OBSERVATIONS ON CLEANER SHRIMPS OF THE GENUS *PERICLIMENES*

By CONRAD MAHNKEN[1]

CONTENTS

ABSTRACT: Diving teams studied the distribution of anemones and commensal fish cleaning shrimps with relation to major reef and sand flat features during Tektite I. The most abundant shrimp was *Periclimenes pedersoni* Chace, followed by *P. yucatanicus* (Ives). Both species were almost invariably associated with the anemone *Bartholomea annulata*. Physiognomic features observed as representing different environments were: back reef; back reef re-entrant or canyon; reef front; unvegetated sand strip, an area at the base of the reef grazed clean by fishes; and algal plain, an area of scattered boulders and sparse vegetation.

The anemone *B. annulata* was about equally abundant in all five habitat types, but the number of shrimps per anemone varied from lowest on the reef front for both species to highest on the sand strip for *P. pedersoni* and highest on the algal plain for *P. yucatanicus*. Variation in abundance of *P. pedersoni* between survey areas is believed to be less related to physical habitat than to the opportunity for meeting fish "clients." Not only is the sand strip the major corridor for fish movement along the reef, but the shrimp-anemone complex is more readily visible to potential fish hosts in the open, unvegetated sand strip. No competitive exclusion was evident between the two species of *Periclimenes*, both shrimps frequently occurring together on the same anemone.

P. pedersoni populations on 23 anemone stations in the unvegetated sand strip were monitored seven times. The notion that *Periclimenes* is territorial and remains for extended periods within a meter or less of the same spot was not borne out, for significant variation ($P = .05$) in shrimp populations on individual anemones as well as in total populations did occur between surveys.

[1]National Marine Fisheries Service, Northwest Fisheries Center, Seattle, Washington 98102

There was no significant difference in individual length of shrimp in populations between surveys (P = .05). The relatively low abundance of *P. pedersoni* in all but the sand strip area and the significant variation in population size with time suggests that the movements in the population that do occur are confined primarily to the unvegetated sand strip.

INTRODUCTION

A symbiotic cleaning behavior exists between certain brightly colored tropical shrimps of the genus *Periclimenes* and cooperating reef fishes. The shrimps, which are almost invariably associated with an anemone, have been observed to pick and eat parasites, injured tissue, and other particles from a variety of fishes. These shrimps are highly specialized, and largely dependent upon cleaning for their food (Limbaugh, 1961; Limbaugh et al., 1961). The shrimps may remain stationed on or near an anemone for a long time, attracting fishes by their brilliant colors, conspicuous patterns, and their actions (Feder, 1966).

"Cleaners" are key organisms in many community ecosystems. Their activity may play a major role in the well being of many species of reef fishes. Since many important food fishes may be largely dependent on the outcome of cleaning for their health, and possibly in some instances for their continued existence, the economic value of cleaners may be great (Feder, 1966). The present study indicates that the abundance of such reef fishes in the Virgin Islands may be indirectly related to the occurrence of the anemone, *Bartholomea annulata* (LeSueur), to which cling the two most abundant shrimps, the Pederson cleaning shrimp *Periclimenes pedersoni* Chace and the spotted cleaner *P. yucatanicus* (Ives). Observations on cleaning by fishes in the area around the Habitat are noted by Collette and Talbot (this volume).

The importance of such symbiotic behavior was not recognized until diving equipment and techniques allowed biologists to observe undersea life directly. The duration of such observations were significantly extended with the recent advent of saturation diving techniques. Saturation diving from manned underwater laboratories, such as the Tektite Habitat, has largely eliminated the restraints imposed by depth and time on conventional SCUBA methods and afforded many advantages for prolonged underwater studies. In the present field study, conducted from the Tektite Habitat during Tektite I (February 15-April 15, 1969), the distribution and abundance of both cleaner shrimp and host anemones were investigated.

DESCRIPTION OF THE STUDY AREA

Physical features and type of bottom

The distribution and abundance of *Periclimenes* was surveyed in five distinct physiognomic reef areas that I believed to be different ecological zones (Fig. 39), all within easy swimming distance of the Tektite Habitat. Anemones and associated shrimp were completely enumerated within each zone at least once during the study.

The back reef plot is located in relatively shallow water between the Tektite Habitat and the bedrock outcrop along the beach. It extends 65 m across the reef in a narrow 3.3 m corridor that intersects several canyons or re-entrants running normal to the transect, but in general is constant in depth at 13 m. Throughout the back reef are scattered coral boulders, rubble, profuse stands of alcyonarians, exposed areas of carbonate sand, and a diverse fauna of actively growing hard corals corresponding in species composition to the "*cervicornis*" zone of Goreau (1959). The plot terminates to the seaward where the reef face breaks and falls away rapidly to the sand-algal plain at a depth of 17 m.

The canyon (survey plot #2) is the same north-south re-entrant in which the Tektite Habitat was located. Near Tektite the canyon was steep-sided and distinct, rising 1 or 2 m above the canyon floor. At the south end it became diffuse and ill-defined, coalescing with the open sand areas of the back reef. Moderate numbers of herbivorous fishes grazed this corridor, keeping it clean of algae.

The deeper parts of the seaward reef front (survey plot #3) are typical of deep Caribbean reefs as described by Goreau (1959) except for the lack of an intermediate buttress zone and a shallow stand of *Acropora palmata*, presumably because of the low energy sea condition that prevails in Lameshur Bay. The steep reef face is typified by *Montastrea annularis*, the primary hermatypic species, but no single species of hard coral is clearly dominant.

Seaward of the reef wall, lie the extensive sand flats that occupy the major portion of Lameshur Bay (survey plot #5). The primary vegetation on the plain is *Thalassia*, *Udotea*, and *Syringodium*, sprinkled with patches of forms such as *Penicillus* and *Halimeda* (see also Earle, this volume). An unvegetated sand strip (survey area #4) averaging 10 m wide separates the reef from the grass and algae covered plain.

This band of bare sand between inshore fringing reef and offshore beds of marine vegetation is a persistent and important bottom feature in the Virgin Islands. Using aerial photographs, Kumpf and Randall (1961) were able to delineate the sand strip along more than one-half of the total 58-mile coastline of St. John and nearby islets.

The unvegetated sand strip results from the grazing activity of herbivorous reef fishes, and width of the strip probably coincides with the maximum distance that these fish will venture from shelter of the reef (Randall, 1965). The bare sand zone is also seen as concentric bands around patch reefs. Randall noted that sharpness of the seaward border of the sand strip was most distinct where the reef is

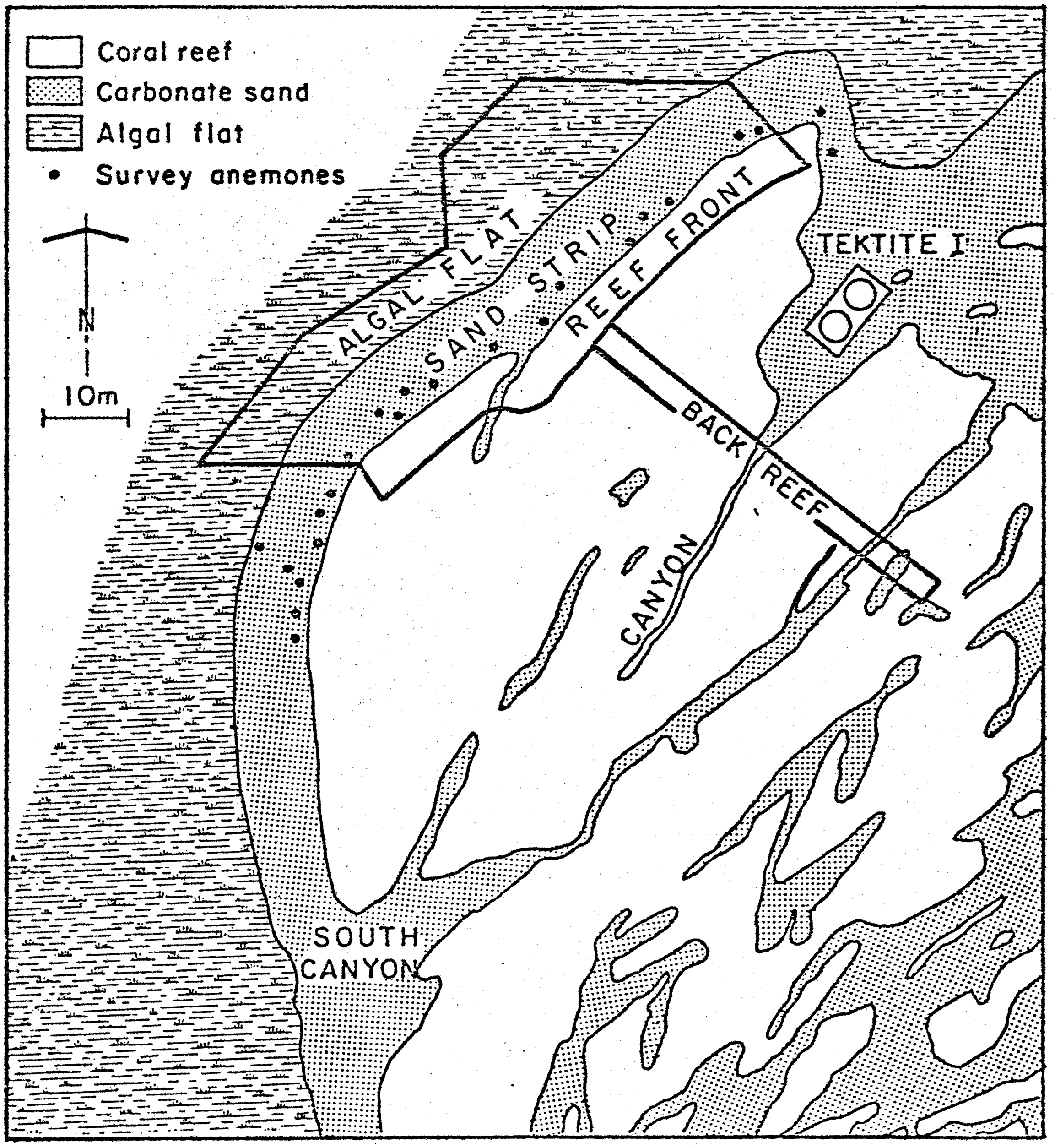


FIGURE 39. Location of Tektite Habitat, survey anemones and five survey plots.

bordered by sea grasses, *Thalassia* and *Syringodium*. I have also observed that the bare zone is most distinct where the adjoining reef is best developed. Thus, where the reef is massive and well developed, affording cover for more grazing fish, the outer border of the sand strip is distinct. Conversely, where the reef is fragmentary or composed of scattered coral boulders and rubble, the sand strip usually becomes diffuse and at best difficult to recognize. Causal relation for formation of the sand strip are treated in greater detail elsewhere in this volume (Earle).

Importance of the sand strip zone is emphasized here because it contained the largest population of Pederson cleaner shrimp among the five areas surveyed. Fish activity is probably the primary factor in determining the abundance of *P. pedersoni* in the sand strip. For this reason, survey anemones were established in the sand strip and surveyed on seven separate occasions.

Bartholomea annulata and its associates

In the Virgin Islands, *B. annulata* is associated with a complex community of organisms, mostly crustaceans, including at least four species of the shrimp genus *Periclimenes*. The interrelations between the organisms in this microcosm are poorly known, but it is probable that many are associated with the anemone for protection against predators, and, in the case of the cleaner shrimp, for a platform easily recognized by soliciting fishes.

The anemone is usually attached to a hard substrate buried in mud or fine sand from just below the low tide mark to at least 23 m (Holthuis, 1951). *B. annulata* is the numerically dominant solitary anemone in Lameshur Bay, and is most often found attached to the base of coral heads or to buried objects such as dead coral or empty conch shells.

Periclimenes pedersoni is a small species of shrimp with a maximum carapace length of not more than 6 cm. It occurs in the Bahamas, Virgin Islands, Antigua, and Florida. In general, it inhabits areas protected from violent surge along the coral-sand boundary, particularly near prominent underwater points or passes between coral heads. Everywhere, except off west Florida, it associates with *B. annulata*, usually hanging directly on the annulated tentacles of the anemone or occupying the same hole (Limbaugh et al., 1961). The shrimp's bright coloration makes it conspicuous against the drab background of the anemone. The shrimp is best termed an ectocommensal as there is no evidence of benefit derived by the anemone—only by the shrimp.

P. yucatanicus is a similar small species of shrimp less than 3 cm long. It is widely distributed between Colombia and southern Florida (Holthuis, 1951). Off the Bahamas, Puerto Rico, and the Virgin Islands, it is found associated with two common anemones, *Bartholomea annulata* and *Condylactis gigantea*, either nestling in the anemone or occupying the same crevice (Limbaugh et al., 1961). I found this shrimp associated with at least two other anemones and one medusa. On three occasions the flat-belled medusa, *Cassiopeia* sp., was observed resting on the sand, ex-umbrellar surface up, with one to three individuals of *P. yucatanicus* in the tentacles.

Periclimenes yucatanicus has some limited ability to assume background coloration matching the host coelenterate. The normal appearance while on *B. annulata*, aside from the bright colored markings, is a clear transparent color. Two large green anemones attached to the shell of an angular triton, *Cymatium femorale*, collected on the algae-covered sand flats at the base of the reef, contained six *P. yucatanicus* that had assumed a darker green shading of the primary body color to match the color of the anemones. Individuals found on the medusa *Cassiopeia* also were darker in coloration.

Other species of *Periclimenes* were collected in direct or loose association with *B. annulata*. One species, was identified by Dr. Fenner A. Chace, Jr., (U.S. National Museum), as similar to *Periclimenes rathbunae* Schmitt; Chace, however, believes possibly two undescribed species may be involved and that positive identification must await further study (personal communication). The drab colored individuals of these species were observed on several species of anemone, but never cleaning or attempting to attract fish. However, they were observed too seldom to eliminate them conclusively as cleaners. Like *P. pedersoni* and *P. yucatanicus*, they moved with impunity among tentacles of the anemones and, when disturbed, burrowed deeper until almost completely hidden by the tentacles. At depth, these shrimps appeared transparent brown peppered with black spots and were well camouflaged in the anemone.

Periclimenes americanus (Kingsley) is one of the most common species of the genus in tropical American waters. Two individuals of *P. americanus* were observed picking through sand at the base of a *B. annulata* beneath the protection of but not touching the extended tentacles. *P. americanus* may be more than a casual visitor to *B. annulata*, for F. A. Chace, Jr. (personal communication) also has observed this association during the Smithsonian-Bredin Caribbean expeditions.

Two other shrimps known to be cleaners were fairly common in Lameshur Bay, the red banded coral shrimp *Stenopus hispidus* (Oliver), largest of known cleaner shrimps, and the smaller *S. scutellatus* Rankin. *S. scutellatus* was observed most often in coral boulders on the algal plains, but, unlike its occurrence in the Bahamas (Limbaugh et al., 1961), there were no extensive beds of eel grass in the near vicinity. *S. hispidus* frequented the reef proper. Despite the fact that many specimens of *Stenopus* were present, they were infrequently observed cleaning fishes. Their importance as cleaners in this area is considerably less than *Periclimenes.*

One final shrimp, an unidentified species of *Thor,* was found regularly in small numbers on certain anemones. Not only did they occur on *B. annulata* but also on several unidentified anemones, one in particular with extremely powerful nematocysts. Individuals lived among the tentacles or clinging to the sides of the anemones.

Chace (1958) also noted a number of other organisms associated with *B. annulata*: red mysid, *Heteromysis actinae*; the purple snapping shrimp, *Alpheus armatus*; hermit crabs; the arrow crab, *Stenorynchus seticornis*; and two fishes, *Paraclinus* sp. and an apogonid. All the above mentioned species occurred during the present study.

ANEMONE DISTRIBUTION

The back reef and reef front contained the greatest species diversity and abundance of anemones because of the solid substrate available in those areas. By far the most common single species, *Bartholomea annulata,* was about equally abundant in all areas except the algal flat (Fig. 40). In the canyon, back reef, and reef front areas *B. annulata* constituted 43-65% of all anemones. On the sand strip and algal flat where there was a lack of suitable hard substrate for other anemones, *B. annulata* became even more dominant constituting 87 and 74% of all anemones, respectively. It may be the prevalence of *B. annulata* on the reef and in the Caribbean generally that has led to its acceptance as a host for cleaner shrimp. But a major question that remains unanswered is why has *B. annulata* alone among all local reef anemones developed such a profusion of symbionts?

DISTRIBUTION AND ABUNDANCE OF *PERICLIMENES PEDERSONI* AND *P. YUCATANICUS*

The most abundant cleaner shrimp found in association with *B. annulata* was *P. pedersoni,* followed by *P. yucatanicus. P. pedersoni,* was the most abundant shrimp per unit area on the sand strip and reef front. *P. yucatanicus* was most abundant on the algal plain (Fig. 40). Large populations of both species were maintained at the base of the reef despite the decrease in anemones available for occupancy in these areas compared to the reef.

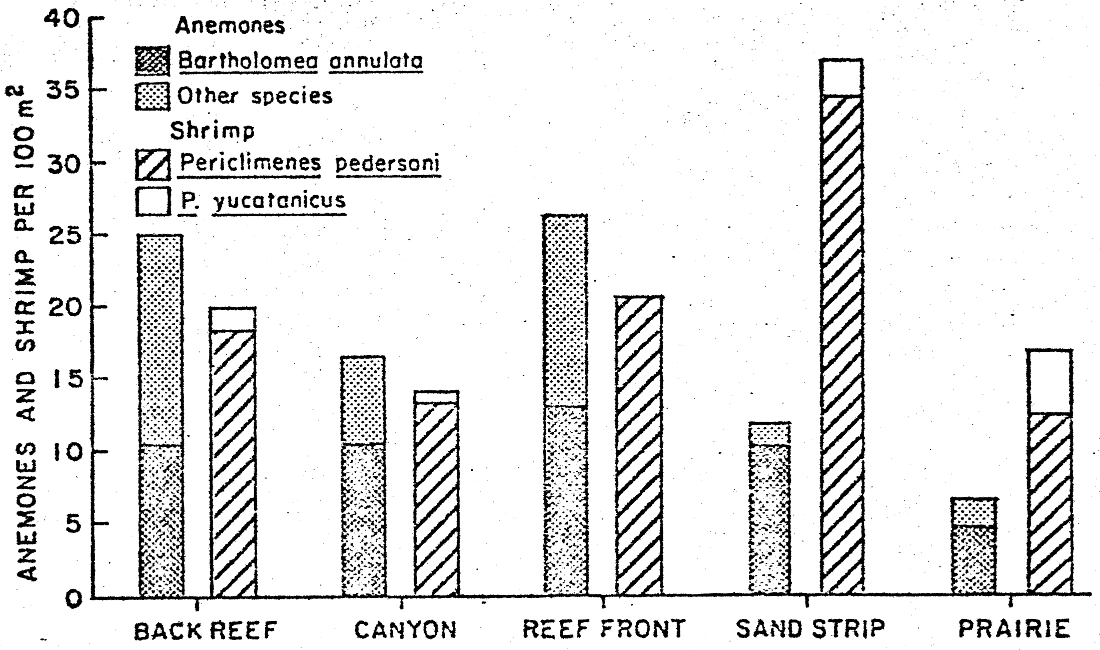


FIGURE 40. Abundance of *Periclimenes pedersoni* and *P. yucatanicus* in five survey plots on reef and sand substrates.

TABLE 3

Abundance of two common species of *Periclimenes* on *Bartholomea annulata* and other anemones

Area	*P. pedersoni* Shrimp per *B. annulata*	*P. pedersoni* Shrimp per all other anemones	*P. yucatanicus* Shrimp per *B. annulata*	*P. yucatanicus* Shrimp per all other anemones
Back reef	1.68	0.04	0.11	0.04
Canyon	1.15	0.14	0.08	0.00
Reef front	1.12	0.48	0.00	0.00
Sand strip	3.30	0.55	0.20	0.09
Algal flat	2.47	0.31	0.72	0.46

Both species of shrimp were far more abundant per anemone in the sand strip and algal flat (Table 3). Tests of all comparisons between means of samples showed that there was a significant difference ($P = .05$) in the average number of *P. pedersoni* on *B. annulata* between survey areas.

There was a high degree of preference for *B. annulata* as a host by both shrimps, but neither species occurs exclusively on this anemone (Table 4). For both cleaner shrimps, the differences in frequency of occurrence on *B. annulata* in different tracts are significant (chi square, $P = .05$). This varying density is dependent upon availability of other anemones and competition for space by the shrimp. For example, on the reef front where other anemones were most abundant, *P. pedersoni* occurred 59% of the time on *B. annulata*, occupying only 45% of the available individuals (Table 4). On the sand strip, where other anemones are scarce and shrimp are abundant, the competition for space is great. In this zone, *P. pedersoni* occurred on *B. annulata* 95% of the time, occupying 83% of the available individuals.

P. pedersoni were most abundant in the sand strip where fish traffic was greatest. I observed the greatest cleaning activity and diversity of host fish in the northern portion of the sand strip where large localized populations of *P. pedersoni* occurred on certain anemones (Fig. 41). Large colonies of the shrimp invariably coincided with the popularity of an anemone as a cleaning station for fish.

P. yucatanicus occurred most often in habitats characterized by isolated coral boulders on a sand substrate, not as often in the sand strip and seldom on the main reef. The greatest abundance was on the algal flat, especially the northern part adjacent to the portion of the sand strip where *P. pedersoni* was also concentrated (Fig. 42).

Reef stations seem to attract smaller, more territorial species of fish and are frequented less by large fishes unable or unwilling to work into crevices between coral boulders where anemone stations are located. Some reef-dwelling *B. annulata* do locate in sand-filled cracks atop living *Montastrea annularis*, and, although the locations are good vantage points, they contained few cleaner shrimp. It is significant to note that midwater fishes such as the yellowtail snapper, *Ocyurus chrysurus*, and the bar jack, *Caranx ruber*, were rarely (a single instance for each species) observed soliciting cleaning from *Periclimenes*. Collette and Talbot (this volume) have observed both of these fishes being serviced by cleaner fishes such as the Spanish hogfish, *Bodianus rufus*, and the bluehead, *Thalassoma bifasciatum*. It was my observation that the more sessile shrimp tend to clean fishes in open areas of good accessibility, while cleaner fishes like *Bodianus rufus* are more successful in soliciting clients in the water column above the main reef areas.

Both species of cleaner shrimp were concentrated near the tip of the reef which juts into the bay and intercepts a large expanse of algal flat. Moving fishes encountering the reef barrier and fishes dependent on the reef for protection may find a natural corridor for movement in the space above the sand strip. The shrimp seek out anemones located where fish traffic is greatest—in the sand strip. The abundance of *P. pedersoni* varies from low on the reef face to high on the sand strip and probably represents a response to the availability of fish hosts (food) rather than a change in habitat or ecotone. I concur with Feder (1966) to the extent that local concentrations of fishes may be dependent on cleaners for their well being, but disagree with his contention that concentrations of fishes are maintained at many fishing grounds primarily by the presence of suitable cleaners. Certainly there is no conclusive evidence here to indicate that the abundance of *P. pedersoni* in the sand

→

FIGURE 41. Abundance of *Periclimenes pedersoni* on anemones on seaward reef face and adjoining sand bottom. Numbers indicate shrimp on each anemone.

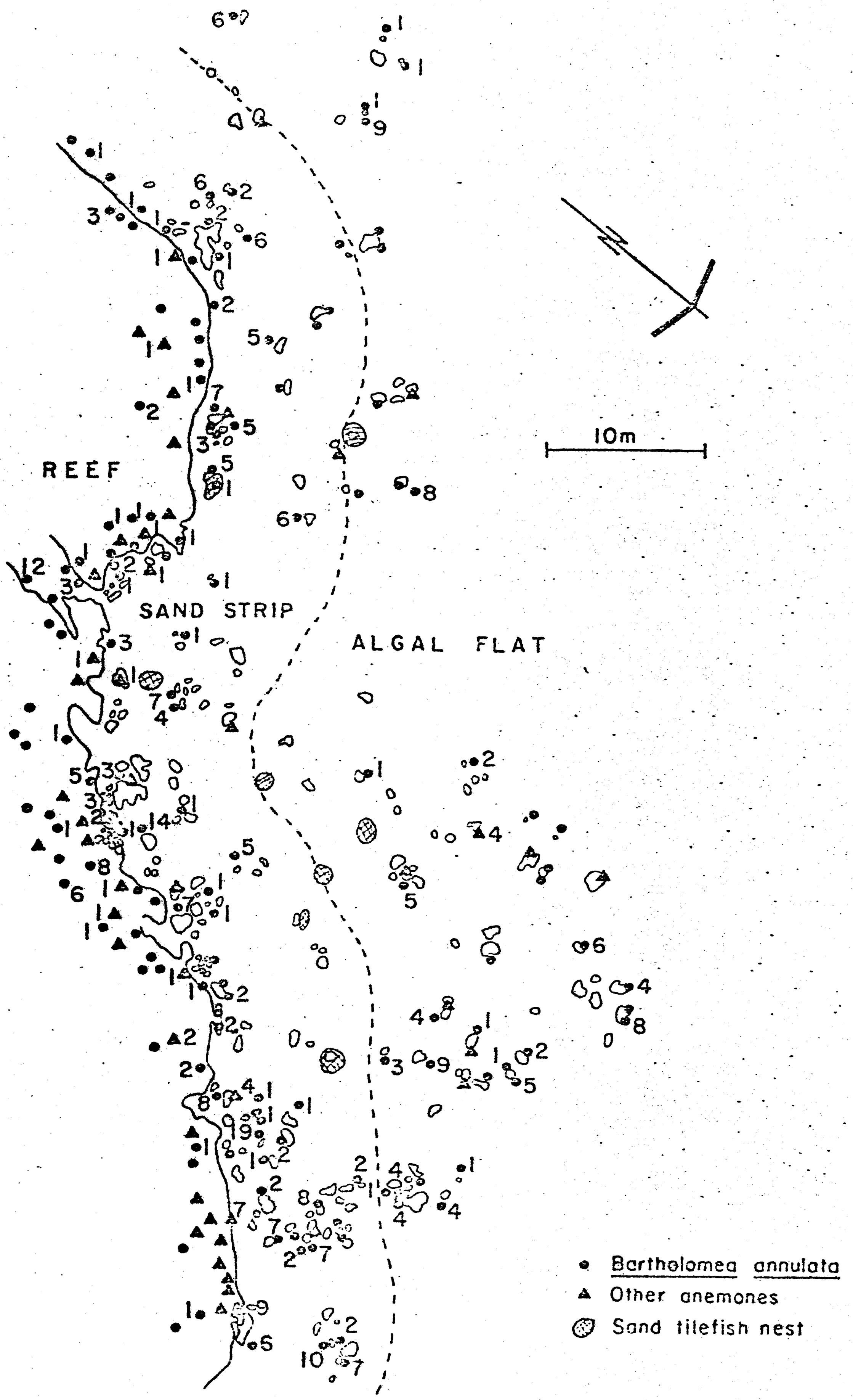

REEF
SAND STRIP
ALGAL FLAT
10m
Bartholomea annulata
Other anemones
Sand tilefish nest

TABLE 4

Percent occurrence of two common species of *Periclimenes* on the anemone *Bartholomea annulata*

	P. pedersoni			*P. yucatanicus*		
Area	Percent occurrence on *B. annulata*	Percent occurrence on other anemones	Percent *B. annulata* occupied	Percent occurrence on *B. annulata*	Percent occurrence on other anemones	Percent *B. annulata* occupied
Back reef	92	8	58	67	33	11
Canyon	83	17	38	100	0	8
Reef front	59	41	45	0	0	0
Sand strip	95	5	83	90	10	13
Algal flat	95	5	58	75	25	50

strip is anything more than an opportunistic aggregation in response to an abundance of fish hosts.

One further factor may ensure the success of shrimp cleaners in open sandy areas. The dark colored anemone *B. annulata* contrasts with the light sandy substrate and presents a good focal point for potential fish clients. The visual cue is heightened by the lashing, light-colored shrimp antennae against the dark anemone background which in turn contrasts with the large interspaces of cleanly grazed sand.

POPULATION SIZE OF *PERICLIMENES PEDERSONI* AND *P. YUCATANICUS* ON MARKED ANEMONES

Populations of *Periclimenes pedersoni* on 23 individual *Bartholomea annulata* located in the unvegetated sand strip were monitored seven times in the 25-day period from March 2 to 26. Each anemone was marked with a small numbered styrofoam cube tied to a sandbag with a nylon string. The foam cube was visible to diving teams some distance away, and adjacent anemones surveyed usually were within visual range of one another. The anemones surveyed were distributed in the sand strip from the reef front adjacent to the Habitat, south to within 40 m of the south canyon (Fig. 39).

The shrimp were rather fearless and could easily be enticed to browse along the back of a diver's hand where they assiduously picked at hairs. It therefore became a matter of routine during each survey to count and measure with calipers the total body length of each living shrimp on the anemone without harming or removing the shrimp. This fearlessness led to testing the theory that *Periclimenes pedersoni* is territorial, remaining for extended periods within a meter or less of the same spot (Limbaugh et al., 1961), and to rechecking the observation that on occasion they may completely disappear, or show up on a new anemone a short distance away.

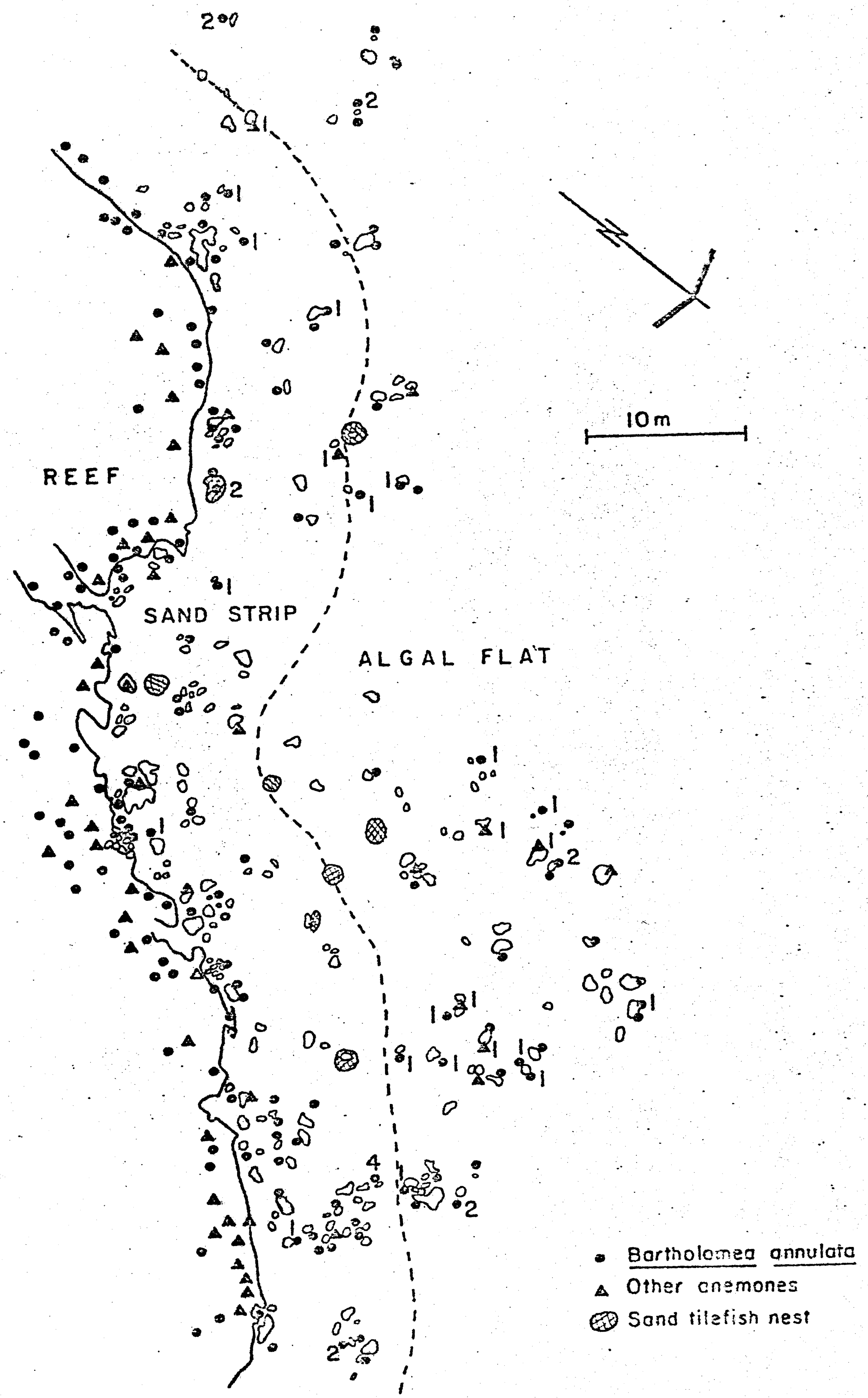
Statistical tests show that there is variation in the number of shrimp per anemone per survey. Subjective evidence indicates a limited movement of shrimp to and from the anemones. A number of natural and artificial movements were observed that might contribute to this population flux.

In an analysis of variance there was significant variation ($P = .05$) in the numbers of *P. pedersoni* on individual anemones between surveys as well as in the total population between surveys. In general this variation, although statistically significant, was limited to moderate changes in the number of shrimp per anemone (Fig. 43). For example, if an undisturbed anemone held a large number (7-11) of shrimp (station 1) then it consistently contained an abundant shrimp population. Conversely, anemones with few shrimp (0-3) remained sparsely populated throughout the surveys (station 10) *P. yucatanicus* and *P. rathbunae* were found infrequently but recurrently on the same anemones (stations 4, 13).

Limited movement of *P. pedersoni* is indicated by the slow rate of repopulation when shrimp are removed from the anemone host. All shrimp on four anemones in the sand strip were removed on March 30, and the anemones visited daily thereafter to determine the rate of repopulation (Table 5). Repopulation was slow at all removal sites despite an abundance of shrimp on nearby anemones. Anemones were resettled at a rate of about one shrimp per 3.5 days. At the first site, for example, 10 shrimp were removed from a large *B. annulata* centrally located in an area of scattered coral boulders. Within a radius of six m there remained 36 *P. pedersoni* and two *P. yucatanicus*

→

FIGURE 42. Abundance of *Periclimenes yucatanicus* on anemones on seaward reef face and adjoining sand bottom. Numbers indicate shrimp on each anemone.


REEF
SAND STRIP
ALGAL FLAT
10m
Bartholomea annulata
Other anemones
Sand tilefish nest

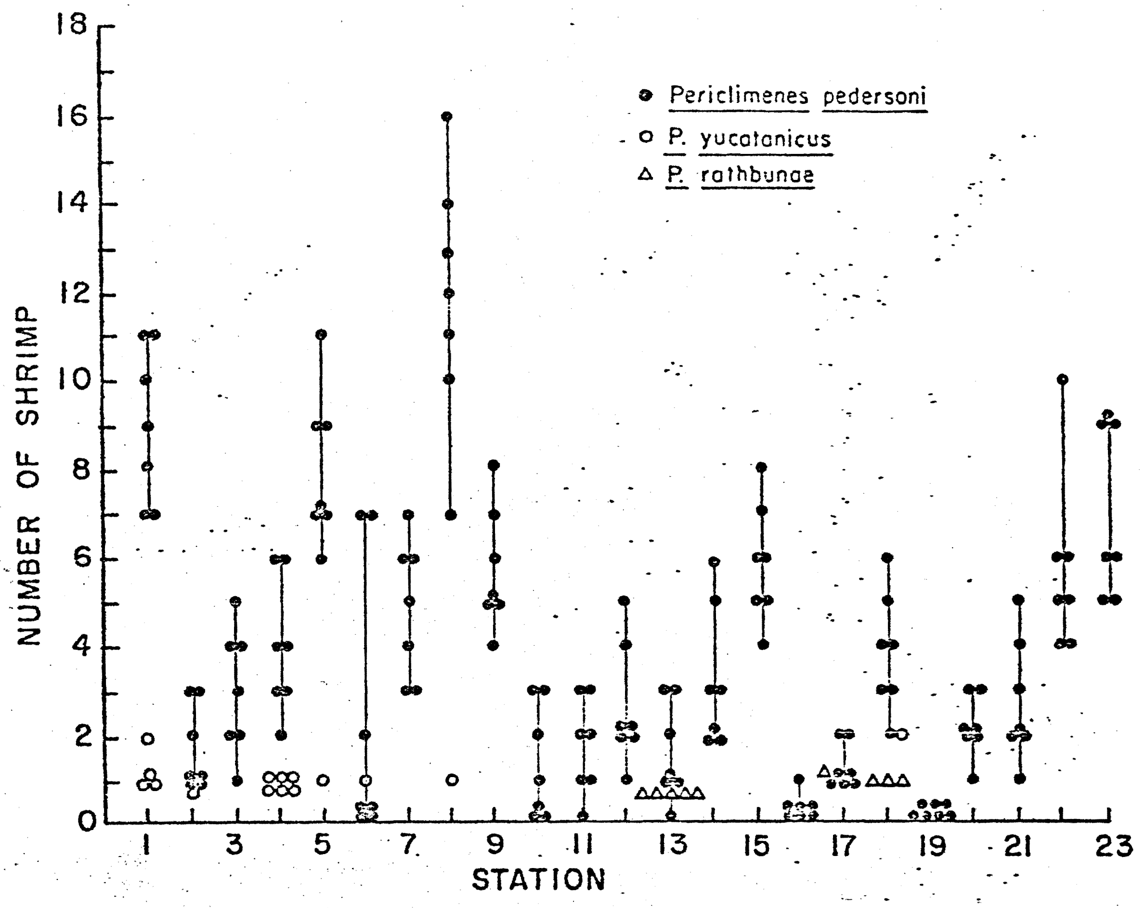


FIGURE 43. Abundance of three species of *Periclimenes* on 23 anemones (stations) located on the sand strip. Each anemone was surveyed seven times in a 25-day period.

occupying a total of 11 anemones; yet after nearly two weeks, only three *P. pedersoni* had settled on the depopulated anemone. Fishes were observed near the first anemone on the first day, but none attempted to solicit cleaning. No soliciting fishes were observed to loiter at any removal sites after the second day.

Sampling error undoubtedly accounts for some of the variation. It was difficult to see the smaller transparent shrimp when they were located on the sand around the base of the anemone, and counting error may account for part of the observed variation in numbers.

In large aggregations larger individuals chased smaller shrimp from the anemone. The displaced small shrimp would take up residence on a nearby vantage point like a sponge or coral or on the sand near the anemone. Small shrimp located on the sand, away from the contrasting brown anemone were especially difficult to see. The population at removal site 4 (26 shrimp, Table 5) was so large that it was scattered about the adjoining coral boulder with about half the individuals occupying a nearby branching sponge.

Shrimp were seen to "ride" fish clients when disturbed during cleaning and this inadvertent dislocation via a fleeing fish may account for some movement to and from anemones.

Recruitment of juveniles onto the anemones may be a slow steady process. Ovigerous females have been observed in the Virgin Islands from April through August (Chace, 1958) and from February to April during the present survey. There was no significant variation ($P = .05$) in shrimp size (length) between samples taken in the surveys and few juveniles were found in a sample of 104 shrimp collected in April (Fig. 44). The occurrence of ovigerous females for at least seven months out of the year, the similar size frequency distribution of the population throughout the survey period, and the relatively small number of juveniles in April indicate a lengthy reproductive period with

TABLE 5

Repopulation of *Periclimenes pedersoni* after removal from the anemone *Bartholomea annulata*. Day zero indicates the number of individuals present before removal

Days after removal	Anemone no. 1	2	3	4
0	10	15	6	26
1	0	0	0	0
2	0	2	0	1
3	0	2	0	1
4	1	2	0	1
5	1	2	0	1
6	1	2	0	1
7	1	3	0	2
8	3	3	0	—
9	4	—	—	6
10	4	3	0	—
11	—	—	—	—
12	3	—	—	—

a slow continuous recruitment of juveniles onto the anemones.

One is tempted to conclude that shrimp populations on individual anemones tend to be relatively static as a result of slow continuous reproduction, and recruitment. However, several other factors could account for the observed but limited variation in populations with time—opportunistic moves in response to the availability of fish clients, overcrowding, sampling error, and translocation by "hitchhiking" on fleeing fish.

CLEANING BEHAVIOR AND SUPPLEMENTARY FEEDING OF *PERICLIMENES PEDERSONI*

The cleaning activity of *P. pedersoni* was described by Feder (1966) and Limbaugh et al. (1961). The shrimp attracts the attention of a great variety of reef fishes by whipping its antennae and by swaying back and forth from a prominent position on or near the anemone. Fishes often line up or crowd around the anemone station, waiting their turn to be cleaned. When approaching an anemone station, a fish often changes color, alights on the bottom, and assumes a submissive posture with mouth open and opercula flared. Nassau groupers, *Epinephelus striatus*, and spotted goatfish, *Pseudupeneus maculatus*, were observed to lie against the anemones while being cleaned. On one occasion I observed *P. pedersoni* cleaning an unidentified parrot fish while the latter was lying on its side on the sand next to the anemone.

The shrimp stops whipping the antennae as soon as the fish is close or when it has come to rest and is quiescent. The shrimp then swims or walks to the client. On occasion shrimp were observed to swim out to meet the approaching fish even before the fish had settled on the bottom. While swimming toward a fish the chelae are open and forward and the body rocks to and fro along the meridional axis.

On occasion, the fish opens its gill covers and allows the shrimp to enter and clean the oral and gill cavities. Shrimp may exit via the gill opening. I observed, as did Limbaugh et al. (1961), that if the fish is disturbed during the cleaning operation, the shrimp is ejected from the fish's mouth before the fish retreats.

Among the most common fish visitors to anemones inhabited by *P. pedersoni* were: the Nassau grouper, *Epinephelus striatus*; yellowtail snapper, *Ocyurus chrysurus*; mutton snapper, *Lutjanus analis*; dog snapper, *Lutjanus jocu*; spotted goatfish, *Pseudupeneus maculatus*; yellow goatfish, *Mulloidichthys martinicus*; and the gray angelfish, *Pomacanthus arcuatus*.

A school of bigeye, *Priacanthus arenatus*, near the south canyon was almost always present in the daytime, suspended beneath alcyonarians along the reef face. They moved singly to anemone stations on the sand strip below, where they were often seen being cleaned. Sand divers, *Synodus intermedius*, were frequently observed being cleaned on the southern portions of the sand strip. I have never observed fish to prey upon *P. pedersoni* or *P. yucatanicus* and it has not been reported in the

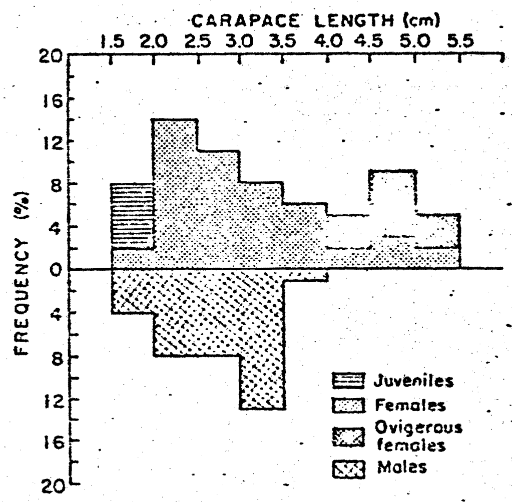


FIGURE 44. Carapace length-frequency histograms for *Periclimenes pedersoni*. Juveniles and females represented above the line, males below. A total of 104 shrimp from 14 *Bartholomea annulata* were measured.

literature, although Randall (1967) listed unidentified *Periclimenes* in the stomach contents of the yellowtail hamlet, *Hypoplectrus chlorurus*, the barred hamlet, *H. puella*, and the high hat, *Equetus acuminatus*.

Mixed schools of creole wrasse, *Clepticus parrae*, and bogas, *Inermia vittata*, frequently worked parallel to the slope of the reef front where the creole wrasse visited cleaning stations amongst coral on the face of the reef.

Observations in aquaria inside the Habitat indicate that *P. pedersoni* are not altogether dependent upon a fish host for food, although it is generally conceded that cleaning activity furnishes the major portion of food (Feder, 1966).

Live specimens of *Bartholomea annulata* attached to empty conch shells were transferred to small aquaria in the Habitat. Shrimp were introduced to the anemone for the purpose of observing their behavior. No fish were present. After two days, cyclopoid copepods were netted from a swarm in the entry trunk of Tektite and placed in the aquarium. The shrimp were observed to snap the copepods from the water with their chelae and eat them. They may resort to such fare only in the absence of fish to clean.

Mixed swarms of the mysid, *Heteromysis actinae*, and an unidentified brown copepod were observed twice at anemone stations on the sand strip the day after all cleaner shrimp had been removed. The absence of such copepods on all but depopulated anemones may also indicate that the cleaners prey on small copepods.

There was a strong degree of competition among individual shrimp for a prominent position on the anemone. Agonistic behavior between individuals for prominent position was observed in aquaria. The largest individuals stationed themselves on the tentacles or near the oral disc of the anemone while medium and small shrimp occupied positions either aligned around the anemone on the sand or on surrounding vantage points such as coral or branching sponges. This distribution is largely size dependent and was most obvious when large numbers of shrimp were competing for the limited space on a single anemone. It is possible that the large individuals, by virtue of their size and hence their ability to establish a commanding position on the anemone, are better able to attract fish, and the success of the cleaning station may be enhanced by the number of large shrimp present.

Subordinate sized shrimp exhibited relatively passive display behavior when approached by a fish. The smaller shrimp were far less obvious in their positions on the surrounding sand where there was less contrast between the shrimp and their background. Usually, the large shrimp were more active in soliciting fish and were the first to approach a client. At that point all individuals usually joined in cleaning the fish. Similar peck order behavior was noted among individuals of *P. pedersoni* held in the aquarium. At first they quarreled with one another over positions on the anemone. Eventually the largest shrimp won out, occupying the dominant positions on the tentacles or oral disc of the anemone.

SPECULATIONS ON THE EVOLUTION OF CLEANING BEHAVIOR

It is tempting to theorize about the course of behavioral evolution in the genus *Periclimenes* beginning with a casual relationship with the coelenterate as exhibited by *P. americanus* to the close knit dependence and complex cleaning behavior of P. *pedersoni*. *Periclimenes americanus* was found as an occasional associate of *B. annulata*, living around the base of the anemone beneath the protective umbrella of extended tentacles. It was never observed to come in direct contact with the anemone nor to undertake cleaning. The hiding behavior and camouflage of *P. rathbunae* implies a closer but simple commensal relationship, being dependent on *B. annulata* primarily for protection against predation. *Periclimenes rathbunae* did not dance to attract fish, were never observed to undertake cleaning, and when approached by a diver, buried themselves in the tentacles of the host coelenterate.

Periclimenes yucatanicus danced and waved its antennae but was not as active in soliciting fish clients as *P. pedersoni*, and although fish were attracted to the anemone, the shrimp were never observed to clean fish. Limbaugh et al. (1961) has noted some attraction betwen fish and *P. yucatanicus* where contact was momentary and the shrimp did not leave the substrate. He suggested that these shrimp may possibly be mimics and not cleaners. I never saw *P. yucatanicus* leave the protection of the anemone. The purpose of the bright coloration and pre-cleaning behavior remains a mystery.

But the suggested role of *P. yucatanicus* as a mimic of *P. pedersoni* is not altogether satisfactory either. The color patterns are dissimilar, with *P. pedersoni*, bearing predominant longitudinal markings, and *P. yucatanicus*, bearing several distinct saddles and spots. Both species occurred together on anemones on the sand strip and algal plain as often as could be expected on a random basis (X^2 test for independence $P = .05$); therefore no competitive exclusion occurred, and because the species were sympatric, there must be a niche separation—probably in the preferred food organism.

Yet, if *P. yucatanicus* is a mimic then it must be regarded as inimical and competitive with *P. pedersoni*, and the two species should not occur together on the same anemones. An example of mimicry among cleaners has been reported with the blenny, *Aspidontus taeniatus*, mimicking the most common Indo-Pacific cleaner wrasse, *Labroides dimidiatus*, in color pattern and behavior (Eibl-Eibesfeldt, 1959). The blenny imitates *Labroides* in order to approach fish and tear pieces from their fins. The cleaner wrasse attacks *A. taeniatus* when the two meet. Furthermore, *P. pedersoni* can be induced to pick at hairs on a diver's arm as if removing parasites. *P. yucatanicus* does not exhibit such definite cleaning tendencies because it can not be induced to approach a diver.

It has been suggested that the cleaning association could only have arisen between shrimps and fishes in which there was a continued danger of predation by the latter on the former (Davenport, 1966). I suggest that *P. yucatanicus* is not a cleaner but is similar enough in appearance to *P. pedersoni* to be mistaken as such and therefore it occupies an intermediate position between a simple commensal and a true cleaner. Warning coloration may be the purpose of the bright patterns and markings of *P. yucatanicus* as a stage along an evolutionary pathway protecting a potential cleaner from predation prior to the development of true cleaning behavior.

ACKNOWLEDGMENTS

All specimens of *Periclimenes* were identified by Fenner A. Chace, Jr. U.S. National Museum (USNM). The entire collection is in the USNM. The mysid *Heteromysis actinae*, was identified by Thomas Bowman (USNM).

I wish to thank my fellow divers, Edward Clifton, John VanDerwalker, and Richard Waller for their patience and helpful suggestions during Tektite I.