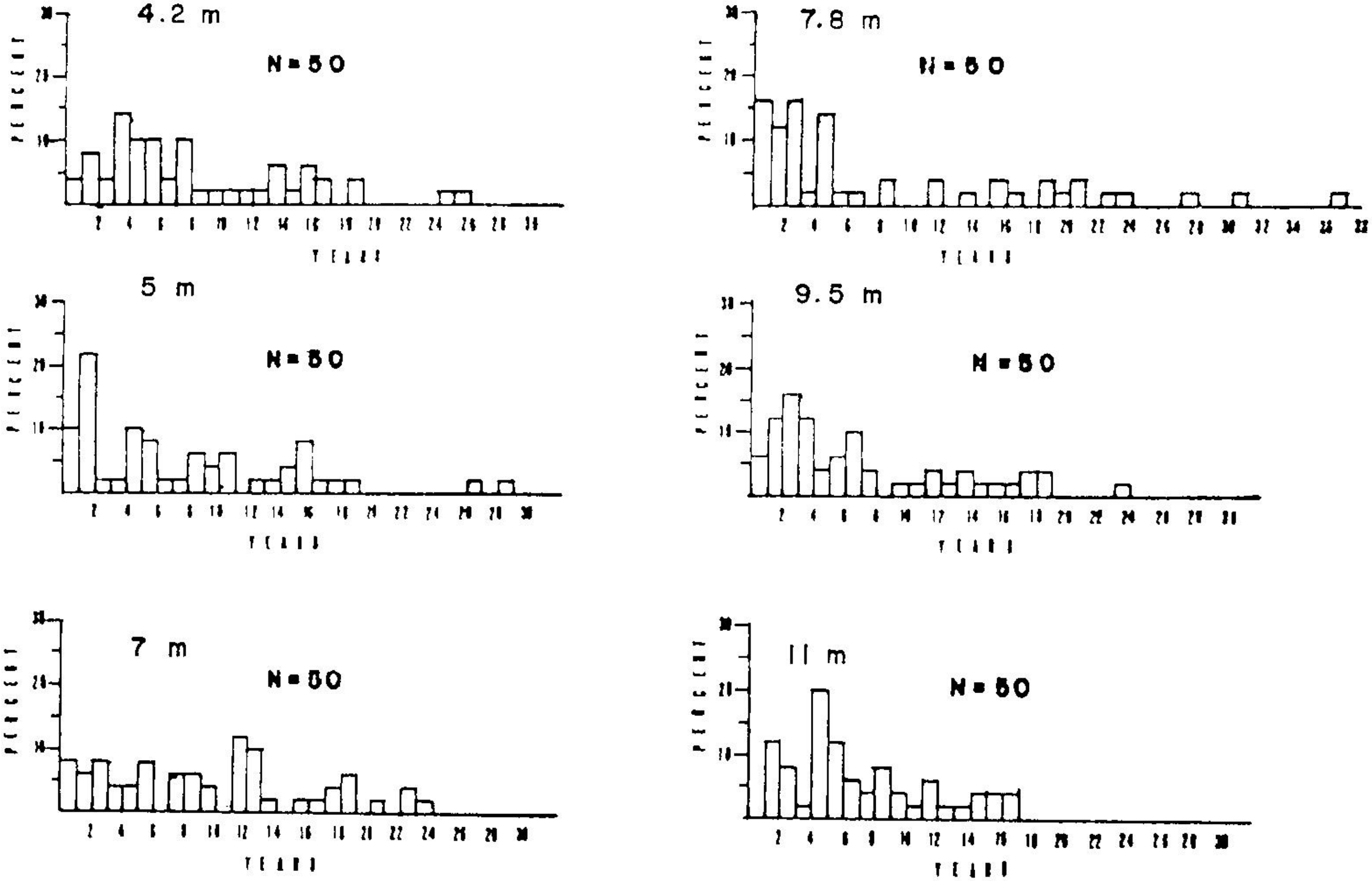
Size frequency data were converted to age frequencies using mean growth rates calculated for each species on each site (see growth section). Figures 3 through 8 show age frequency distributions for each species within sites at different depths and between sites. Age frequency distribution for *P. americana* on El Negro reef is shown in Figure 8. Cumulative percentages for age classes between species, within depths on a site, and between sites were compared using the Kolmogorov-Smirnov test (Tate and Clelland, 1957). Cumulative percentages were from youngest to oldest age classes. Tables 6 through 12 show probabilities for comparisons between these cumulative frequency percentages.

Age frequencies of *P. americana* or *P. acerosa* within each depth at each site were not significantly different in most cases (Table 6). Some significant differences within depths may be due to multiple testing error where significance may be an artifact of the large number of comparisons made.

Where no or few significant differences were found for cumulative size frequencies, the data were pooled for a species on a particular site. This allowed comparisons between sites. Thus age frequency data for *P. acerosa* on all sites and for *P. americana* on sites (1) and (3) were pooled.

Figure 3. Age frequency distributions of *Pseudopterogorgia americana* at different depths on site (1). N = number of colonies used.

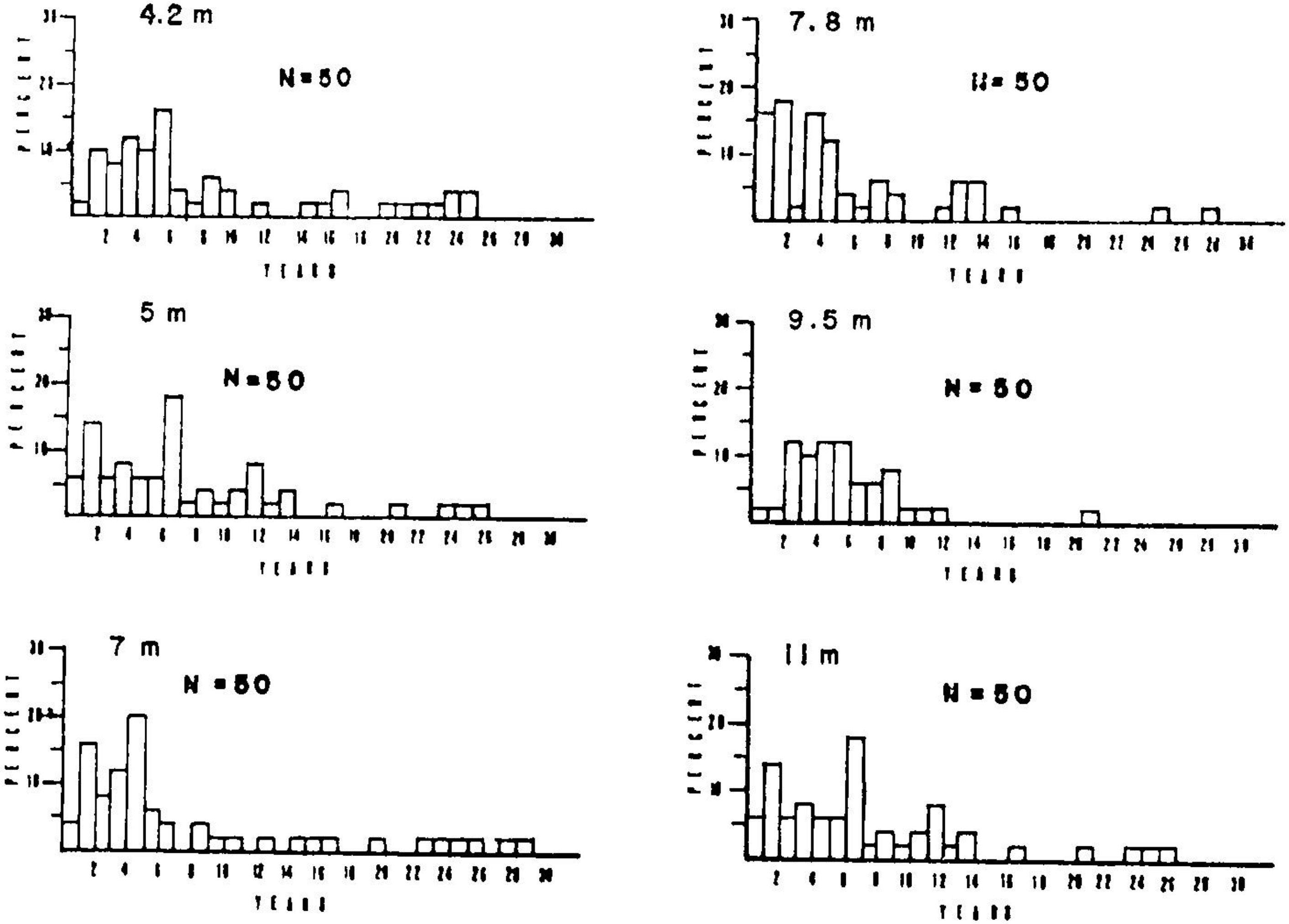
Site 1



Pseudopterogorgia americana

Figure 4. Age frequency distributions of *Pseudopterogorgia acerosa* at different depths on site (1). N = number of colonies used.

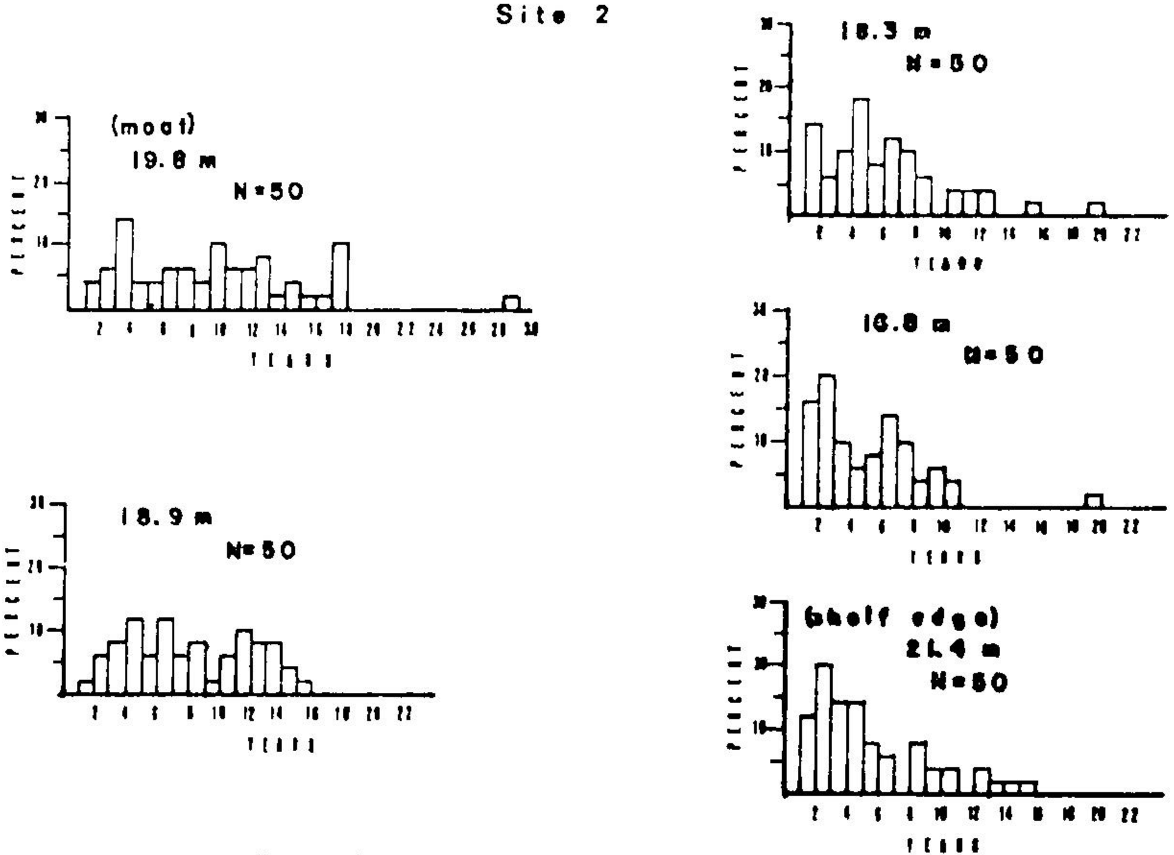
Site 1



<u>Pseudopterogorgia</u> <u>acerosa</u>

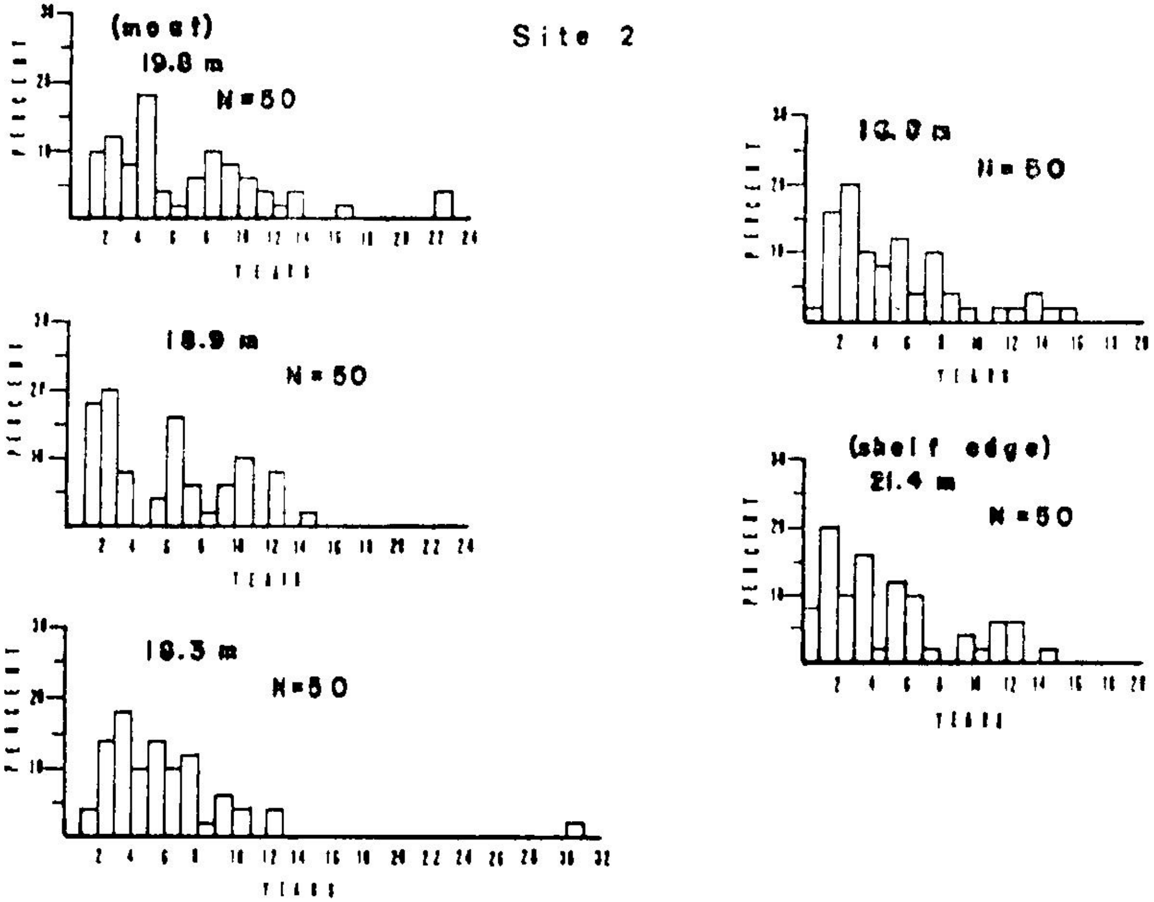
Figure 5. Age frequency distributions of *Pseudopterogorgia americana* at different depths on site (2). N = number of colonies used.

Site 2



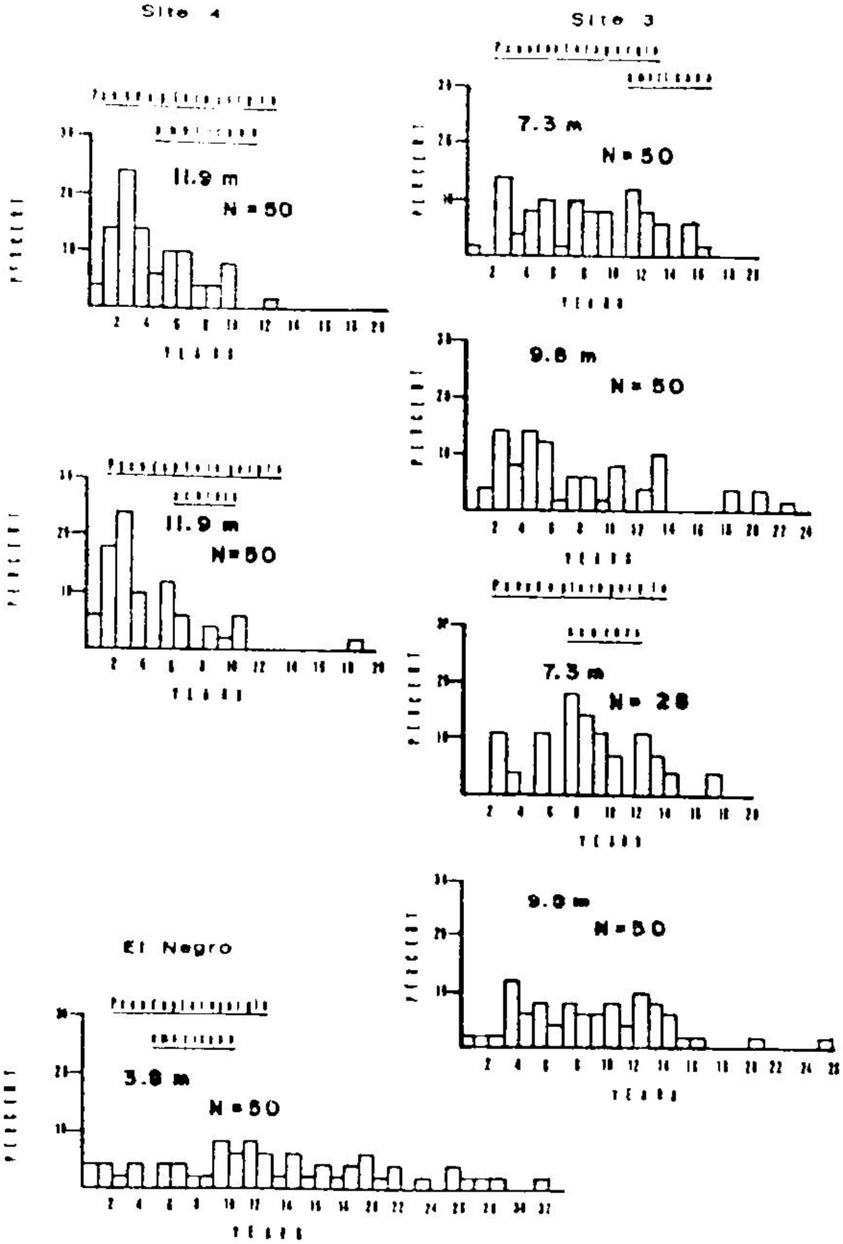
Pseudopterogorgia americana

Figure 6. Age frequency distributions of *Pseudopterogorgia acerosa* at different depths on site (2). N = number of colonies used.



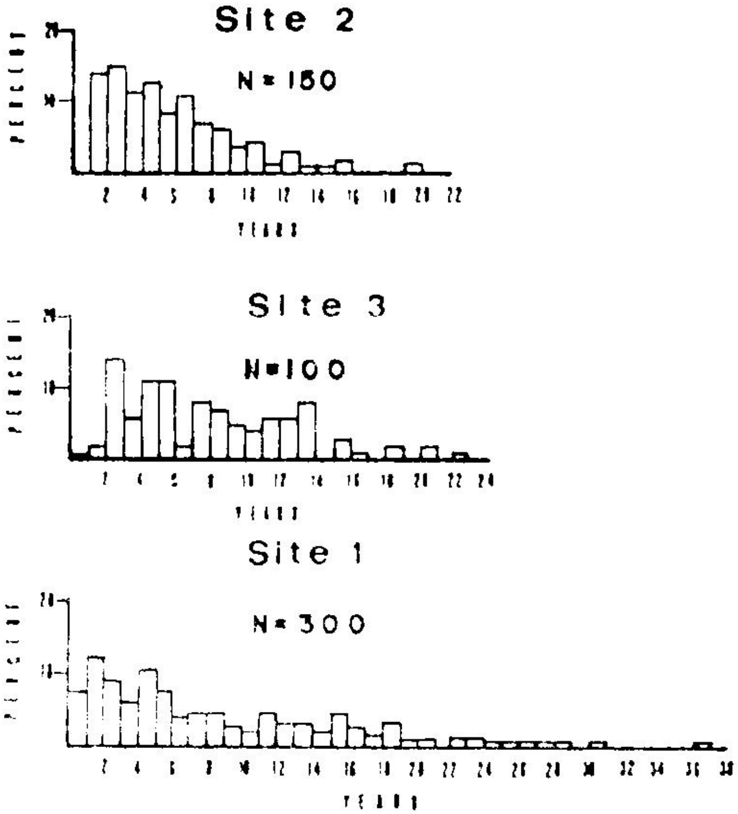
Pseudopterogorgia acerosa

Figure 7. Age frequency distributions of *Pseudopterogorgia americana* and *Pseudopterogorgia acerosa* at different depths on site (3), one depth on site (4), and one depth for *P. americana* on El Negro reef. N = number of colonies used.

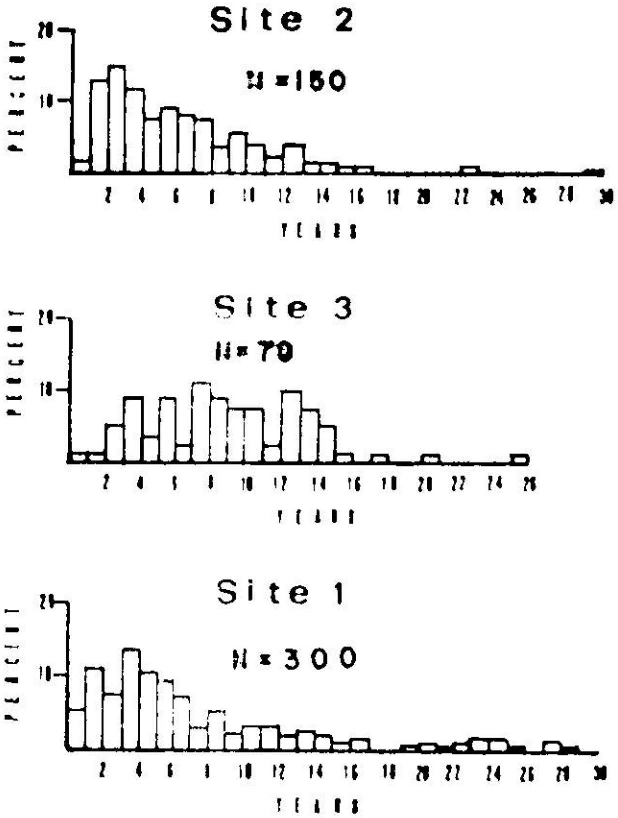


Site 4
Pseudopterogorgia
americana
11.9 m
N = 50
PERCENT
YEARS
Pseudopterogorgia
acerosa
11.9 m
N=50
PERCENT
YEARS
Site 3
Pseudopterogorgia
americana
7.3 m
N = 50
PERCENT
YEARS
9.8 m
N = 50
PERCENT
YEARS
Pseudopterogorgia
acerosa
7.3 m
N = 28
PERCENT
YEARS
9.8 m
N = 50
PERCENT
YEARS
El Negro
Pseudopterogorgia
americana
3.8 m
N = 50
PERCENT
YEARS

Figure 8. Age frequency distribution of *Pseudopterogorgia americana* and *Pseudopterogorgia acerosa* on sites (1), (2), and (3). N = number of colonies used.



Pseudopterogorgia americana



Pseudopterogorgia acerosa

Age frequencies for *P. americana* on site (2) showed highly significant differences ($p < .01$) between 19.8 m and all other depths except 18.9 m which was significantly different ($p < .02$) from one other depth. Therefore, data for these two depths were treated separately, while the data for the other three depths were pooled. The 19.8 m data were taken on a sand-reef interface, and are not significantly different from site (1) or the 11 m depth on site (1) which is also a sand-reef interface. Although 19.8 m is significantly different from El Negro reef which is located near site (4) ($p < .05$) for age frequencies of *P. americana* this only becomes apparent at the older age classes (Table 12). El Negro was a shallow protected reef area with frequent large sand patches.

The results of Tables 6 through 12 are summarized by Table 13 which ranks sites from those containing the greatest proportion of young to those containing the greatest proportion of old colonies. Station ranks are similar for both species with the exception of the 19.8 m depth for site (2). Thus, younger colonies of both *P. americana* and *P. acerosa* are more abundant at site (4) and older colonies at site (3).

Recruitment and Mortality

The mean number of recruits per m^2 was 1.1 for *P. americana*, 0.1 for *P. acerosa*, and 2.4 for other gorgonians. A two way analysis of variance (ANOVA) for recruitment be-

TABLE 13. Sites ranked according to those containing the greatest proportion of young colonies. Underlining indicates no significant differences.

Youngest %						Oldest %
			P. americana			
Site (4)	Site (2)	Site (2) 18.9 m	Site (1)	Site (3)	Site (2) 19.8 m	El Negro
			P. acerosa			
Site (4)	Site (2)	Site (1)	Site (3)			

TABLE 14. A two way analysis of variance (ANOVA) for recruitment between *Pseudopterogorgia americana* and *Pseudopterogorgia acerosa*.

	SS	df	MS	F ratio	Significance
Between species	1.016	2	0.508	$F_{2,27}=7.82$	$p< .01$
Between depths	0.048	2	0.024	$F_{2,27}=0.37$	NS
Interaction	0.139	4	0.048	$F_{4,27}=0.74$	NS
Error	1.766	27			
Total	2.969	35			

SS= sum of squares, df=degrees of freedom, MS=mean square, F=F-test tween depths and between *P. americana*, *P. acerosa*, and other gorgonians on site (1) showed no significant differences in recruitment between species (Table 14). (Variances were equalized and data were normalized by log transformations.) *P. acerosa* had significantly fewer recruits than "other gorgonians" ($p<.05$, Neuman-Keuls, Sokal and Rohlf, 1969). All other comparisons were not significant. Estimates of recruitment are probably low for "other gorgonians" as they were checked only every six months.

Mean number of recruits per m^2 in all of the cleared quadrats was 9.2 for *P. americana*, 2.8 for *P. acerosa*, and 4.2 for other gorgonians. Recruitment in the uncleared (permanent) quadrats on transect 1 was compared to the quadrats cleared of gorgonians and to the totally cleared quadrats. A two way analysis of variance (ANOVA) with log transformed data showed significant differences between quadrat treatment and between species (Table 15). *P. americana* had significantly higher recruitment than *P. acerosa* ($p<.05$, Neuman-Keuls). Other comparisons were not significant. Totally cleared quadrats and quadrats cleared of gorgonians did not differ significantly, but both were significantly different from the uncleared quadrats ($p<.05$, Neuman-Keuls). Therefore, recruitment is increased by the removal of adult gorgonians and encrusting organisms. Scoured corals and encrusting organisms in the totally cleared quadrats showed recovery within four months. This may explain why recruitment between totally cleared quadrats and gorgonian cleared quadrats was not significantly different. Recruits were noticeable at a height of 1 cm, and the most recruits for *P. americana* were seen in June and July. These recruits may be as old as 5 to 6 months (see discussion).

Densities of *P. americana* and *P. acerosa* in a 20 m^2 quadrat near site (2) at the buoy scar site were compared to densities in two 20 m^2 quadrats at the same depths and comparable positions at site (2). The 95% confidence limits for *P. americana* and *P. acerosa* for the two positions at site (2) were from 0 to 11.3 colonies per 20 m^2 with a mean of 2.5 colonies for each species. The observed values for the buoy scar area were 14 colonies for *P. acerosa* and 17 colonies for *P. americana* per 20 m^2 suggesting that recruitment is also higher in cleared areas at site (2).

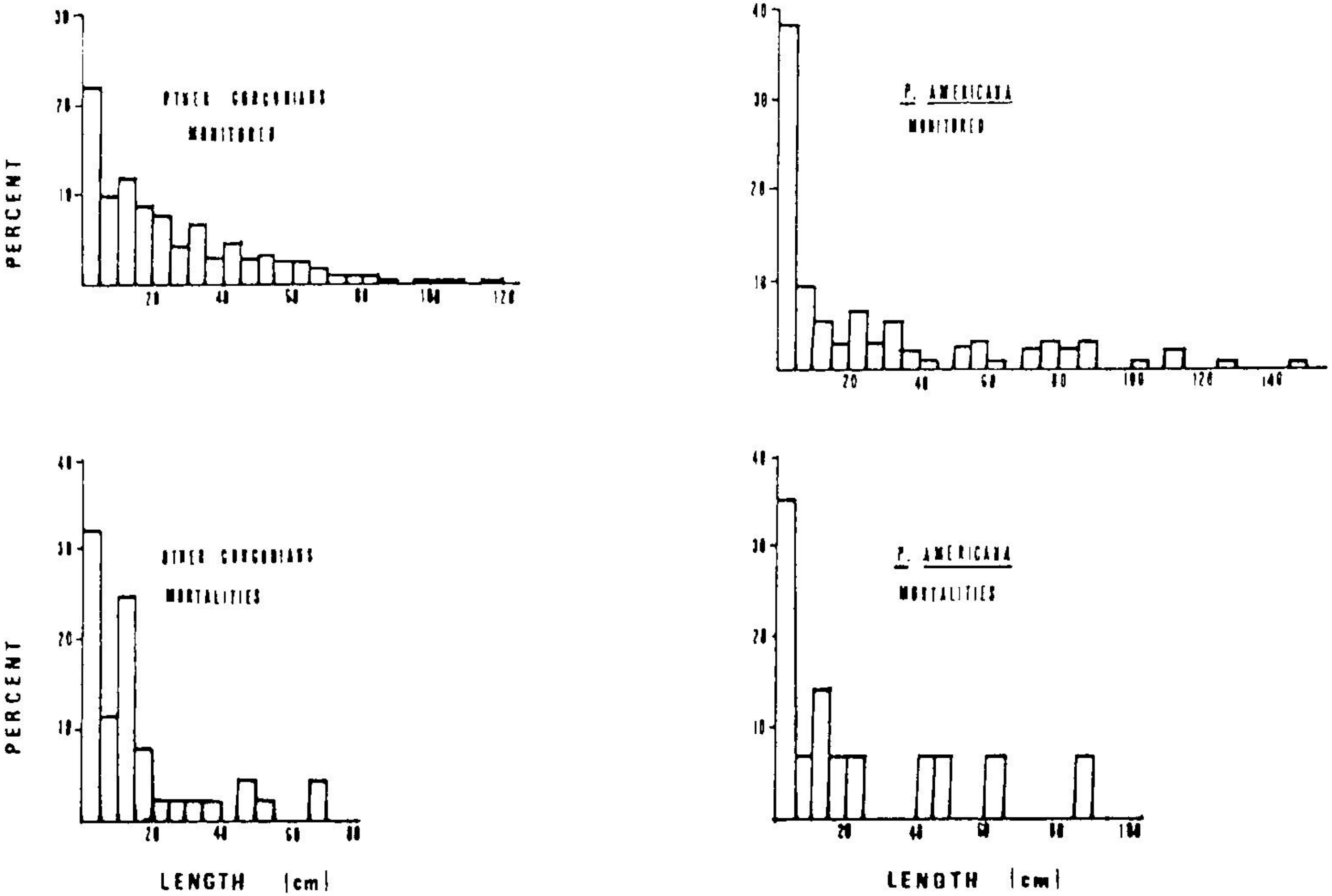
Mortality rates in the permanent quadrats on site (1) for *P. americana*, *P. acerosa*, and other gorgonians were calculated by dividing the number that died by the number monitored over one year. These percentages were 15.6% for *P. americana* (14/90), 6.7% for *P. acerosa* (1/15), and 17.3% for other gorgonians (43/249). None of these percentages were significantly different when compared by an arcsine transformation for comparing percentages (Sokal and Rohlf, 1969).

Size frequencies of mortalities for *P. americana* and other gorgonians were compared with size frequencies of the gorgonians monitored (Figure 9). Cumulative frequency percentages showed no significant differences for *P. americana*. Thus mortality of a given size class is proportional to the relative abundances of that size class. There is a significantly higher percentage of mortalities for small sizes in other gorgonians ($p<.05$, Kolmogorov-Smirnov test). *Pseudopterogorgia acerosa* was not included as there was only one mortality.

The number of mortalities were not significantly different from the number of recruits in the uncleared (permanent) quadrats for *P. americana* and other gorgonians (t-test) implying stable population sizes of gorgonians at site (1). *P. acerosa* was not included as there was a total of one mortality and one recruit.

The causes of mortality could seldom be ascertained. Two or three mortalities appeared to be caused by weakening of the basal stalk due to encrustations. One colony under 15 cm tall had the axial skeleton completely stripped of tissue when the mortality was first recorded. A month later the skeleton was gone. This was probably the result of grazing by *Cyphoma gibbosum* or an amphinomid polychaet. High mortalities occurred among the very small colonies (under 2 cm) in one of the cleared quadrats, and the cause could not be attributed to smothering by sediments or algae or to scouring by wave action.

Figure 9. Comparisons of the length frequency distributions of the gorgonians monitored in the 12 permanent quadrats to the length frequency distributions of mortalities in these quadrats. "Other gorgonians" does not include *Pseudopterogorgia americana* or *Pseudopterogorgia acerosa*.



OTHER GORGONIANS
MONITORED
P. AMERICANA
MONITORED
OTHER GORGONIANS
MORTALITIES
P. AMERICANA
MORTALITIES
PERCENT
PERCENT
30
20
10
40
30
20
10
20
40
60
80
100
120
140
LENGTH (cm)
LENGTH (cm)

TABLE 15. A two way analysis of variance (ANOVA) between *Pseudopterogorgia americana* and *Pseudopterogorgia acerosa* and quadrat clearing treatments.

	SS	df	MS	F ratio	Significance
Between species	1.35	2	0.675	$F_{2,45}=5.31$	p .05
Between treatments	1.80	2	0.900	$F_{2,45}=7.09$	p .05
Interaction	0.61	4	0.153	$F_{4,45}=1.20$	NS
Error	5.73	45			
Total	9.49	53			

SS=sum of squares, df=degrees of freedom, MS=mean square, F=F-test

TABLE 16. Annual growth rates (cm/yr) based on growth rates for *Pseudopterogorgia americana* and *Pseudopterogorgia acerosa* at the study sites.

	P. americana			*P. acerosa*		
Site	cm/yr	SD	N	cm/yr	SD	N
(1)	5.6	2.1	43	6.0	2.0	19
(2)	5.9	2.5	20	6.9	2.1	38
(3)	5.5	1.2	21	5.4	1.9	15
(4)	5.3	2.3	23	5.9	1.6	29

SD=standard deviation, N=number

Figure 10. Least squares length-weight regressions for *Pseudopterogorgia americana* (r_1) and *Pseudopterogorgia acerosa* (r_2) collected at site (1). *P. americana* is represented by ✱ and *P. acerosa* is represented by ● .

Sites (1), (2), and (3) were briefly inspected after storm waves generated by Hurricane David devasted many shallow water reefs on 30 August 1979. On site (1) wave energy was strong enough to topple a large head of *Dendrogyra cylindrica*. *Acropora cervicornis* stands were broken and pieces scattered over the reef. The most commonly detached gorgonians were *Plexaurella* spp., *Muricea* spp., and *Plexaura* spp. on site (1). *Pseudopterogorgia americana* and *P. acerosa* were seldom detached. *Pseudoplexaura* spp., *Pseudopterogorgia americana*, and *P. acerosa* were frequently damaged by abrasion to branch tips. The removal of tissue on the bases of colonies as described by Cary (1914) was not seen on site (1), but was common on sites (2) and (3). The rock substrate on these two sites appeared to be scoured.

Growth

Length-weight regressions using log-log plots for the two species at the four sites are shown in Figures 10 through 13. All regressions were highly significant ($p<.001$, F-test, Sokal and Rohlf). The linear equation form for the regressions, $\log Y = \log b + m \log X$, can be written $Y = b X^m$. Therefore the slope, m, of the linear form is the exponent of length in this case. These exponents were between 2 and 3 in all cases indicating that both species weigh somewhere between the square and the cube of the length times some constant (always far less than 1). Slopes (or exponents) did not differ significantly for any comparisons between species

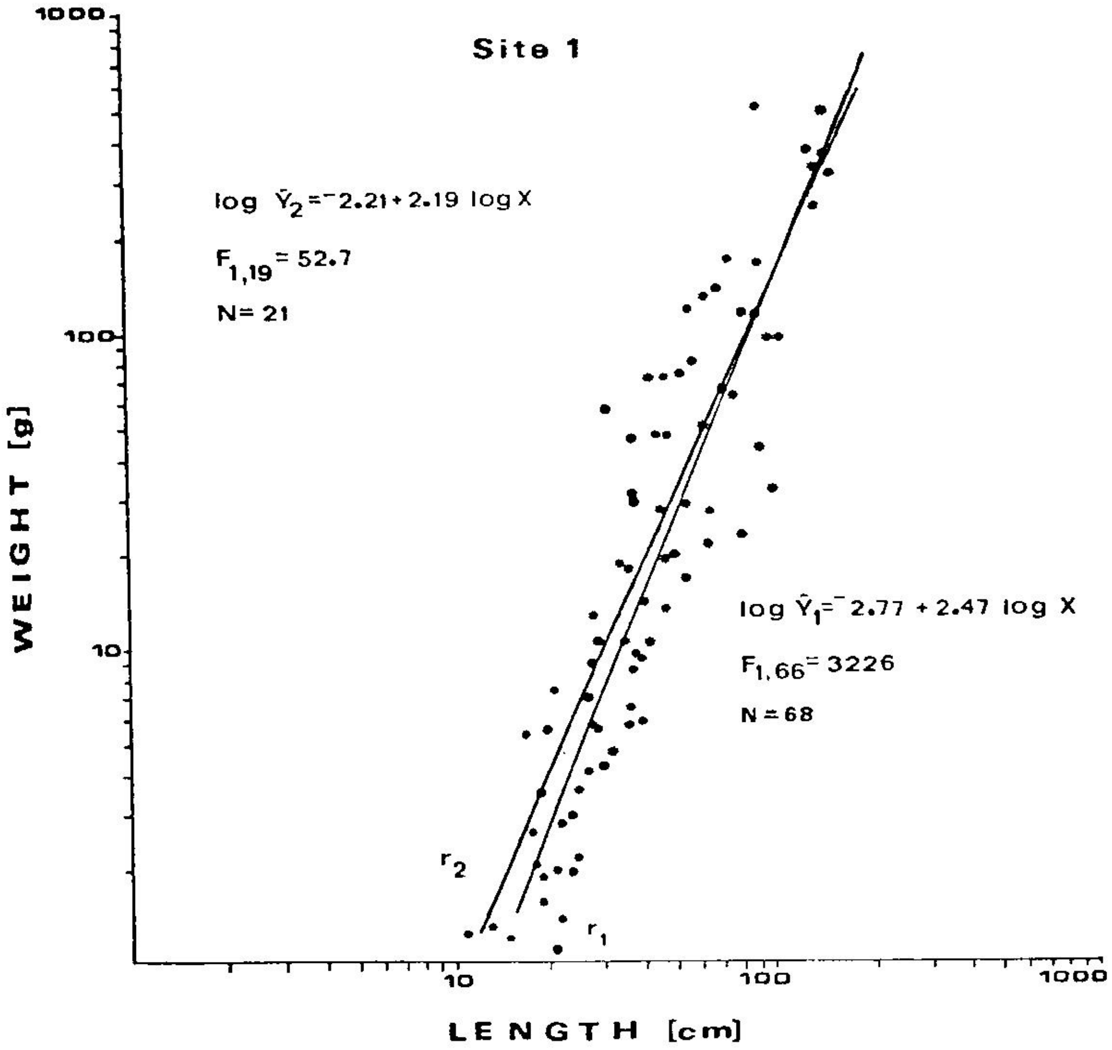

Site 1
log Ŷ2=⁻2.21+2.19 log X
F1,19= 52.7
N= 21
log Ŷ1=⁻2.77 + 2.47 log X
F1,66= 3226
N = 68
r2
r1
WEIGHT [g]
1000
100
10
LENGTH [cm]
10
100
1000

Figure 11. Least squares length-weight regressions for *Pseudopterogorgia americana* (r_1) and *Pseudopterogorgia acerosa* (r_2)[1] collected at site (2). *P. americana* is represented by ✱ and *P. acerosa* is represented by ●.

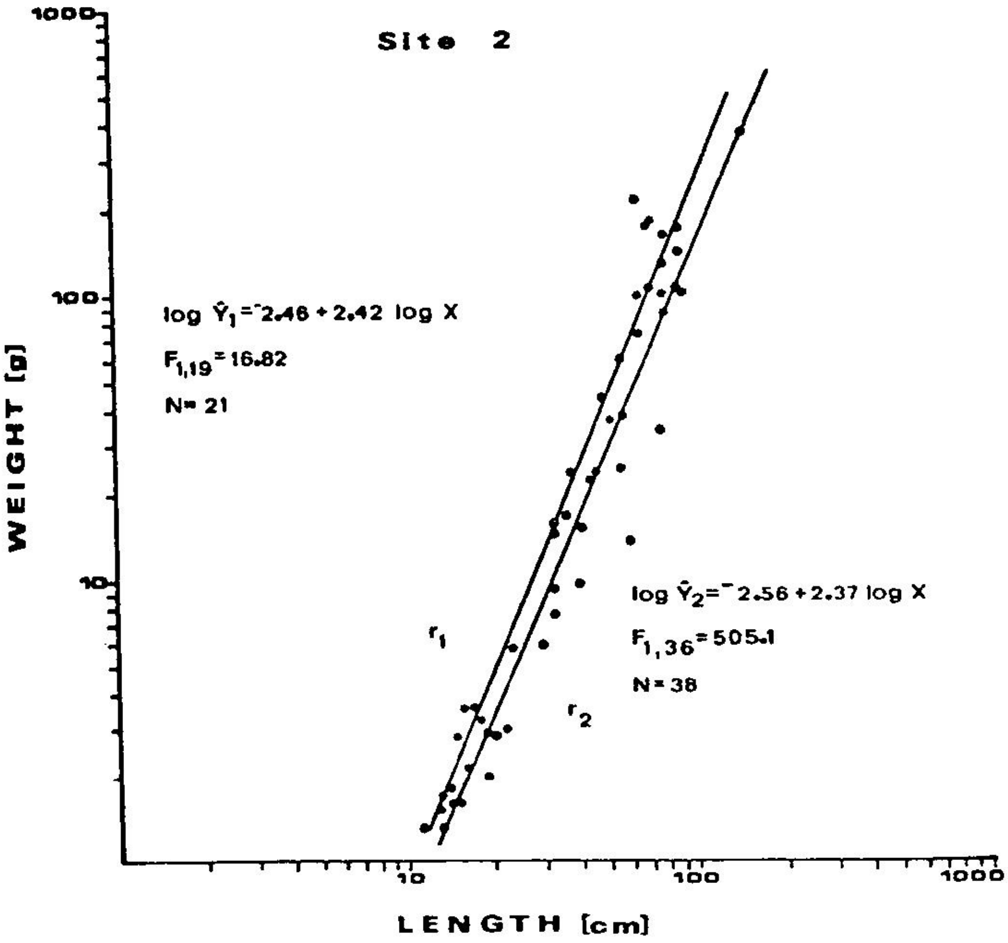

Site 2
WEIGHT [g]
LENGTH [cm]
1000
100
10
10
100
1000
log Ŷ1 = ⁻2.46 + 2.42 log X
F1,19 = 16.82
N = 21
log Ŷ2 = ⁻2.56 + 2.37 log X
F1,36 = 505.1
N = 38
r1
r2

Figure 12. Least squares length-weight regressions for *Pseudopterogorgia americana* (r_1) and *Pseudopterogorgia acerosa* (r_2)[1] collected at site (3). *P. americana* is represented by * and *P. acerosa* is represented by ●.

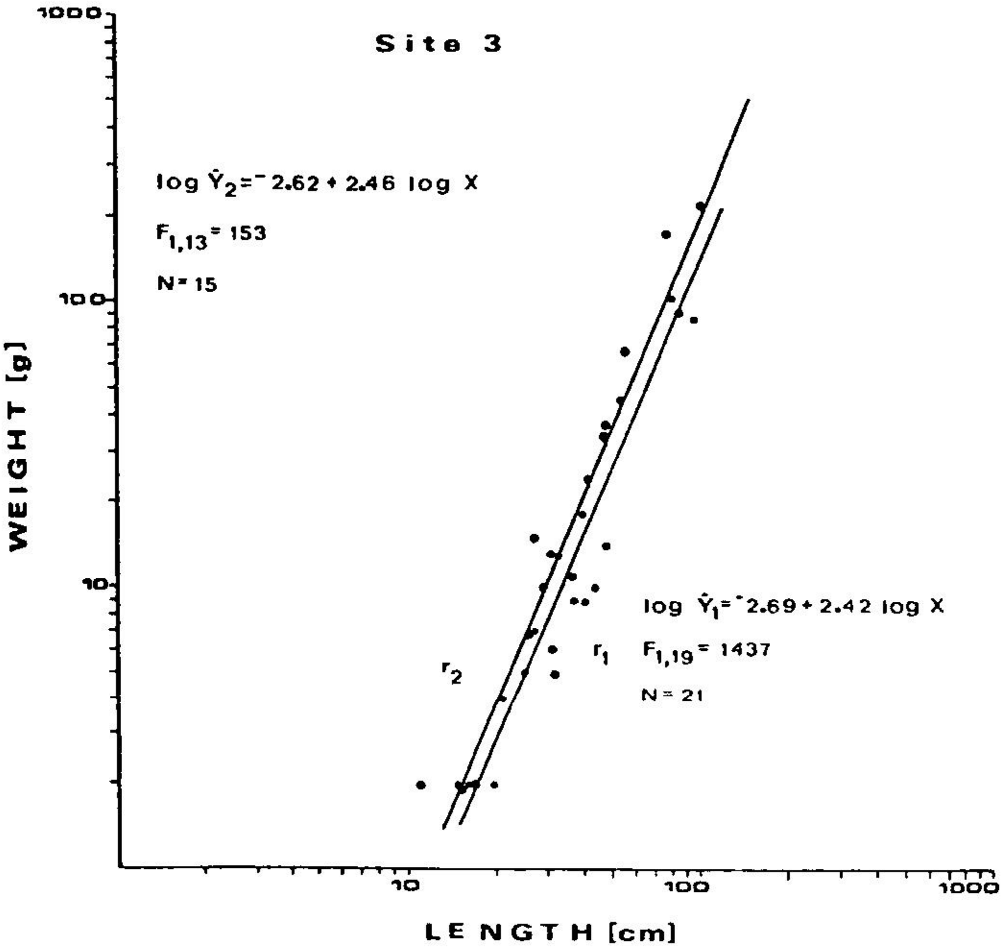
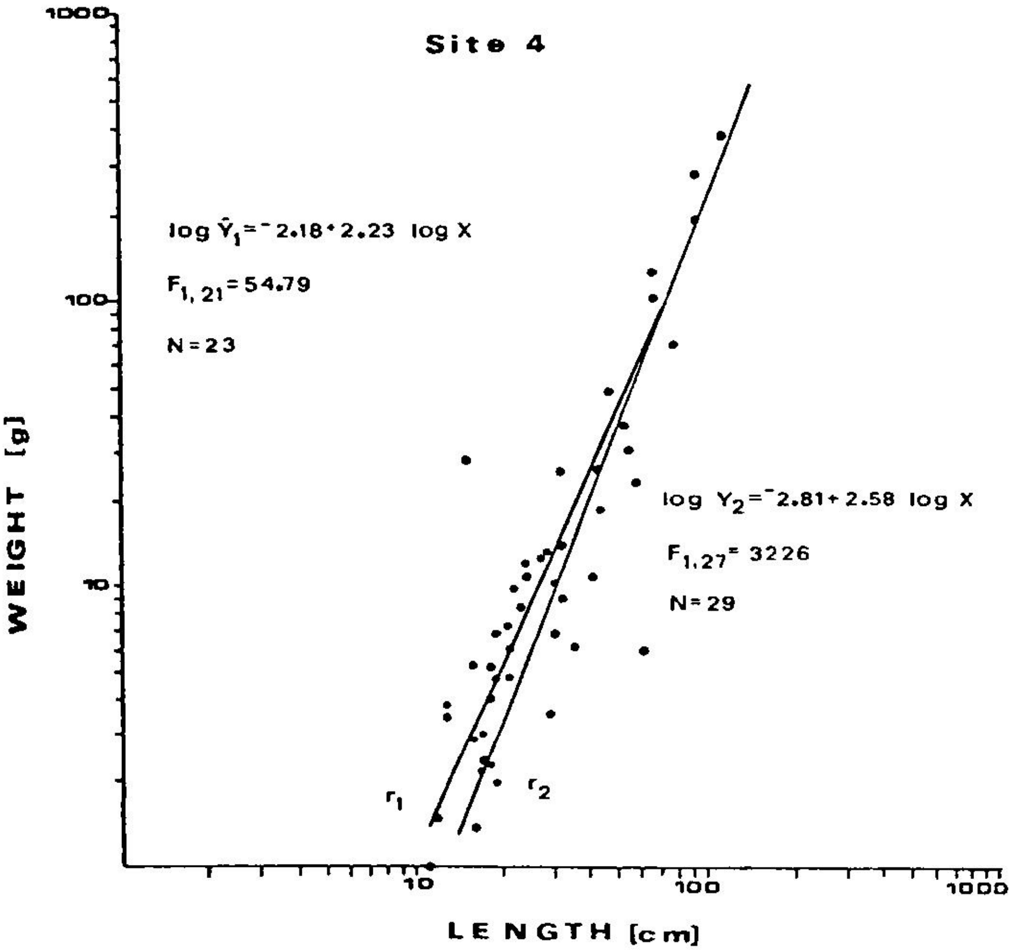

Site 3
log $\hat{Y}_2 = {}^{-}2.62 + 2.46 \log X$
$F_{1,13} = 153$
$N = 15$
log $\hat{Y}_1 = {}^{-}2.69 + 2.42 \log X$
$F_{1,19} = 1437$
$N = 21$
r_2
r_1
WEIGHT [g]
1000
100
10
LENGTH [cm]
10
100
1000

Figure 13. Least squares length-weight regressions for *Pseudopterogorgia americana* (r_1) and *Pseudopterogorgia acerosa* (r_2)[1] collected at site (4). *P. americana* is represented by ✱ and *P. acerosa* is represented by ● .



Site 4
$\log \hat{Y}_1 = {}^{-}2.18 + 2.23 \log X$
$F_{1,21} = 54.79$
$N = 23$
$\log Y_2 = {}^{-}2.81 + 2.58 \log X$
$F_{1,27} = 3226$
$N = 29$
r_1
r_2
1000
100
10
10
100
1000
WEIGHT [g]
LENGTH [cm]

or sites. Significant differences in the regressions for position were found between the two species at sites (2) and (4) ($p<.01$) indicating that *P. americana* weighed more for a given length than *P. acerosa* at these sites. This difference appears to come from a difference in growth pattern of *P. americana* which is significantly heavier ($p<.01$) for a given length at sites (2) and (4) than at sites (1) and (3), while *P. acerosa* shows no significant differences between sites.

Growth rates measured for *P. americana* and *P. acerosa* were highly variable. Only colonies measured for at least 8 months were used. Mean growth was 4.4 cm/yr for *P. americana* and 5.3 cm/yr for *P. acerosa* on site (1), and 6.4 cm/yr for *P. americana* and 6.3 cm/yr for *P. acerosa* on site (2). Growth rates were not significantly different between sites (1) and (2) or species (t-test). Growth rates did not vary with colony length on site (1) (least squares regression, Figure 14). No relationship was found with growth rates versus depth on site (1) (Tukey corner test), but a significant positive relationship accounting for about 20% of the variability was found between growth rates and light for *P. americana* (least squares regression, Figure 15). *Pseudopterogorgia acerosa* had too few colonies measured to show significance. Although light decreases with depth, individual colonies at the same depth may receive very different light levels due to shading. The amount of light

Figure 14. Annual growth versus initial colony length for *Pseudopterogorgia americana* ● (r_1) and *Pseudopterogorgia acerosa* □ (r_2) on site (1). No relationship was found between growth rates and colony length (Tukey corner test).

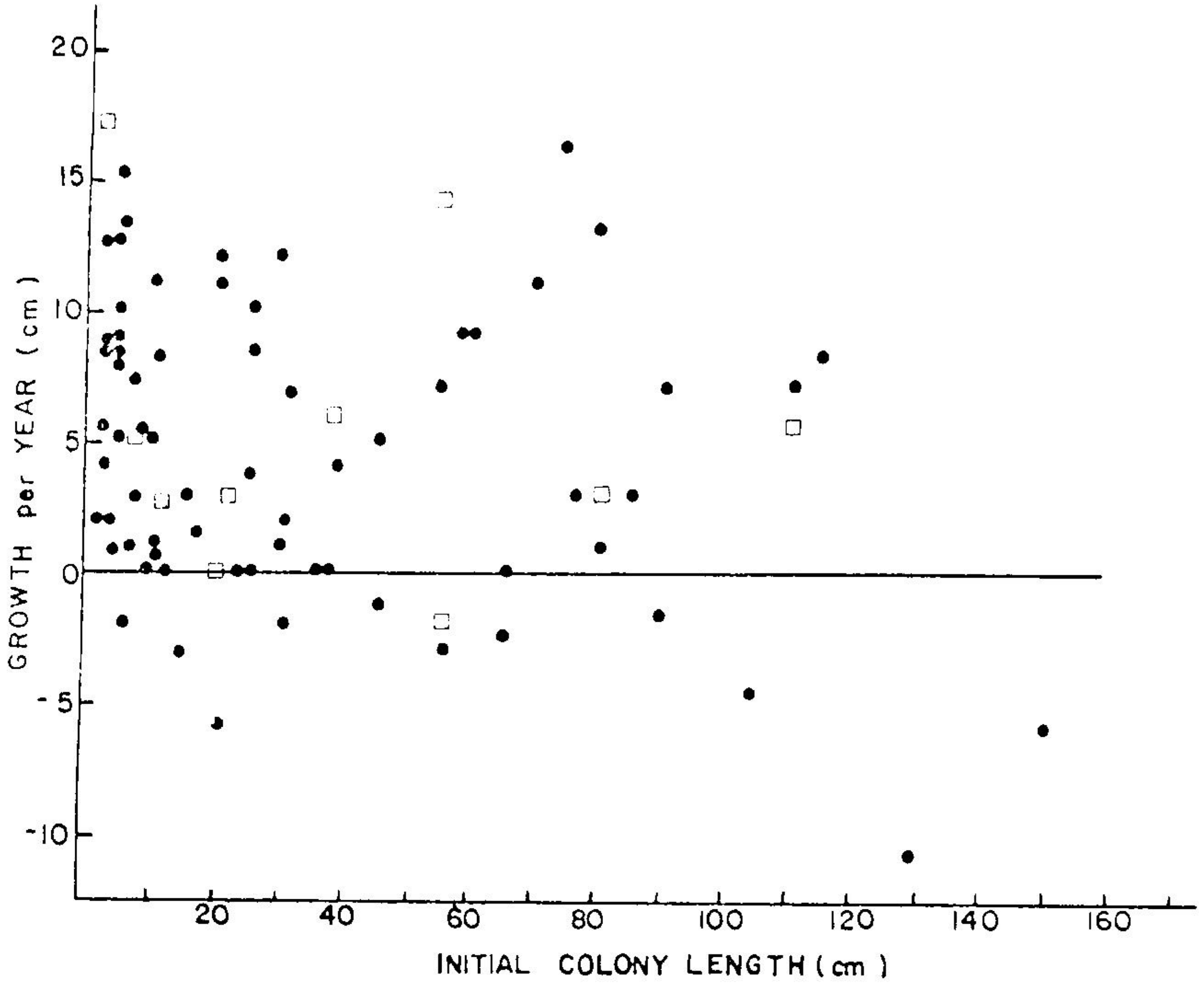
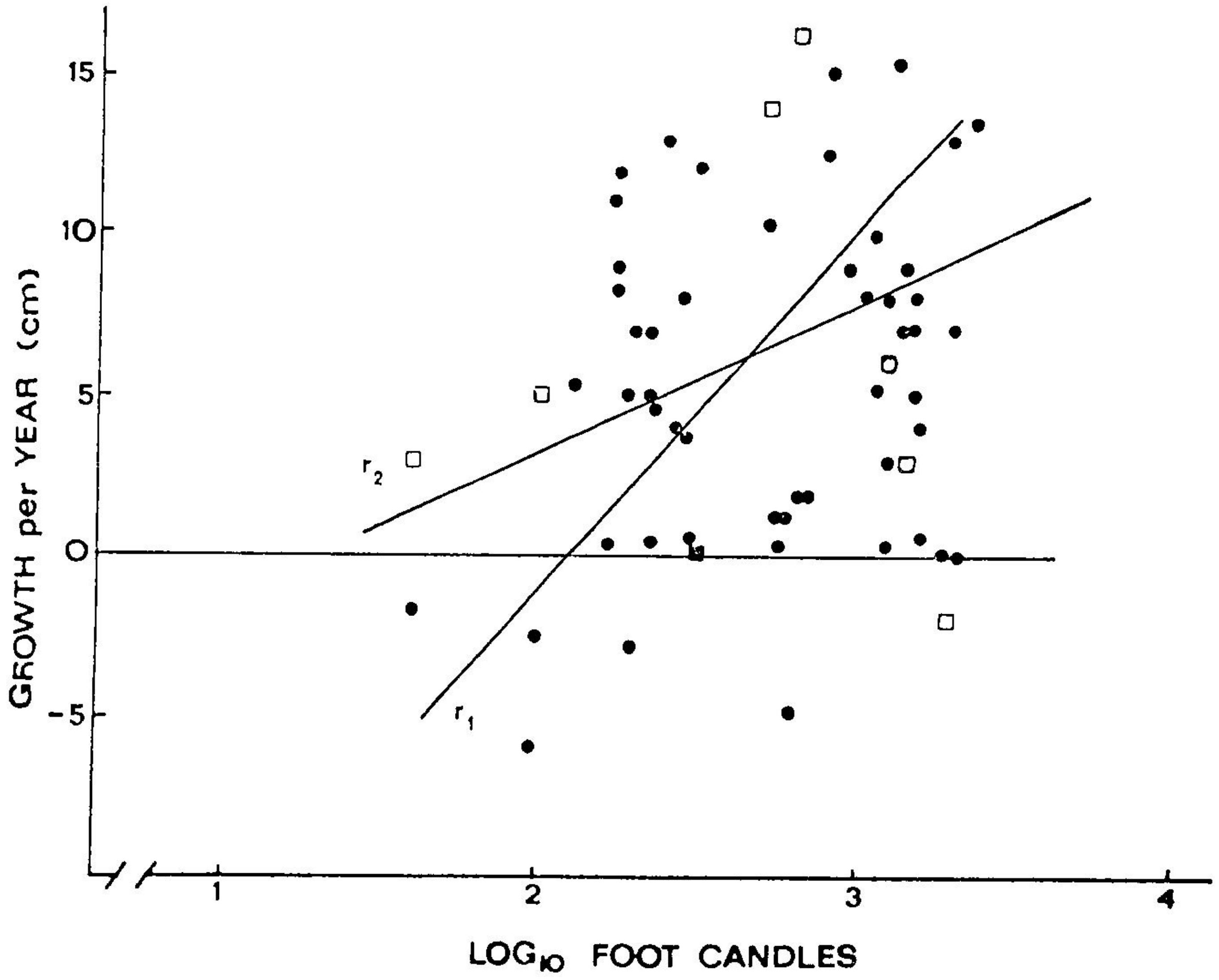

20
15
10
5
0
-5
-10
GROWTH per YEAR (cm)
2
20
40
60
80
100
120
140
160
INITIAL COLONY LENGTH (cm)

Figure 15. Annual growth versus relative light levels for *Pseudopterogorgia americana* ● (r_1) and *Pseudopterogorgia acerosa* (r_2) □ on site (1).


GROWTH per YEAR (cm)
15
10
5
0
-5
LOG10 FOOT CANDLES
1
2
3
4
r2
r1

shown in Figure 15 has no absolute meaning but should be considered as relative between colonies since it was measured only on one day.

Growth ring versus length regressions on log-log plots are shown in Figures 16 through 19. All regressions were significant ($p<.01$, F-test). Colony length was divided by the number of rings to give length per ring (cm/ring) for each colony and means cm/ring were calculated. Means of length per ring were not significantly different from annual growth rates for *P. americana* or *P. acerosa* on sites (1) and (2) (t-test). Mean length per ring for *P. americana* on site (1) was also compared to semiannual and biennial growth rate estimates and found to be significantly different from either one. Several colonies known to be under one year old did not have apparent growth rings. These considerations indicate that rings are added annually. Growth rings are probably a better measure of growth rates than measured rates as they average growth over the life of the organism, and are therefore less affected by shorter term variations in growth rates. However, growth rings in larger colonies were more difficult to distinguish resulting in higher linear growth estimates for older colonies. Mean growth rates based on growth rings for each species at each site were used to make age estimates (Table 16).

Figure 16. Least squares length-growth ring regressions for *Pseudopterogorgia americana* (r_1) and *Pseudopterogorgia acerosa* (r_2) collected at site (1). *P. americana* is represented by ✱ and *P. acerosa* is respresented by ●.

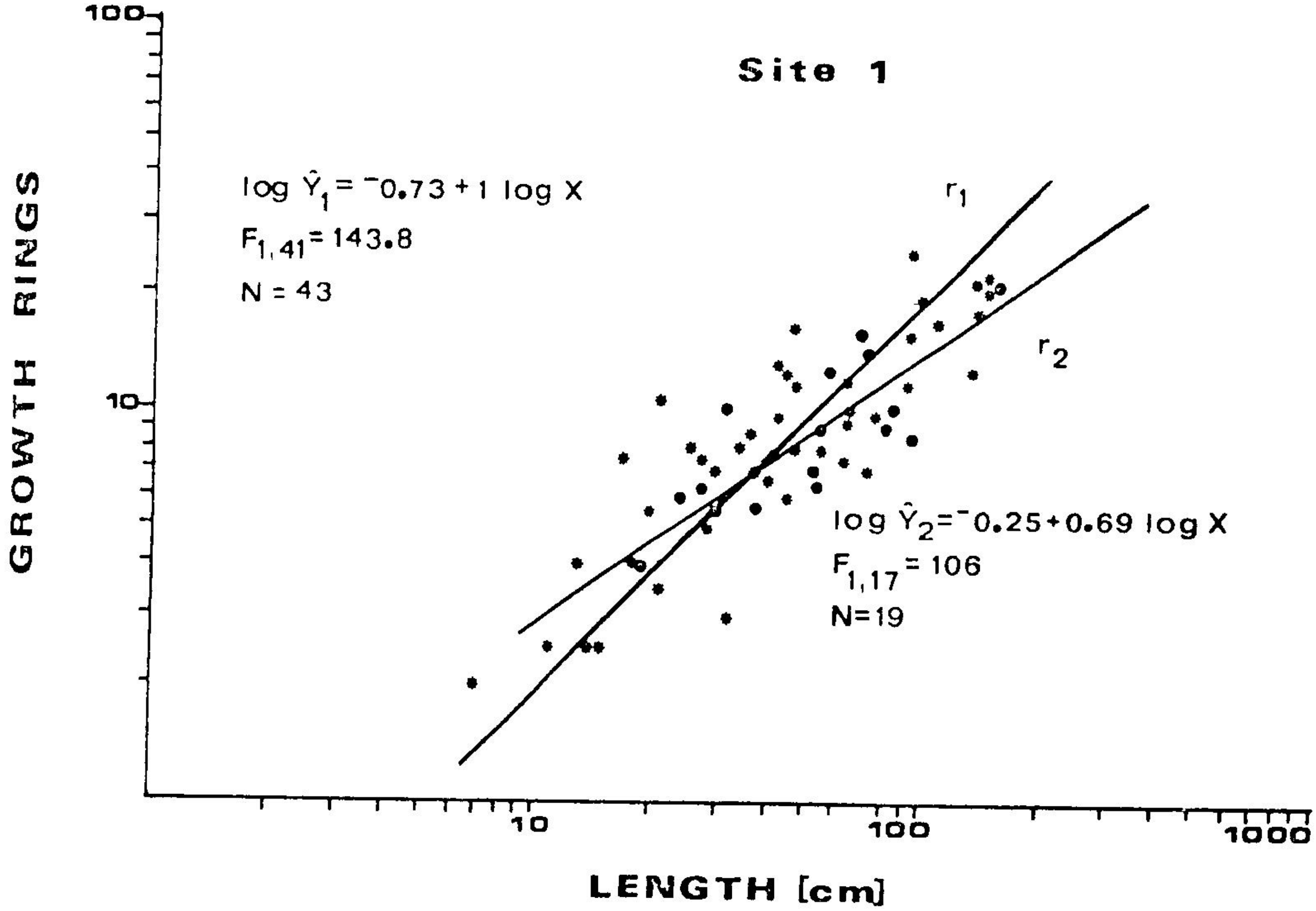

Site 1
GROWTH RINGS
LENGTH [cm]
100
10
10
100
1000
r1
r2
log Ŷ1 = ⁻0.73 + 1 log X
F1,41 = 143.8
N = 43
log Ŷ2 = ⁻0.25 + 0.69 log X
F1,17 = 106
N=19

Figure 17. Least squares length-growth ring regressions for *Pseudopterogorgia americana* (r_1) and *Pseudopterogorgia acerosa* (r_2) collected at site (2). *P. americana* is represented by ✱ and *P. acerosa* is represented by ●.

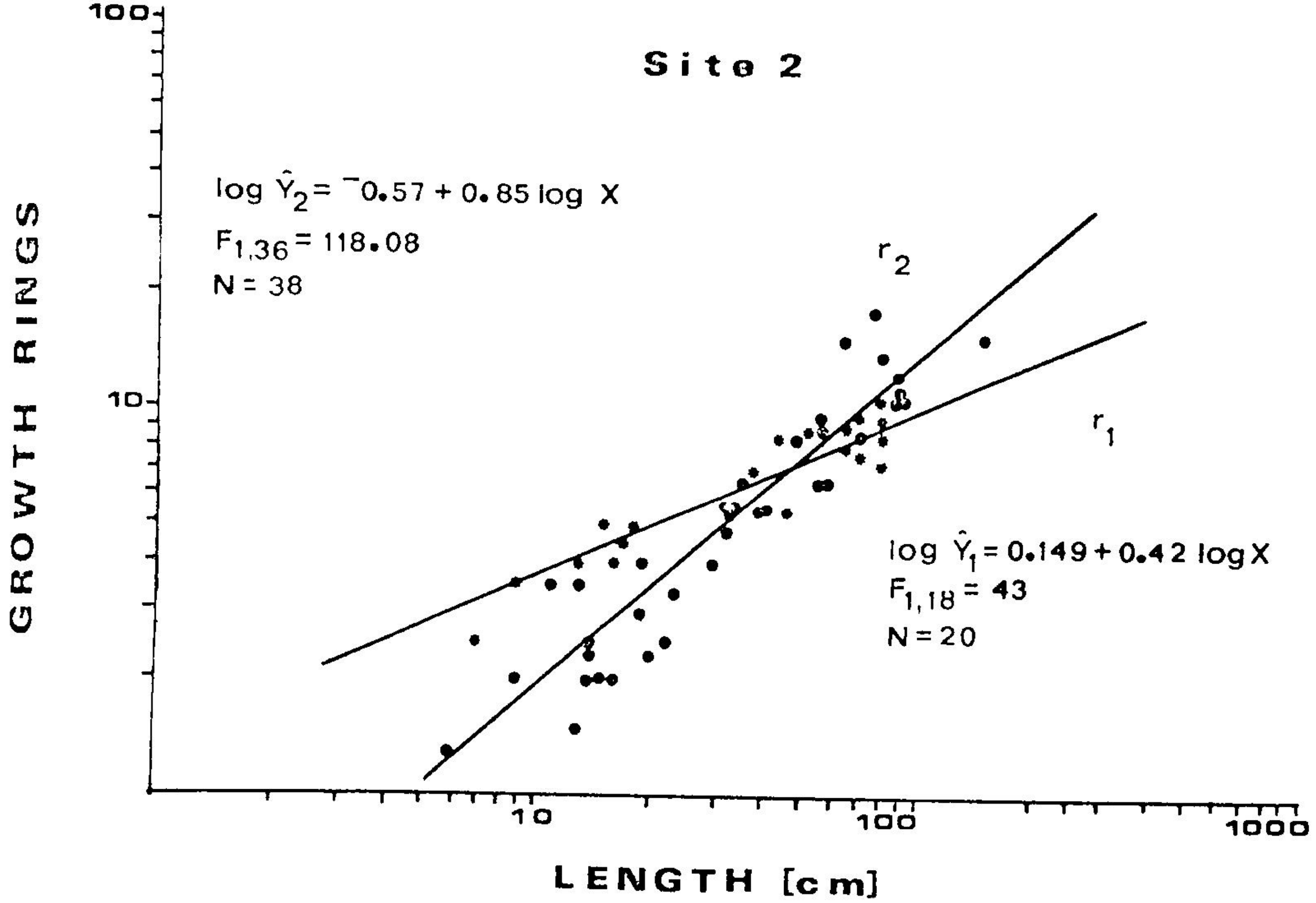
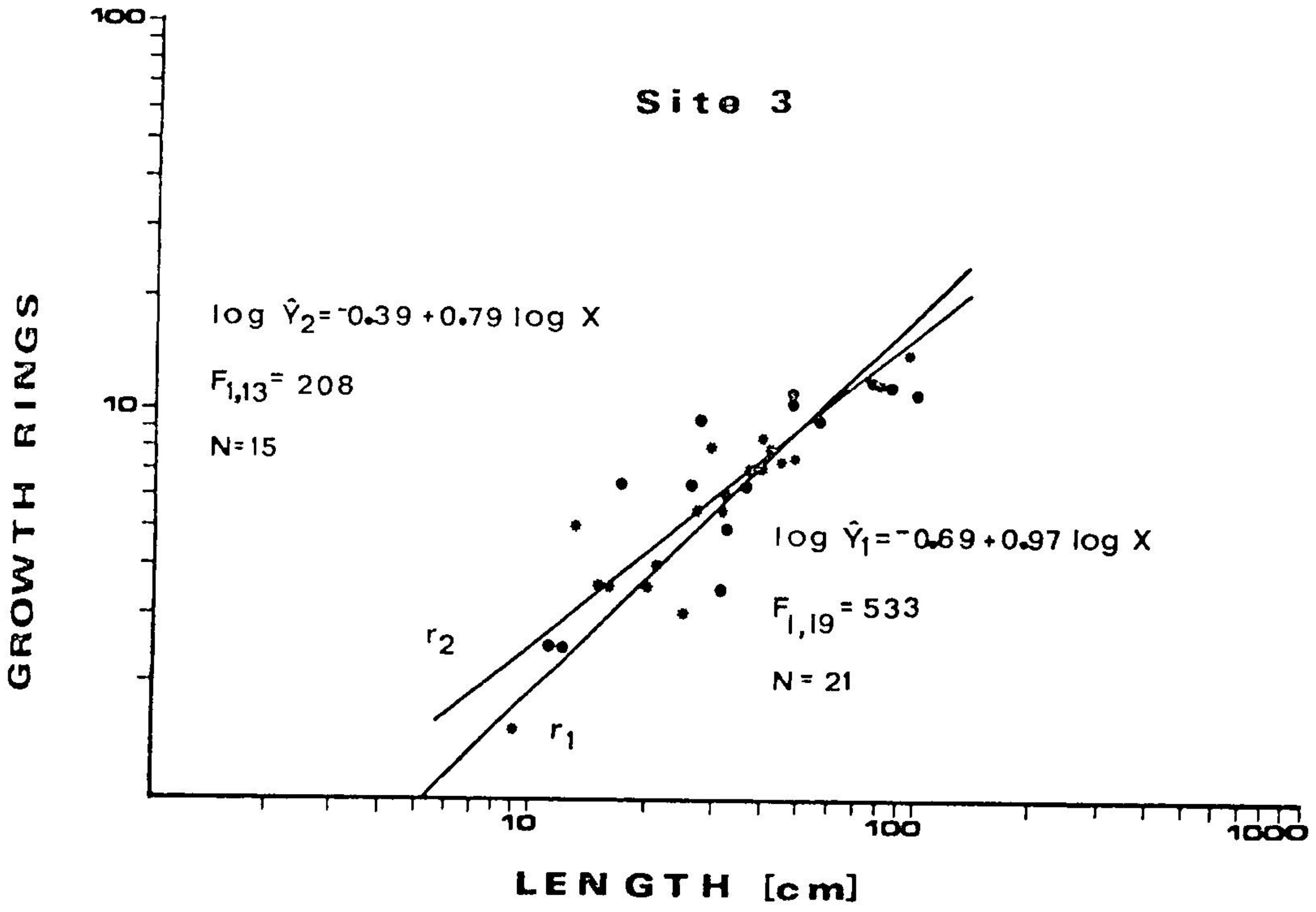
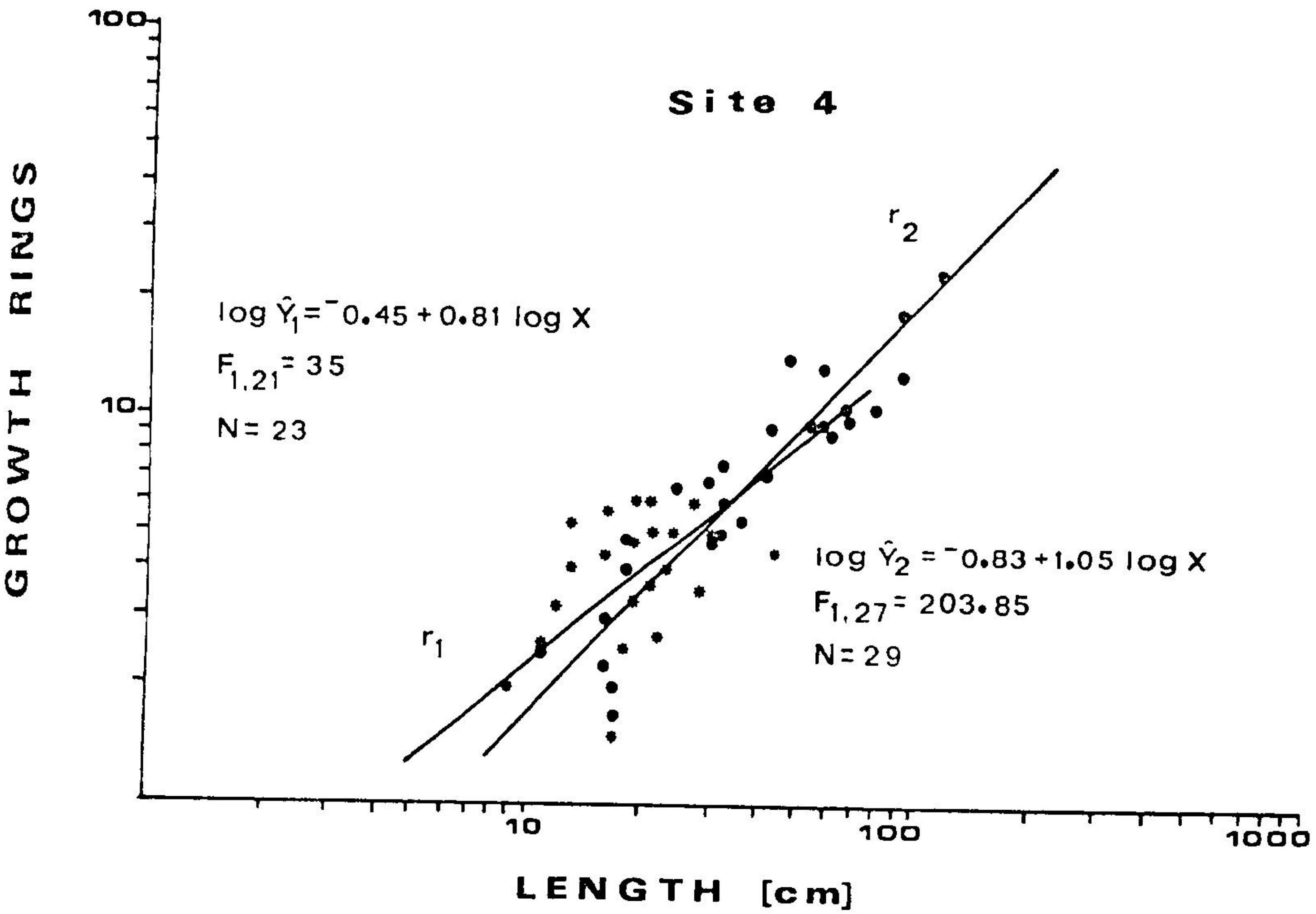

Site 2
log $\hat{Y}_2 = {}^{-}0.57 + 0.85 \log X$
$F_{1,36} = 118.08$
N = 38
r_2
r_1
log $\hat{Y}_1 = 0.149 + 0.42 \log X$
$F_{1,18} = 43$
N = 20
GROWTH RINGS
100
10
LENGTH [cm]
10
100
1000

Figure 18. Least squares length-growth ring regressions for *Pseudopterogorgia americana* (r_1) and *Pseudopterogorgia acerosa* (r_2) collected at site (3). *P. americana* is represented by ✱ and *P. acerosa* is represented by ● .



Site 3
log $\hat{Y}_2 = {}^-0.39 + 0.79$ log X
$F_{1,13} = 208$
N=15
log $\hat{Y}_1 = {}^-0.69 + 0.97$ log X
$F_{1,19} = 533$
N = 21
r_2
r_1
100
10
GROWTH RINGS
10
100
1000
LENGTH [cm]

Figure 19. Least squares length-growth ring regressions for *Pseudopterogorgia americana* (r_1) and *Pseudopterogorgia acerosa* (r_2) collected at site (4). *P. americana* is represented by ✱ and *P. acerosa* is represented by ● .


Site 4
GROWTH RINGS
100
10
LENGTH [cm]
10
100
1000
r1
r2
log Ŷ1 = ⁻0.45 + 0.81 log X
F1,21 = 35
N = 23
log Ŷ2 = ⁻0.83 + 1.05 log X
F1,27 = 203.85
N = 29

Reproduction

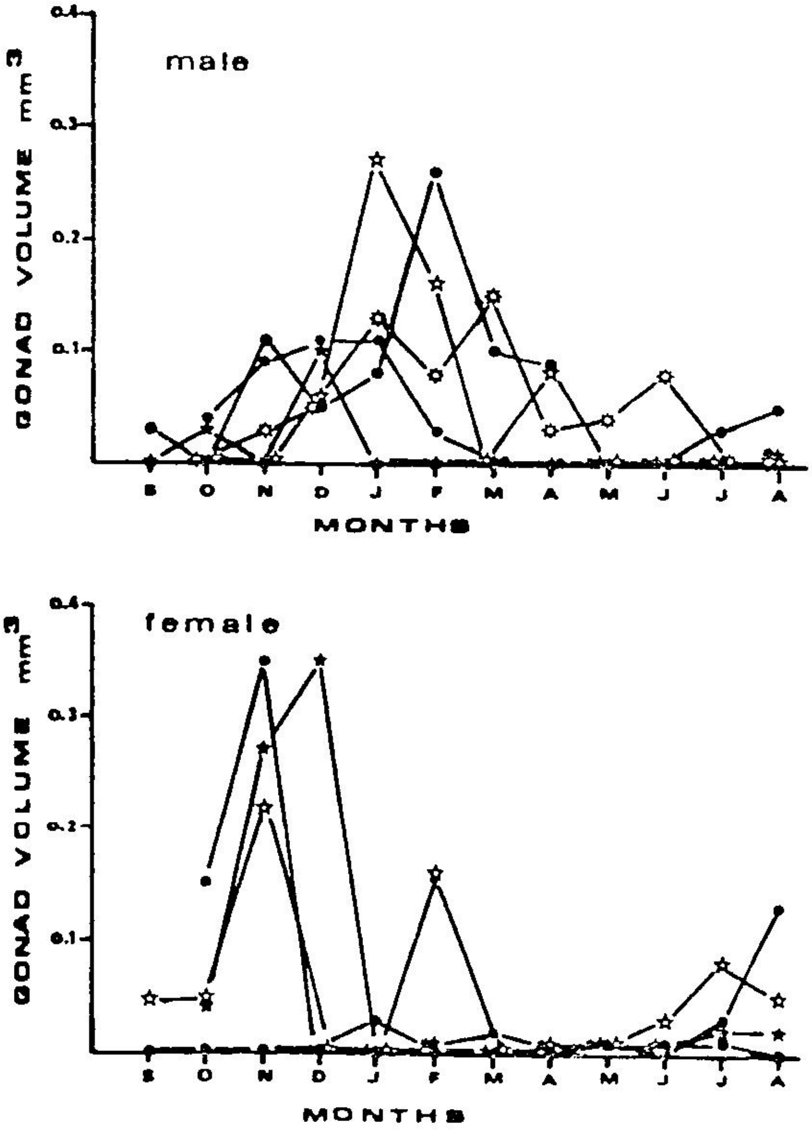
Sexes were found to be separate for all colonies examined at a particular time. Either sex was found in colonies of all sizes which contained gonads. One colony of *P. americana* which was sampled throughout the year appeared to switch from female to male. Sections examined in September contained large eggs while sections examined in December had well developed spermaries. No sign of gonads was found in October. Confusion of the colony with others was unlikely as the colony was tagged and not very close to other colonies. Male to female sex ratios were calculated from all colonies sexed throughout the study. *P. americana* had 65% females to 35% males. The 95% confidence limits for the males ranged from 24% to 47% (population proportion confidence limits, Tate and Clelland) indicating that *P. americana* does have a significantly higher percentage of females (84 colonies sexed). *Pseudopterogorgia acerosa* had 57% females to 43% males, and the 95% confidence limits for the males ranged from 29% to 59% indicating no significant difference from an even sex ratio.

The nearest neighbor technique (Clark and Evans, 1954) dispersion patterns of male and female colonies of *P. americana* from the large 16 m^2 quadrat were examined to determine if members of the same or opposite sex tended to be near to each other. The distribution of males to females was not significantly different from random. Hence the sexes are not significantly associated (or dissociated) with each other. *P. acerosa* had too few colonies to analyze.

As described by Gohar (1940a, 1948), ova and spermaries were found on six of the eight mesenteries. The larger ova or spermaries lie in the bases of the polyps unattached or attached by a very thin peduncle to the mesentery. Ova and spermaries were round or oblong in shape. The largest ova in *P. americana* and *P. acerosa* averaged 0.5 mm while the largest spermaries averaged 0.4 mm in diameter. Females of both species had two to four large ova per polyp when ova diameters were greatest, and males four to six large spermaries at the same stage of development. No difference was found in the sizes or numbers of ova or spermaries from different parts of a colony at any one time.

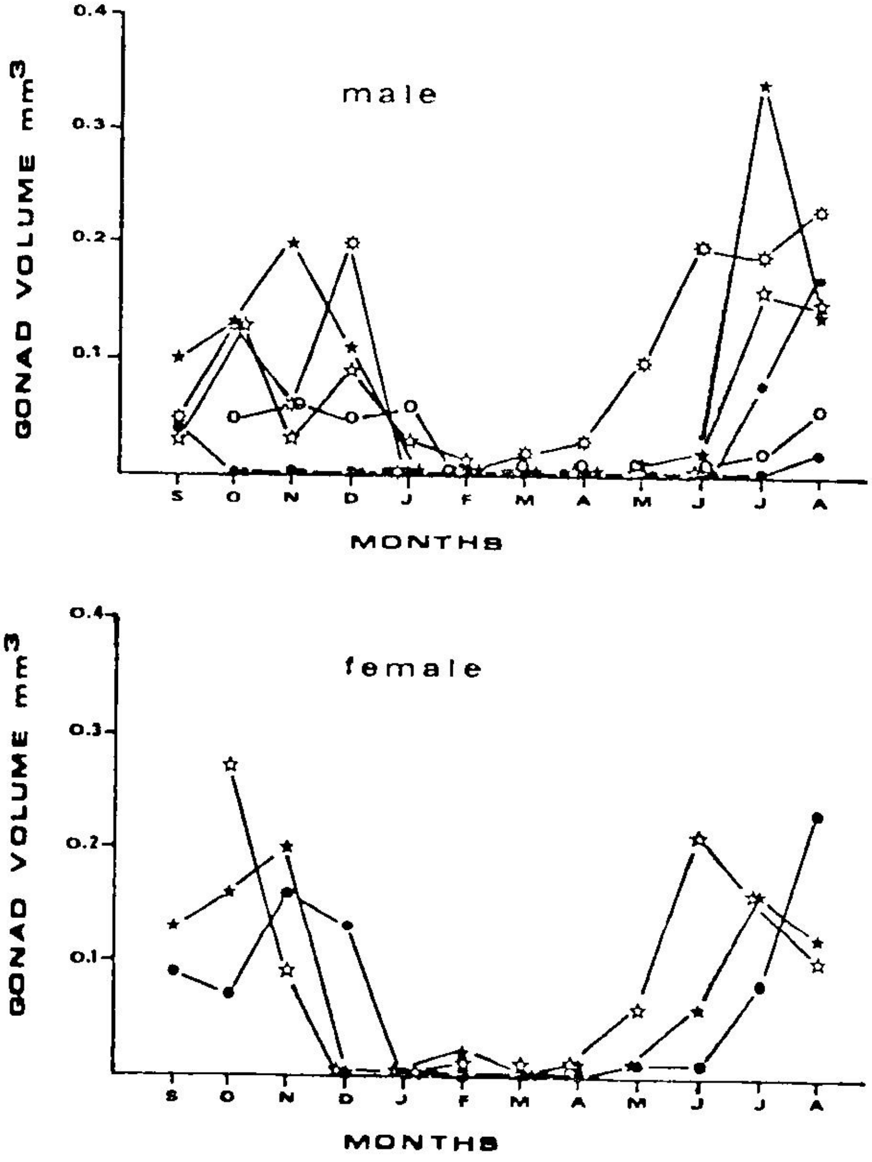
The degree of ripeness of the sperm varied from month to month, and even within a month for four colonies examined. Ripe or very young sperm could be found in the same colony at various times throughout a month. Since colonies were only sampled for gonads once a month, the size of ova or spermaries was used to determine reproductive periodicity. Gonadal volume was calculated monthly for each colony (Figures 20 and 21). The median number of eggs or spermaries per polyp was multiplied by the volume of the median egg or spermary. The median diameters of the five largest eggs or spermaries were used to calculate this volume assuming that eggs and spermaries were spherical. The volume

Figure 20. Volume of gonads per polyp of individual male and female colonies (symbols) of *Pseudopterogorgia americana* sampled at monthly intervals at site (1).



Pseudopterogorgia americana

Figure 21. Volume of gonads per polyp of individual male and female colonies (symbols) of *Pseudopterogorgia acerosa* sampled at monthly intervals at site (1).



Pseudopterogorgia acerosa

of a sphere is $4/3\pi r^3$ where r = radius. Since r = (d)iameter/s, this equation can be written volume = $\pi d^3/6$.

The periodicity of gonadal volume was compared within a sex and between sexes for *P. americana* and *P. acerosa* by a Kendall concordance test. Colonies which failed to reproduce actively (gonadal volume less than 0.1 throughout the year) were excluded from analysis as well as the month of September for which some values were missing. *P. americana* showed strong synchrony between males ($p<.005$) and weak synchrony between females ($p<.10$). *P. acerosa* showed strong synchrony between males ($p<.005$) and between females ($p<.025$). Synchrony between males and females was not significant for *P. americana*, but was quite strong for *P. acerosa* ($p<.01$, Kendall-Tau rank correlation). Since there was not strong synchrony between males and females for *P. americana*, comparisons were not made between the two species. *Pseudopterogorgia acerosa* appears to peak in reproduction from August to October while *P. americana* seems to reproduce anywhere from September to April on site (1). Reproductive periodicty was not obtained for site (2) as most of the colonies tagged there never reproduced. This was an artifact of small sample size since several collections of colonies from site (2) had gonads in over 50%.

Egg production probably does not vary much between colonies of *P. acerosa* and *P. americana*. Estimates of the average number of polyps per colony of a given height are only different where one of the species is bushier than the other. Since both species produce from two to four eggs per polyp in a season, estimates for egg production would be similar. *Pseudopterogorgia americana*, however, has proportionally more females than *P. acerosa* so a given number of colonies will produce more eggs (at least on sites (1) and (2) where reproduction was examined). Otherwise the relative advantage of one species over the other reproductively would depend on their relative abundances at different sites.

No gonads were found in colonies of *P. acerosa* (n = 16) or *P. americana* (n = 24) under 15 cm long. Ten of these showed no sign of gonads in histological sections. No sign of gonads was found in 85% (17/20) of *P. americana* and 89% (16/18) of *P. acerosa* colonies examined between 15 and 30 cm long. Observed percentages of older colonies (greater than 30 cm) with no gonads collected at the same times and locations as the small colonies were 58% (29/50) for *P. americana* and 67.5% (27/40) for *P. acerosa*. An arcsine transformation was used to compare the equality of percentages (Sokal and Rohlf, 1969) between the adult ratio of those without gonads to the observed ratios for small colonies. For colonies under 15 cm, highly significant differences were found for *P. americana* and *P. acerosa* ($p<.001$). For colonies between 15 and 30 cm long, *P. americana* was significantly different from percentages in older colonies (p<.02) and *P. acerosa* was not quite significantly different (p<.06). A colony of *P. acerosa* or *P. americana* of 30 cm would be about five years old and a colony of 15 cm about three years old. The five colonies found with gonads were between 16 and 19 cm long. Therefore, reproduction is usually delayed for at least three to five years in both species. More samples would be needed to determine if one starts reproducing at a slightly younger age than the other.

No dividing eggs or developing larvae were seen during this study, although clippings of *P. acerosa* were collected several times a week for several weeks when the eggs were largest.

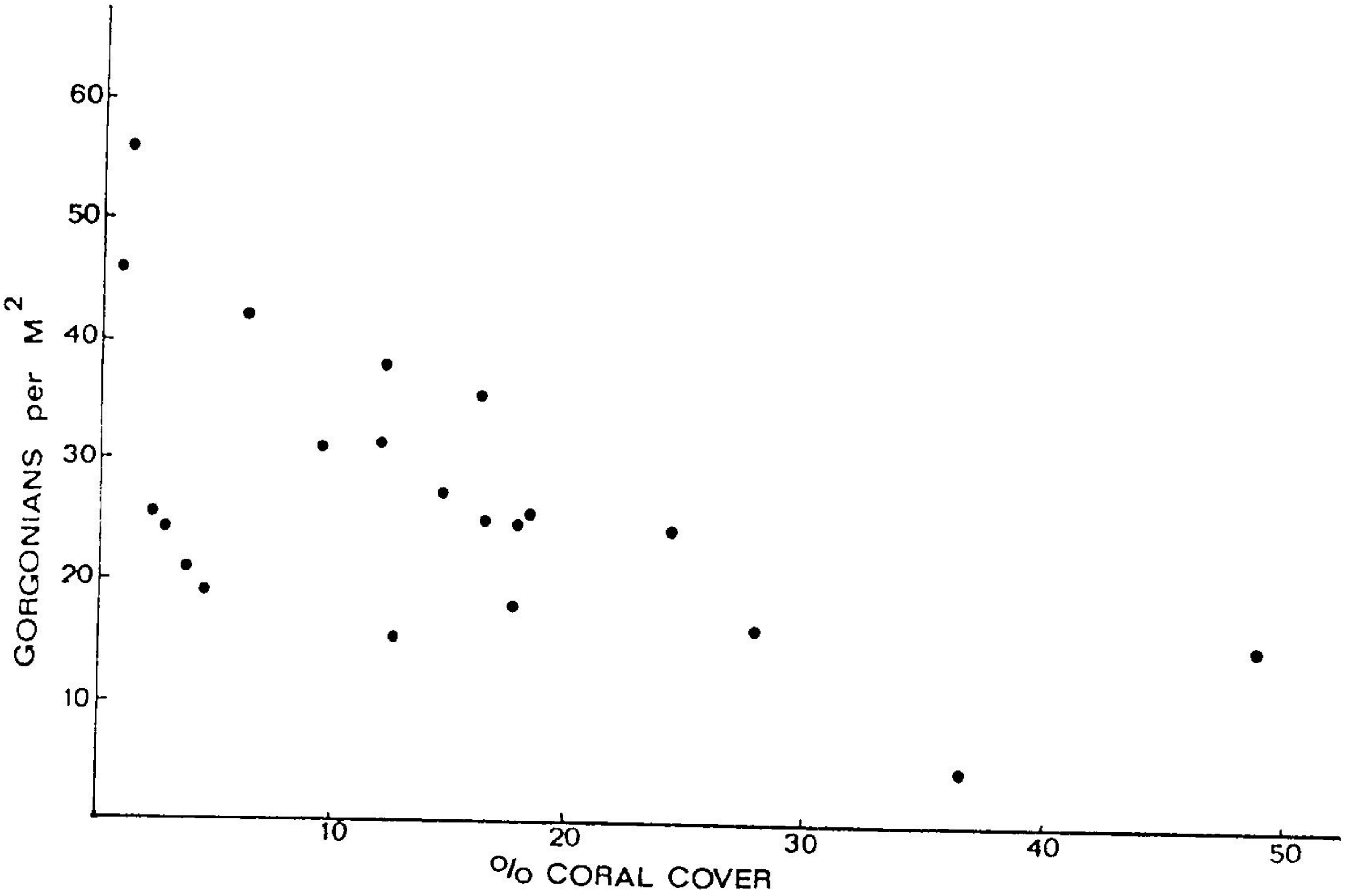
Ecological Interactions

Coverage by corals and other encrusting organisms was negatively correlated with gorgonian densities (Figure 22, p<.05, Tukey corner test). This might contribute to the aggregated dispersion patterns of the gorgonians on site (1).

Recruitment was enhanced in quadrats which were totally cleared or cleared of gorgonians only compared to uncleared quadrats (see recruitment and mortality). This was probably a response to the greater availability of hard substrate suitable for gorgonian settlement.

Gorgonians of both species were often observed with the bases in contact with each other or other gorgonians. The

Figure 22. Number of gorgonians versus percent of cover from corals and other encrusting organisms.


60
50
40
30
20
10
GORGONIANS per M²
10
20
30
40
50
% CORAL COVER

only damage of one gorgonian by another was minor fraying at the points where branches of colonies were in contact. Abrasive damage to *Pseudopterogorgia* spp. colonies by other gorgonians was most often by *Muricea* spp. which was most common near the base of the reef on site (1). However, contact with hard corals or other hard surfaces was the most frequent cause of fraying damage. Tips of colonies damaged by fraying were often briefly colonized by hydroids or the small anemone *Bunodiopsis antilliensis*. Tips usually healed subsequently or fell off, but damage was seldom permanent.

Encrusting organisms are found most frequently on the base of large gorgonians. New encrustations were only observed on the bases of previously damaged colonies. Many organisms such as barnacles, algae, and hydroids are eventually overgrown by regrowth of the gorgonian tissue. This was apparent when cross sections of colony bases revealed intact barnacle shells or traces of calcareous algae within the axial skeleton. Several sponges, *Briarium* (a scleraxonian gorgonian), and *Millepora alcicornis* appear to be more successful at maintaining the infestation.

Sponges and *Briarium* on the bases of gorgonian colonies in the permanent quadrats were measured over a year. Sponges and *Briarium* usually advanced slowly (about 3 cm/yr) if at all by overgrowing and smothering the gorgonian tissue.

Millepora alcicornis found on the bases of four gorgonian colonies in the permanent quadrats grew up the gorgonian stalks at an average rate of 9.3 cm/yr varying from 6 to 12 cm/yr. A narrow band of dead gorgonian tissue in advance of the *Millepora* is a good indication that the fire coral actively kills the tissue. A colony usually breaks off at some point on the basal stalk before being covered by *Millepora*. Many clumps of *Millepora alcicornis* on site (1) revealed gorgonian stumps when they were broken apart.

New encrustations during the study period on gorgonian colonies were only seen to occur on portions of axial skeleton which had been previously denuded. One common cause of damage to gorgonians is *Cyphoma gibbosum*. *Cyphoma gibbosum* grazes on the tissue leaving behind a denuded patch of axial skeleton. *C. gibbosum* was seen on 1 out of 500 gorgonians examined on site (1). This was low compared to some areas such as site (3) which had 2 *C. gibbosum* out of 200 colonies examined. *C. gibbosum* occurred on *Pseudopterogorgia americana* half as often as on any other gorgonians on site (1) out of 29 observations. This is a disproportionately large number as *P. americana* accounted for less than one third of the total number of gorgonians. *C. gibbosum* was seen on *P. acerosa* only once, and basal damage or encrustation was uncommon on *P. acerosa* on site (1). This suggests that *C. gibbosum* is selective for *P. americana* on site (1).

Ten out of 16 tagged colonies of *P. americana* with *C. gibbosum* healed within two months after the gastropod left. The other six were infested with sponges or bryozoans.

Cyphoma were often found in pairs and when one moved to a different colony, the other usually followed within a few days. Most of the grazing damage was near the base of the gorgonians where *C. gibbosum* was usually found. *Cyphoma gibbosum* were not usually seen high on the colonies except at night. The ability of the gorgonian to heal over a scar was less related to the extent of the scar than to what had colonized the area. One colony was completely girdled for over 5 cm on the base and healed within a month. Four of the 16 colonies had *Cyphoma* return to them at least once.

Coralliophila caribaea, another gastropod, was found frequently near the bases of colonies. This genus is known to associate with sea fans. Damage to the gorgonians seemed to be limited to the immediate vicinity of the gastropod. *C. caribaea* were not seen to change position on the gorgonians.

Polychaets of the family Amphinomidae were occasionally seen on gorgonians on site (1), but almost always on the steep slope or near the base of the reef where hard corals are not abundant. Usually they were seen feeding high in the branches of gorgonians.

A polychaet of the family Syllidae was found within the coenchyme of *Pseudopterogorgia acerosa*. The larger polychaets were usually free within the tissue, while smaller specimens were encysted within a capsule possibly of their own making. The polychaets were usually not visible externally, and specimens were only found in polyps dissected for gonads. They were found in all of the *P. acerosa* which were sampled monthly and were usually common. Only one polychaet was found in *P. americana* and it appeared to be the same species. Some members of the family Syllidae are known to be parasitic on other invertebrates such as sponges. Since the polychaet appears to live internally in the gorgonian, it is probably a parasite. Other species of gorgonians were not examined for its presence.

An isopod of the genus *Excorallana* was commonly found on *P. acerosa* but rarely on *P. americana*. It appears to be free-living and the nature of its relationship to *P. acerosa* is not known.

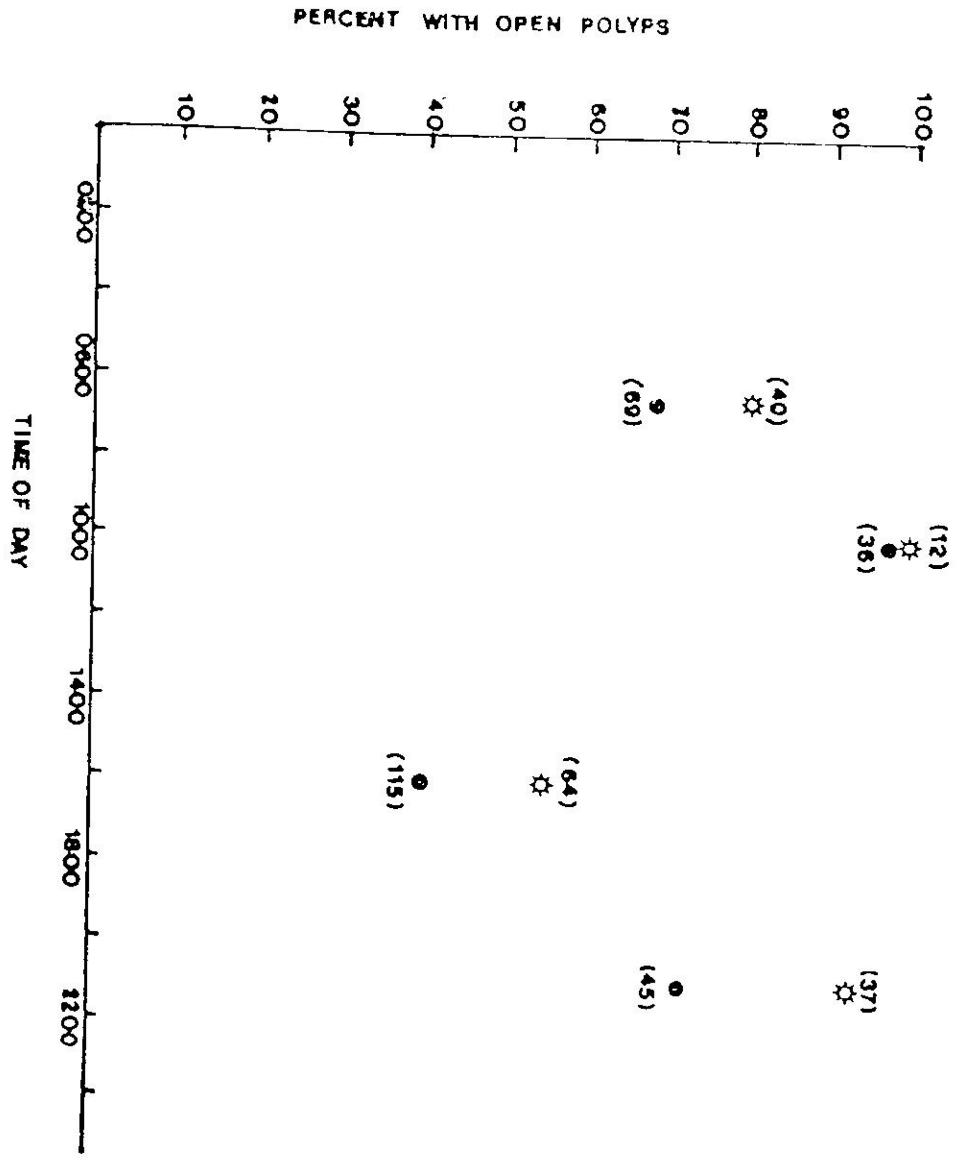
Other invertebrates known to associate with *Pseudopterogorgia* were seen frequently. These included *Astrophyton muricatum*, the basket star, and *Pteria colymbus*, the Atlantic winged oyster. *Astrophyton* appears to cause little damage when it wraps itself in the *Pseudopterogorgia* branchlets, but may cause some abrasive damage to the colony. It is common on either species of *Pseudopterogorgia*. *Pteria* seems to only cause damage at the attachment site. Small crinoids were seen once clinging to several *P. americana* at site (2), but were not seen again. The caridean shrimp, *Tozeuma carolinense*, was not observed on gorgonians in this study, but was seen once on a *Pseudopterogorgia* sp. by Joseph Kimmel (personal communication).

Bluehead wrasses, *Thalassoma bifasciatum*, were observed frequently picking at gorgonians. The gut contents from seven individuals revealed mostly isopod parts, a few small crab and shrimp parts, ophiuroid arm parts, sponge spicules, and only once a few gorgonian spicules. The small isopods occurring on *P. acerosa* are probably a common prey, though this was not confirmed by gut content examinations. *Thalassoma bifasciatum* appears to "clean" gorgonians rather than graze on them. The red banded parrotfish, *Sparisoma aurofrenatum*, was observed picking at gorgonians occasionally, and appeared to actually bite off small pieces (Ileana Clavijo, personal communication).

Experiments using cages on the cleared quadrats were mostly unsuccessful. The enclosure versus exclosure caging for *Diadema antillarum* on two cleared quadrats which had high recruitment did indicate that *D. antillarum* had no apparent effect on these recruits.

Day versus night polyp expansion data showed that *P. americana* and *P. acerosa* follow the same trend and that usually over 50% of the colonies have expanded polyps at any one time (Figure 23). *Pseudopterogorgia americana* also tended to have a slightly higher percentage of colonies with open polyps, and this trend was significant at 1600 hours ($p=.05$) and 2130 hours ($p<.001$, arcsine transformation for comparing percentages). Since no replicates were taken for the same time periods, the diurnal pattern was not analyzed.

Figure 23. Percent of colonies with the polyps expanded at different times of the day. *Pseudopterogorgia americana* is represented by ☼ , and *Pseudopterogorgia acerosa* is represented by ● .


PERCENT WITH OPEN POLYPS
10
20
30
40
50
60
70
80
90
100
0200
0600
1000
1400
1800
2200
TIME OF DAY
(40)
(69)
(12)
(36)
(64)
(115)
(37)
(45)

Discussion

Distributional Studies

Small Scale Dispersion Patterns

Grigg (1970) used variance to mean ratios to examine the dispersion patterns of *Muricea californica* and *M. fructicosa* on a 1 m^2 scale. He found *M. californica* to be aggregated and *M. fructicosa* to be too rare to test. On a smaller scale using a nearest neighbor analysis on an area which had great physical heterogeneity of the substrate and on an area with very even substrate, he found that although both areas were not significantly different from a random distribution, gorgonians had a tendency to be aggregated on the heterogeneous substrate and evenly distributed on the homogeneous substrate. He concluded that substrate heterogeneity was the strongest factor causing aggregation.

Pseudopterogorgia americana, however, was found to be aggregated on a 1/16 m^2 scale in both areas indicating that larvae may tend to settle close to a colony of the same species. The even distribution of total gorgonians on a 1/16 m^2 scale over the more homogeneous substrate may be a result of negative interactions between colonies due to very high densities. An area of lower densities of gorgonians and more even substrate than found on site (1) could provide more complete answers to small scale dispersion patterns.

Densities and Size Frequencies

Although the relative abundances of *P. americana* and *P. acerosa* do not differ significantly at different depths within a site, they do differ between sites. For instance, *P. americana* was at least three times more abundant at site (1) than *P. acerosa*, while *P. acerosa* was slightly more abundant than *P. americana* at site (2). The area with the highest densities of *Pseudopterogorgia* spp., site (1), had a much higher relative abundance of *P. americana* than *P. acerosa*. Sites of lower *Pseudopterogorgia* spp. density showed an almost equal or even higher abundance of *P. acerosa* than *P. americana*. Therefore, densities of these species may imply an advantage for one species over the other at a particular site.

Low numbers of colonies in the first year age classes for both species of *Pseudopterogorgia* are probably due to the difficulty of seeing very small colonies (less than 2 cm long). The fact that comparisons of the age frequencies between the two species did not differ within sites indicates that the species are not affected differentially by those factors influencing these age distributions. These factors include variations in recruitment rate and mortality rate which may be due to factors such as light, surge, sedimentation, competition, and predation.

If populations are in a fairly steady state, the high proportion of young colonies at site (4) indicates higher mortality for younger colonies than at other sites. The more even age distributions and the large relative abundances of older colonies at site (3) and El Negro reef (for *P. americana*) implies low recruitment rates and low mortality rates evenly distributed over the age spectrum.

Grigg (1975) used the variability between successive age classes as an indicator of habitat "stability". Variability due to high recruitment and/or mortality would indicate unstable habitat. He used the relative longevity of the species to determine habitat "suitability". In these terms, site (1) would be the most "suitable" and "stable" site for both species. Site (3) shows the greatest variability between age classes for both species, but this may be due to lower numbers (100 for *P. acerosa* and 78 for *P. americana*). Due to the higher percentage of older colonies, site (3) is more "suitable" than site (2) and perhaps as suitable as site (1). Recruitment at site (3) appears to have been low for several years.

Recruitment and Mortality

Although the abundance of *P. americana* is significantly higher than *P. acerosa* on site (1), recruitment was not significantly higher for *P. americana*. This may be due to small sample size or to proportionately greater reproductive success for *P. acerosa*. Recruits were noticeable at a height of 1 cm, and the most recruits for *P. americana* were seen in June and July. Since most estimates for larval life span are short (about 30 hours for *Eunicella singularis*, Weinberg and Weinberg, 1979) and the most active reproduction period for *P. americana* is during the winter months (see Reproduction), recruits may be as old as five to six months when they are visible in the field. Therefore, estimates for mortality of young gorgonians do not include the earliest, and perhaps most crucial, period of life.

The higher recruitment of *P. americana*, *P. acerosa*, and other gorgonians in cleared versus uncleared quadrats implies that space is a limiting factor for gorgonians at least on site (1). Since recruitment was significantly higher in quadrats cleared only of gorgonians on site (1), gorgonians appear to compete with each other for space. The higher densities of *P. americana* and *P. acerosa* at the buoy scar site compared to areas of similar position at site (2) indicate that space is limiting at site (2) even though overall gorgonian densities are lower.

The higher recruitment of *P. americana* than of other gorgonians in the cleared quadrats is an indication that *P. americana* may be a colonizing species. Although the recruitment of *P. americana* was not significantly higher than that of other gorgonians, relative recruitment rates are higher because the abundance of *P. americana* does not equal the abundance of other gorgonians on site (1). The lower number of recruits for *P. acerosa* does not necessarily mean that it is not a colonizing species; rather it may be a result of the low abundances of *P. acerosa* compared to *P. americana* or other gorgonians.

Since the percentages of mortalities were not significantly different for *P. acerosa*, *P. americana*, and other gorgonians, the prominent causes of mortality are apparently not species specific (at least for the two species of *Pseudopterogorgia*). The number of mortalities in a given size class of *P. americana* was proportional to the relative abundance of that size class indicating that the rate of mortality is evenly distributed over all size classes of *P. americana*. Other gorgonians (not including *P. acerosa*) had a proportionately higher rate of mortality in the younger size classes.

As the numbers of recruits did not differ significantly from the number of mortalities for *P. acerosa*, *P. americana*, or other gorgonians, the populations of both species of *Pseudopterogorgia* and other gorgonians were stable over the period of the study.

Although causes of mortality are most commonly either detachment from the substrate from bioerosion and/or wave force or encrustation by *Millepora* spp. or sponges, the disappearance of large numbers of very young colonies in one of the cleared quadrats may be the result of grazing (see ecological interactions). *Cyphoma gibbosum*, shown to be a "prudent predator" by Birkeland and Gregory (1975), was rarely a direct source of mortality on any of the sites examined.

Growth

The great similarity between length-weight regressions of *P. americana* and *P. acerosa* at all sites indicates that the two species grow very similarly under a variety of conditions. The greater weight of *P. americana* at two sites is probably due to its greater "bushiness" at these two sites since it is unlikely that the density of the material which makes up the colony would vary.

The variability of linear growth increments in colonies measured over one year is real although some measuring error may be involved. Since there were no significant differences between growth rates of colonies of different length or at different depths, the effects of colony lengths and depth were not distinguishable, if present, due to the high variability in growth rates. Available light accounts for only about 20% of the variability. Grigg (1970, 1977) attributes the high variability in the growth rates of *Muricea* spp. to damage by abrasion, grazing, and intrinsic variability between individuals. As many incidents of negative growth occurred for *P. americana* and *P. acerosa*, especially on a bimonthly time scale, abrasion or grazing probably are responsible for much of the variability. Colonies showing no negative bimonthly growth increments also had a great deal of variability in growth rates suggesting intrinsic differences in growth rates between colonies. (Kinzie (1970) and

Weinberg and Weinberg (1979) also found high variability in growth rates for the species they studied and attributed it to abrasion, predation, and intrinsic differences.

Mean growth rates of about 5 cm/yr for *P. americana* and 6 cm/yr for *P. acerosa* (as determined by length per growth ring) were very close to or higher than other reported growth rates. Grigg (1970, 1974) found a mean growth of about 1.5 cm/yr for *Muricea californica.* Cary (1914) reported growth ranges of 0 to 8.3 cm/yr for *Gorgonia flabellum* and *Plexaura flexuosa. Plexaura homomalla* grew at a mean rate of 2 cm/yr (Kinzie, 1974). Kinzie (1970) measured growth rates in a variety of gorgonian species and found them to vary from 2.8 to 8 cm/yr depending upon the site and depth. Weinberg and Weinberg (1979) reported growth rates of 0 to 4.9 cm/yr in *Eunicella singularis.* The growth rates reported by Kinzie (1970, 1974) and Weinberg and Weinberg (1979) excluded incidents of negative growth and therefore are optimal and probably higher than would be expected in nature. Growth rates used in the present study included incidents of negative growth so that they could be used to determine age of colonies of a given length.

The positive relationship of growth rates to the relative amount of light indicates that zooxanthellae enhance growth. *Pseudopterogorgia americana* contains more zooxanthellae than *P. acerosa* (Bayer, 1961). If growth rates were dependent upon zooxanthellae, *P. americana* should show a faster growth rate than *P. acerosa*. This, however, is not the case and may indicate that growth rates are also dependent upon other factors.

Annual periodicity in growth rings of gorgonians has been demonstrated in a temperate species (Grigg, 1970, 1974). The existence of growth rings was shown in a tropical gorgonian, *Plexaura homomalla*, by Opresko (1974), and he assumed rings to be annual. The agreement between measured growth rates and estimates based on length per growth ring in *P. americana* and *P. acerosa* indicates that growth rings are annual. Since growth rings are found in young colonies that are not reproductively active, they cannot be due to slowing of growth during reproductive periods. Seasonal fluctuations in temperature or light (in the number of daylight hours) are probably responsible for these rings. Growth rings are most easily distinguished in gorgonians from site (1) and may be due to greater seasonal influences there. Although site (1) had the shallowest depths, visibility there was frequently so low that light levels are probably not much, if at all, greater than at the other sites.

The length per growth ring data indicate that larger colonies grow faster than small ones. However, as actual measured growth rates did not vary with colony length, this is considered to be an error due to the difficulty of distinguishing all the rings in large colonies. Grigg (1970, 1974) plotted growth rings against age based on height and measured estimates of growth and found agreement (one to one) except for the largest colonies. He concluded that the age estimates for large colonies using growth rings were low due to the difficulty in distinguishing the rings on the periphery of cross sections. Grigg also found that measured linear growth rates in *Muricea californica* decreased slightly with increasing colony size, while growth rings in large colonies indicated an increased linear growth rate over small colonies. Mean growth rates based on colony length per growth ring compared well with annual growth increments measured in *P. americana* and *P. acerosa*; therefore, mean growth rates were used for all colony sizes to estimate age.

Reproduction

Sexes are separate in both species of *Pseudopterogorgia*. Gohar (1940a) and Gohar and Roushdy (1961) found some Red Sea octocorals to be hermaphroditic although most were dioecious. Grigg (1970) examined over 1300 colonies of *Muricea californica* and *M. fruticosa* and concluded that sexes were separate since only four colonies (all *M. fruticosa*) contained male and female sex cells. Sex change, if it does occur, is a rare event as only one colony (*P. americana*) out of 18 sampled monthly on site (1) could have changed sex. Goldberg and Hamilton (1974) reported that several colonies of *Plexaura homomalla* out of 75 appeared to change sex, but they attributed this to sampling error.

If colonies do occasionally change sex, one reason might be to increase the proximity of males to females. Therefore, a nearest neighbor technique should demonstrate if one sex tends to be closer to the other sex than to members of the same sex. In material discussed here, the sexes were not significantly associated or dissociated with each other. Since either males or females were found in colonies of all sizes, sex change, if it occurs, is not an age or size phenomenon.

Pseudopterogorgia americana was found to have a higher percentage of females than males, while *P. acerosa* had a one to one ratio. The higher proportion of females in *P. americana* assumes that colonies which could not be sexed did not contain a higher proportion of males than females. It was not possible to determine if this was true for *P. americana* since only nine colonies were sampled monthly. If *P. americana* does have a higher proportion of females than males, while *P. acerosa* has an even ratio, *P. americana* might have an advantage over *P. acerosa* if the fertilization rate is the same. No studies have been reported of fertilization rates in gorgonians.

Reproductive periodicity shows stronger synchrony between sexes of *P. acerosa* than *P. americana* at least on site (1) for the year studied. Although *P. americana* may reproduce for a longer period of time each year, the strong synchrony between sexes in *P. acerosa* might enhance its fertilization rate. This could give *P. acerosa* and advantage over *P. americana* in areas of lower density of the two species such as sites (2), (3), and (4). Work on reproductive periodicity in an area of lower densities might be valuable to determine if synchrony patterns were the same for the two species. Unfortunately not enough colonies of the two species were sampled at site (2) to provide any information on reproductive periodicity there.

Grigg (1970, 1977) found that both Pacific species of *Muricea* delayed reproduction for four to six years, and gonads did not achieve the size found in large colonies for up to 10 years old. *Pseudopterogorgia americana* and *P. acerosa* also appear to delay reproduction for at least three to five years. Since the reproductive potential of a colony would depend upon the numbers of polyps and therefore the size of the colony, areas with a high proportion of larger (older) colonies should have a higher reproductive potential than areas with a higher proportion of small (young) colonies. In addition areas with a higher proportion of older colonies should have a far higher proportion of reproductively active colonies. Likewise, if one species is reproductively active at a smaller size than the other, it could have a reproductive advantage. Many more samples would have to be taken to determine just when each species becomes reproductively active. No previous work on the size of the colony at onset of reproduction has been reported for other species of West Indian gorgonians. Great reproductive potential may be an important factor between species, but space limitation will control the total number of recruits.

Since space is limiting for gorgonians and the availability of space may occur at any time, the slight seasonal differences in reproductive periodicity between the two species of *Pseudopterogorgia* may be thought to temporally separate the species. The cleared quadrats, however, were not settled substantially until amost a year after the clearing. This is probably not due to a need to "age" the substrate, as other substrate which was cleared in the same manner was settled on within a few months by gorgonians (Paul Yoshioka, personal communication).

Gohar (1940a, 1940b, 1948), Gohar and Roushdy (1961) found oviparous and larviparous octocorals, Kinzie (1970) found planulating individuals of *Pseudopterogorgia bipinnata, P. elisabethae, Briarium asbestinum,* and *Muriceopsis flavida,* although in the last two species only one planulating individual of each was seen. Several species of *Eunicella* have been shown to be larviparous (Theodor, 1967b; Weinberg, 1979b; Weinberg and Weinberg, 1979). Bayer (1974) and Goldberg and Hamilton (1974) found no sign of larvae or dividing eggs in *Plexaura homomalla.* No larvae or dividing eggs were found in *P. americana* or *P. acerosa*, although colonies with large eggs were checked frequently. Reproduction did occur as recently settled colonies were found. Therefore, these two species are probably oviparous. More work should be done to determine if a particular species can be both oviparous and larviparous.

Ecological Interactions

The negative relationship between coral coverage and gorgonians indicates that they do compete with each other for space and may be partially responsible for patchiness on site (1). Grigg (1970, 1977) concluded that the two *Muricea* spp. he studied appear to compete more strongly with other organisms than with each other for space. No new coral polyps were noticed in the cleared quadrats on site (1) suggesting that gorgonians colonize an area faster than corals. Stoddart (1963)indicated that gorgonians recover more rapidly than corals in storm devastated areas. This may be due to both heavy recruitment of gorgonians in cleared areas and relatively rapid growth rates compared to many corals.

Gorgonians showed little obvious ability to damage each other. *Muricea* spp. did cause some damage, and this was also reported for *Muricea laxa* in Jamaica by Kinzie (1970). *Pseudopterogorgia* spp. with their high degree of branching are among the few gorgonians which may have the ability to shade (exclude light from) other gorgonians (Kinzie, 1970). Since gorgonians tend to be evenly distributed on even substrate (small scale dispersion patterns), either larvae tend to avoid other colonies during settlement or interactions do occur. The highly significant even pattern found on the homogeneous substrate on site (1) may be related to extremely high densities of gorgonians which would increase abrasive contact.

No new encrustations were seen on colonies which had not sustained previous damage in this study. Bayer (1961), Kinzie (1970), and Grigg (1970) believe that encrusting organisms need exposed axial skeleton to settle on gorgonians. Therefore, the means by which this damage is caused is very important. Storm damage by heavy wave action is known to be the most prevalent cause of heavy mortalities to gorgonians in many areas (Cary, 1914, 1918; Goreau, 1964; Stoddart, 1962; Birkeland, 1974). Storm waves may also cause damage which exposes the axial skeleton of the bases of colonies as well as abrasion to branch tips (Cary, 1914). Storm damage to the bases of gorgonian colonies was found on site (2) and is probably due to scouring by heavy sediment rather than twisting of the colonies. Even in areas where damage to the basal stalk during high storm waves is not common, as on site (1), encrustations on the bases of gorgonians are common. *Cyphoma gibbosum* occurs infrequently on site (1), but its grazing damage is most common near the bases of gorgonians. Birkeland and Gregory (1975) found that *C. gibbosum* prefers gorgoniid to plaxaurid gorgonians, with a particular preference for *Gorgonia* spp., at least at the Tektite site in St. Johns, Virgin Islands. *C. gibbosum* seemed to prefer *P. americana*, also a gorgoniid, on site (1). *Gorgonia* spp. were rare on site (1). Since *C. gibbosum* moves to new colonies frequently (Birkeland and Gregory, 1975), one gastropod is capable of attacking many colonies. Since as many as 37% (6/16) of these attacks result in permanent encrustations, even small numbers of *C. gibbosum* could have a significant indirect effect on the rate of mortalities. The "successful encrustations" on gorgonians previously attacked by *C. gibbosum* were only observed for several months, and none of these included *Millepora* spp. The actual number of encrustations from organisms other than *Millepora* spp. resulting in mortalities is not known, but they do occur. Although the extent of these infestations frequently does not increase, if they are stable the colony may eventually topple as the weight becomes too great for the basal stalk to support. Amphinomid polychaets which do graze on gorgonians were not seen on the basal stalk where most encrustations are found.

Encrustations by *Millepora* spp. "seals the fate" of a particular gorgonian colony (Kinzie, 1970). Growth rates of *Millepora* spp. of 9.3 cm/yr indicate that the hydrocoral can outgrow a gorgonian, but usually gorgonians break on the weakened basal stalk before being completely overgrown. Kinzie (1970) reported growth rates for *Millepora* spp. of 244 cm^2/yr on *Gorgonia* spp. and 1.44 cm/yr on branch tips of *Plexaurella* spp. *Plexaurella* spp. have a very thick coenenchyme which may be more difficult for the hydrocoral to kill.

Kinzie (1970) reported that periodic algal blooms in some areas may smother young colonies. No dense growths of algae were noticed on sites (1) or (2) until after storm waves from Hurricane David scoured the bottom at site (2). Dense mats of algal growth were not seen during the study.

The occurrence of a parasitic polychaete and an isopod on *P. acerosa* and not on *P. americana* may be due to some chemical repellent in *P. americana* or just to the mechanical difficulties of living in the slime produced by *P. americana*. The sliminess of *P. americana* may have many advantages such as a greater ability to slough off sediments and many disadvantages such as fouling from its own mucus in the absence of water currents. Excessive mucus production is a disadvantage to the species when kept in aquaria (Goldberg, 1973b). Colonies of *P. acerosa* which were infected with the polychaete or isopod appeared to be in good condition.

The presence of *Astrophyton muricatum* or *Pteria colymbus* on colonies of *Pseudopterogorgia* spp. did not appear to cause mortality in gorgonians from excessive weight. However, Weinberg and Weinberg (1979) observed mortality from "benign" encrusting organisms on *Eunicella stricta*. Large individuals of *A. muricatum* are usually found on corals rather than gorgonians (Wolfe, 1978).

Thalassoma bifasciatum appears to "clean" gorgonians rather than graze on them. Randall (1967) noted that *T. bifasciatum* usually feeds on small crustaceans often "picking" at gorgonians. Occasionally the parrotfish, *Sparasoma aurofrenatum*, was also seen plucking at gorgonians.

The disappearance of a large number of very young colonies in one of the cleared quadrats remains unexplained. No large storm waves, unusual algal growth, or heavy sedimentation occurred at the time, and other cleared quadrats had few mortalities. Caging experiments indicated that *Diadema antillarum*, though abundant, was not responsible. Predation from fish or some other source remains a good possibility.

The trend for a high percentage of both species of *Pseudopterogorgia* to be open day and night may indicate dependence upon catching food and zooxanthellae. Neither species was seen actively catching plankton at night, but the role of fine detritus in gorgonian nutrition has not been reported.

Summary

1. The distributions and abundances of *Pseudopterogorgia americana* and *P. acerosa* were studied on four different sites. Mortality, recruitment, growth rates, reproduction, and interactions with other organisms were studied to determine what effect they may have on these distributions and abundances.

2. Substrate heterogeneity is largely responsible for the aggregated dispersion patterns of gorgonians on site (1). The presence of corals and other encrusting organisms may contribute to these aggregated patterns since there is an inverse relationship between coral or encrusting organism cover and the number of gorgonians.

3. Negative interactions may occur between gorgonians in areas of high density as indicated by the even dispersion patterns on relatively homogeneous substrate on site (1). A single species, *P. americana*, was aggregated on relatively homogeneous substrate which may be due to a limited ability for the larvae to disperse.

4. The relative abundances of *P. americana* and *P. acerosa* differ from site to site. Site (1), where the absolute densities of both species are highest, had many more *P. americana* than *P. acerosa*. The other three sites, where the densities of the two species were lower, had almost as many or even more *P. acerosa* than *P. americana*.

5. The age frequency distributions of the two species were very similar on all of the sites studied indicating that the two species are not affected differentially by those factors influencing these distributions.

6. Site (4) had the greatest proportion of young colonies of both species while site (3) had the greatest proportion of older colonies. Therefore, site (4) probably has the highest mortalities among young colonies while mortalities on site (3) were more evenly distributed over the age spectrum.

7. Site (1) appeared to have the most "suitable" and "stable" habitat for both species.

8. Gorgonians compete with each other and other sessile organisms for space as indicated by the significantly higher recruitment in cleared versus uncleared quadrats. *P. americana* may be a colonizing species since its recruitment was higher than that of other gorgonians.

9. The number of mortalities were not different for *P. americana*, *P. acerosa*, and other gorgonians on site (1).

10. The number of mortalities in a size class of *P. americana* on site (1) was proportional to the relative abundance of that size class, while mortalities were proportionately higher in the younger size classes of other gorgonians (excluding *P. acerosa*). This did not include very young colonies (under 2 cm).

11. Recruitment did not differ significantly from mortality in *P. americana*, *P. acerosa*, and other gorgonians indicating that the populations were stable over the period of the study.

12. Although *Cyphoma gibbosum*, a gastropod, rarely causes mortality, its ability to bare the axial skeleton by grazing does allow encrusting organisms to settle on gorgonians. Usually, however, the gorgonian heals over the *C. gibbosum* scars.

13. *Pseudopterogorgia americana* and *P. acerosa* grow at similar rates and have a similar growth form. Linear growth rates as estimated from growth rings or measured over one year are very variable and are about 5 cm/yr for *P. americana* and 6 cm/yr for *P. acerosa*.

14. Growth rings were found to be annual for *P. americana* and *P. acerosa*. Age estimates for older colonies are low due to the difficulty in distinguishing all of the rings.

15. Growth rates did not vary significantly with colony length or depth, but did show a positive relation to increasing light. This accounted for about 20% of the variability in growth rates. Other variability may be due to loss of length from grazing or abrasion, measuring error, and intrinsic differences in growth between colonies.

16. Sexes are separate in *P. americana* and *P. acerosa* colonies. *P. americana* had a higher percentage of female than male colonies on site (1), while *P. acerosa* had an

even ratio of males to females. If the fertilization rates are the same for the two species, this may give *P. americana* some advantage over *P. acerosa*.

17. *Pseudopterogorgia acerosa* had strong synchrony in reproductive periodicity (from gonad volume) both between sexes and within sexes, while *P. americana* had weak synchrony within sexes and was not very synchronous between sexes. *P. acerosa* peaks from late July to September, while *P. americana* appears to reproduce from late September through March. The strong synchrony in *P. acerosa* might be an advantage over *P. americana* in areas of low colony density where the fertilization rate might be affected.

18. Reproduction in both species of *Pseudopterogorgia* may be delayed for from three to five years since small colonies rarely contained gonads.

19. Both species of *Pseudopterogorgia* are probably oviparous since no dividing eggs or larvae were found in the polyps.

20. Few gorgonians showed damage as a result of contact with other gorgonians, although there is some indication that high densities of gorgonians may cause negative interactions. Since light can aid growth, the high degree of branching of *Pseudopterogorgia* spp. may allow them to shade other gorgonians.

21. No obvious damage or mortalities were noticed from the isopods or parasitic syllid polychaets found on *P. acerosa*. *Thalassoma bifasciatum*, a wrasse, was frequently seen picking at gorgonians, but gut contents examinations showed few, if any, gorgonian remains. *Sparisoma aurofrenatum* was only rarely seen picking at gorgonians.

22. A high percentage of colonies of both species expand their polyps during the day or night which may indicate that *Pseudopterogorgia* spp. depend upon their zooxanthellae and active feeding.

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