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THE BEHAVIORAL ECOLOGY OF ALPHEUS CLYPEATUS
COUTIÈRE (DECAPODA, ALPHEIDAE).

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THE BEHAVIORAL ECOLOGY OF *ALPHEUS CLYPEATUS* COUTIERE

(DECAPODA, AIPHEIDAE)

A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION OF THE UNIVERSITY OF HAWAII IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN ZOOLOGY MAY 1970

By

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ABSTRACT

The behavioral and ecological adaptations associated with the construction and inhabitance of algal tubes by Alpheus clypeatus are examined. Shelter procurement of this type differs from that of most other alpheid shrimps which utilize shelter, such as crevices in coral or the canals within sponges, that requires little or no modification.

Field collections were carried out regularly over a 15 month period. Data from the field collections reveal that (1) A. clypeatus breeds throughout the year, (2) the greatest number of juvenile shrimps settle on the coral heads in the summer months, (3) the population consists of three size classes and each size class occupies a specific portion of the coral head, and (4) fishes capable of preying on alpheid shrimps occur in the coral heads. Observations on the positions of algal tubes of A. clypeatus within coral heads show that tubes are located in an area not occupied by other species of alpheid shrimps. The ability to utilize a portion of the habitat with reduced levels of interspecific competition is discussed with respect to the adaptive significance of tube construction.

Laboratory observations on A. clypeatus show that tube construction, a continuous process accomplished by the chelate second pereiopods, plays a significant role in pair formation and spacing of the species within the habitat. Intraspecific agonistic behavioral patterns which contain both ritualized and non-ritualized components are described. The influence of algae on agonistic behavior is shown for a number of different combinations of shrimps. The number of snaps produced by all combinations of shrimps, with
the exception of single females, is significantly reduced for a 72 hour period by the presence of algae. Similar experiments of 25 days duration reveal that the presence of algae increases survival between members of heterosexual pairs of shrimps but not between two shrimps of the same sex or groups of three shrimps which consist of two shrimps of the same sex plus one shrimp of the opposite sex. In the latter two situations, the presence or absence of algae makes no difference, because in these longer duration experiments one of the two shrimps of the same sex ultimately is killed.

The adaptive significance of algal tube construction and the associated behavioral patterns is that it permits *A. clupeatus* to utilize the dead coral head habitat to the greatest advantage. The algal tubes increase the exploitable surface area of the coral head, provide the basis for a territorial social system which allows a higher specific population density, and in addition, three species of algae that are present in the tubes are used as food.
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INTRODUCTION

Alpheid shrimps occur throughout the world and occupy a variety of habitats. Their latitudinal limits are set by the 11°C. winter surface isotherm which closely approximates 40° N. and S. latitude (Johnson, Everest, and Young, 1947). Most species are associated with natural shelter which requires no modification. Such habitats include sand, mud, rubble, crevices in live and dead coral heads, sponges, worm burrows, crinoids and echinoids (Banner, 1953; Banner and Banner, 1966b). In contrast Alpheus clypeatus constructs tubes of filamentous algae.

Only a few alpheids are known to construct and inhabit algal tubes. Banner (1953) and Banner and Banner (1966b) reported Alpheus brevipes Stimpson, A. pachychirus Stimpson, A. bucephalus Coutière, and A. clypeatus to live in algal tubes. Cowles (1913) and Fishelson (1966) described the behavior of Alpheus frontalis H. Milne Edwards, but failed to mention the significance of the behavioral adaptations related to tube occupancy.

The present study is an attempt to demonstrate the significance of behavioral adaptations associated with tube construction and occupancy by asking these questions: What behavioral patterns are involved in the construction and maintenance of algal tubes? Which appendages are most important with respect to tube construction? Is there competition for algae? How are members of the species spaced out within the habitat and what behavioral patterns are involved? By what mechanism does pair formation occur? And finally what is the effect of the ability to construct algal tubes on social behavior, especially agonistic behavior?
Behavioral and ecological studies of *A. clypeatus* have not been published and only taxonomic and zoogeographic accounts of the species are available (for example, Coutière, 1905; Edmondson, 1925; Banner, 1953, 1957, 1958; Banner and Banner, 1964, 1966b, 1968b). Literature which deals with other species of alpheid shrimps and relevant work on other species of Crustacea is discussed where pertinent throughout the paper.

ACKNOWLEDGMENTS

The author wishes to express his sincere appreciation to fellow graduate students Paul Struhsaker and David Olsen for their assistance on the statistical treatment of data in the present study. He further wishes to express profound gratitude to his wife and son for their continued encouragement, support, and sacrifice during the course of this research.
MATERIALS AND METHODS

Collection of Animals

Specimens of *A. clypeatus* used in the present study were collected from similar habitats in two locations. Thirty-three of the 36 collections were made on a reef flat in 60–80 ft. of water immediately seaward of Kaneohe Bay, Oahu (lat. 21° 28' 50" N., long. 157° 46' 45" W.). A second area where three of the collections were made was within Kaneohe Bay in water 2–8 ft. (lat. 21° 27' 30" N., long. 157° 47' 0" W.).

Monthly samples for the period of October, 1968, through December, 1969 (except December, 1968, and March, 1969), were collected from the deep site. Each sample consisted of from six to eighteen dead heads of *Pocillopora meandrina* which were overgrown with algae and encrusting organisms. Intact coral heads were removed from the substratum, placed in separate fine mesh bags, and transported to water tables at the laboratory.

Field Data

Water temperature and clarity, and surge conditions were noted at the time of each collection. The density of *P. meandrina*, at the deep site, was determined from 40 photographs of 685 m² of the bottom. A three meter long scale was used for size reference.

Field Experiment

Estimates of the effectiveness of cover provided by the habitat, with respect to predation, were obtained in two ways: (1) shrimps were deprived of all cover by destruction of the coral head and
(2) intact algal tubes with shrimps inside were taken from coral heads and allowed to drift freely over the reef flat for five minutes. Each experiment was repeated 20 times over a 12 month period.

Treatment of the Collections

The volume of each coral head was estimated by the product of the linear dimensions (L x W x H). Coral heads were then broken apart for removal of the algal tubes and shrimps. Each tube complex together with the shrimps found inside was placed in a separate container. The occurrence of other species of alpheid shrimps and fishes in the coral head was noted. These data were recorded for each specimen of *A. clupeatus*: (1) sex, (2) size (carapace length in mm measured from the tip of the rostrum to the posterior border formed by the joint of the first abdominal segment), and (3) number of eggs carried by gravid females. Additional measurements of 10% of the shrimps in each sample included snapping claw length (greatest distance between anterior and posterior extremities of the detached chela) and abdomen length (from the posterior border of the carapace to the posterior border of the telson excluding setae). Data recorded for each algal tube complex included (1) position in coral head (either at the tips of the coral branches or deep within the interstices formed by the branches), (2) wet weight (weight in grams after tube complex had been placed between several layers of paper toweling for five minutes), and (3) outside diameter of one tube in the complex (the portion measured was estimated to be midway between the largest and smallest diameters of the complex).
The algal tubes and the gut contents of the shrimp were examined microscopically. The different genera of algae and their relative abundance in each case were determined. The gut contents of 23 fishes, found within the coral heads, were examined for crustacean remains.

Orientation to and Choice of Algae

The ability of _A. clupeatus_ to select certain species of algae was tested in a Y-maze (modified from Davenport, 1966) where experimental animals were presented various algae. Four groups of experimental animals were treated as follows: (1) 18 were starved for 30 days; (2) 18 were exposed to algae, normally used for tube construction, for 56 days; (3) 18 were exposed to a brown filamentous alga, which was not normally used for tube construction, for 56 days; and (4) 18 were exposed to a green non-filamentous alga, which was not used for tube construction, for 56 days. Each shrimp was tested in the maze three to four times. Algal choices were reversed every five runs to insure that the shrimp's orientation was a result of the stimuli provided by the algae rather than some other cue in the maze. For each run the shrimp's size and sex, algal choice, and length of time to complete the choice were recorded.

The Y-maze (Fig. 1) was constructed of plexiglass. Preliminary trials revealed that shrimps followed the corner created by the side and bottom of the maze, this introduced a bias at the choice point, therefore a sand bottom and baffles were added which effectively removed the bias. An equal number of control animals
Figure 1. Y-maze used to test the ability of *A. clipeatus* to discriminate chemically between different genera of algae. A. Water inlet. B. Position of algal sample. C. Plastic screen. D. Choice point. E. Baffles. F. Release point. G. Water outlet.
were then observed oriented to either the right or left arm of the maze. The completed maze was placed in the upper 1/3 of an Aqua Flair plastic aquarium that had the top and sides covered with white paper. Sea water taken directly from the system at the laboratory supplied each arm of the maze at a constant 100 ml/min. Samples of algae were placed in the tip of each arm and held there by a plastic screen.

Construction of Algal Tubes

To study the manner in which _A. alveatus_ constructs tubes of filamentous algae normal or ablated shrimps of either sex were placed in test chambers with specially prepared algae. The prepared algae consisted of algal tubes which had been removed from the coral heads and homogenized in a Waring blender with sea water for 30 seconds. The shredded tubes (hereafter referred to as prepared algae) were rinsed of all extraneous debris. The amount of algae given to each shrimp was determined by the relationship between shrimp size (carapace length) and algal tube wet weight (Fig. 5).

The various stages of tube construction were recorded by time lapse motion picture photography with the Sage series 500 cinephotomicrographic apparatus and Bolex H16M camera. Individual shrimps were placed in each of four compartments of a plastic aquarium (22.3 x 17.5 x 6.4 cms) with prepared algae. Light (44 foot candles) was supplied by two fluorescent bulbs that were left on for the duration of each experiment (10--40 hrs).

Close-up (0.2--1.0 object to image ratio) motion pictures of the appendages used in tube construction were obtained with a Bolex
Hi6 Rex camera and 25 mm lens with 5 mm extension tube. Light (100 foot candles) was supplied by a fluorescent ring light.

Shrimps were placed in plastic containers constructed to conform to the field size of the lens and camera. To determine which appendages were most important for tube construction five ablations were performed: both chelae, second, third, fourth, or fifth pereiopods. Intact shrimps served as controls. The appendages were ablated by grasping them with forceps until they were autotomized. Experimental animals were placed in test chambers with prepared algae. Appendage changes, through successive molts, and the success or failure to construct tubes were noted.

Sound Production and Agonistic Behavior

To more clearly understand the snapping mechanism of *A. olypeatus*, two experiments involving modification of the chela were performed: (1) deformation of the propodal oval disc surface and (2) removal of the plunger from the dactylus. The experimental animals were then held in test chambers for a minimum of 24 hours before they were subjected to stimuli that usually released snapping. Any changes in the ability to produce snapping sounds and intensity of noise produced were noted.

Agonistic behavioral patterns were studied with the aid of close-up (0.2–1.0 object to image ratio) motion pictures and video tape recordings. Two shrimps, usually males of approximate the same size, were placed in a plexiglass container that conformed to the field size of the lens and camera used. Light was supplied by the fluorescent ring light. Damage inflicted upon combatants and the
The influence of Algae on Agonistic Behavior

Since snapping sounds accompany agonistic interactions, the number of snaps per unit time and the relative intensity were recorded for 12 different combinations of shrimp and algae. The recordings were made in a test chamber to which a Sony model F-7B microphone was attached. The test chamber was suspended by rubber bands inside a portable ice chest with a clear plexiglass top. Signals from the microphone were fed into a Heathkit model EA-2 amplifier and subsequently into a rectifier circuit. The rectified signals were converted into permanent graphic records by a Texas Instruments model 2990 rectilinear recording milliammeter. Continuous records of snapping activity were made for 72 hours. Light intensity (40 foot candles) was equivalent to that measured in the field. The photoperiod was 13 hours and coincided with natural daylight.

To measure the influence of algae on the survival of shrimps eight experimental combinations were tested. Each combination consisted of two parts (1) with algae present and (2) without algae. Each of the 16 parts was repeated an average of 22 times. The duration of each replicate was 25 days unless death ensued. Test chambers were utilized for all combinations of shrimp. In those experiments which included algae an amount of algae, double that found in nature, was determined by the relationship between shrimp size (carapace length) and algal tube wet weight (Fig. 5).

Pair Formation

To study pair formation in A. clypeatus four or eight small
(1.5—3.5 mm carapace length) shrimps, known to be unpaired, were placed in a test chamber with their original tubes plus an amount of prepared algae equivalent to one-half the wet weight of the original tubes. Other groups of similar individuals were removed from their tubes and placed in test chambers with an amount of prepared algae equivalent to twice the wet weight of the tubes. Tube construction, individuals expelled from tubes or killed, and the pairs formed were recorded for 30 days.

Intermolt Period

The intermolt periods of individual shrimps and heterosexual pairs of shrimps were recorded for 120 days. Either a single shrimp (N = 15) or a pair of shrimps (N = 17 pairs) was placed in a test chamber with an amount of algae determined by the relationship between shrimp size (carapace length) and algal tube wet weight (Fig. 5). The experiments were carried out in an air-conditioned room where the maximum temperature range was 4°C (22—26°C).
RESULTS

Description and Distribution of \textit{A. clypeatus}

\textit{Alpheus clypeatus} was originally described by Coutière (1905) from specimens obtained in the Maldive Archipelago in the Indian Ocean. More recently, Bamber (1953) has given a description of the external morphology based on specimens from the Hawaiian Archipelago. Widely scattered collections (Table I) suggest that the distribution of \textit{A. clypeatus} extends southwest from the Hawaiian Archipelago through Micronesia to the Indian Ocean. Further collections, if made in the habitat of \textit{A. clypeatus}, are likely to extend the known distribution throughout most of the tropical Pacific and Indian Oceans.

Habitat

A discussion of the physical and biological characteristics of the habitat where \textit{A. clypeatus} occurs must involve those factors that affect the survival of \textit{P. meandrina} since its presence appears to be a basic requirement for the occurrence of \textit{A. clypeatus}.

Physical Characteristics

Certain physical characteristics of the habitat are variable while others remain more constant. The variable characteristics include depth, light, surge, and substratum. Depth, although relatively constant for a given location, is considered to be variable in this case because the habitat extends over a depth range of 2--80 feet. Light varies inversely with depth and amount of particulate matter suspended in the water (Raymont, 1963).
### Table I. Locations Where Specimens of *A. Clypeatus* Have Been Collected

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<td>Personal collection, 1967</td>
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Jerlov (1951) has shown that nearly 55% of the total solar energy is absorbed in the first meter of clear ocean water and approximately 82% is absorbed in the first 20 meters. These data suggest that twice as much light is present in shallow (2-8 ft) areas as compared to deep (60-80 ft) areas of the habitat. Surge, produced by surface waves, also varies inversely with depth (Odum and Odum, 1955; Moore, 1958). Shallow areas receive relatively strong surges of short duration while deeper areas are subjected to more gentle surges of longer duration. The substratum in shallow water consists of loose coral rubble and sand. In deeper water the substratum is primarily hard, flat limestone with occasional small pockets of sand.

Temperature is one of the more stable characteristics of the habitat. Monthly records at the deep site indicate a range from 24.0-26.5°C over a period of 15 months (Fig. 2). The few temperature measurements taken in shallow water averaged 2.0°C higher.

The above characteristics describe much of the inshore area of Oahu, Hawaii. Observations on some of these areas (Fig. 3) revealed the presence of *P. meandrina* and *A. clypeatus*. Such observations indicate that the most important physical aspect of the habitat, with respect to *P. meandrina*, is rapid water movement. Calm bodies of water, such as the shoreward portions of Kaneohe Bay, are not suitable for the growth of *P. meandrina*. Although other physical characteristics of the water appear adequate, the lack of relatively strong water movement apparently precludes establishment of this coral.
FIGURE 2. WATER TEMPERATURES MEASURED AT THE DEEP SITE (60 FT) BETWEEN OCTOBER, 1968, AND DECEMBER, 1969. DASHED LINES INDICATE ABSENCE OF DATA.
FIGURE 3. CHART OF OAHU, HAWAII, STATIONS WHERE P. MEANDRINA AND A. CLIPERATUS WERE OBSERVED.

Biological Characteristics

Biological factors that contribute to the formation of the habitat are varied and complex. No attempt has been made to account for all the factors and interrelationships associated with the habitat. Rather, those factors more directly related to the presence of *A. clypeatus* are described.

CORAL: The most important biological factor for the presence of *A. clypeatus* is the presence of dead heads of *P. meandrina*. The interstices in this type of coral are selected by *A. clypeatus* significantly more often than other spaces in the environment. For example, only seven shrimps, out of more than 1200 collected, were not in *P. meandrina* coral heads. An indication of the amount of available habitat space is shown by the crude density (Odum, 1953) and size frequency distribution (Fig. 4) of *P. meandrina* at the deep site. A distinction, in this case, must be made between live and dead coral heads because live heads have little or no algae present and are not occupied by *A. clypeatus*. The crude density for live coral heads is 0.14/m² and that for dead coral heads is 0.10/m².

Examination of the dead coral heads revealed that they can be categorized into four general groups based on the type and amount of encrusting material on the branches. Coral heads in the first group are completely devoid of live *P. meandrina* polyps and are covered with a thin (1 mm) layer of encrusting organisms. This condition is associated with small quantities of filamentous algae and proportionately fewer (0-3) algal tubes. The second group consists of coral heads in which the branches are covered with a
FIGURE 4. RELATIONSHIP OF NUMBER OF ADULT A. CLYPEATUS TO ESTIMATED VOLUME OF P. MEANDRINA CORAL HEADS. INDICATED BY THE REGRESSION LINE $\hat{y} = 0.2596x + 2.084$. $N = 113 \quad p < .001 \quad r^2 = 35.8\%$. DOTTED LINE SHOWS RELATIONSHIP BETWEEN THE SPECIFIC DENSITY OF SHRIMPS AND ESTIMATED CORAL VOLUME. LOWER PORTION OF GRAPH SHOWS THE SIZE-FREQUENCY DISTRIBUTION OF CORAL COLLECTED FROM THE DEEP SITE. THE 95% CONFIDENCE LIMITS ARE SHOWN BY THE DASHED LINES.
NUMBER OF SHRIMPS

SPECIFIC DENSITY (SHRIMPS/UNIT HABITAT SPACE)

ESTIMATED VOLUME OF CORAL HEAD (cm^3 x 10^3)

NUMBER OF CORAL HEADS

0

0.5

1.0

15

20

25

30

35

40

0

5

10

15

0

10

0.0

0.5

1.0
layer of encrusting organisms approximately 1 cm thick. Generally the outer portions of the branches are more thickly encrusted with various species of macroscopic algae while the inner portions are covered with a thin layer of bryozoans, tunicates, sponges, and small bivalve molluscs. The inner branch area also contains several species of filamentous algae that are utilized by *A. clypeatus* in tube construction. The greatest number of algal tubes (0--8) occurs in coral heads of this type. The third group contains coral heads that are heavily encrusted with macroscopic algae on the outer portions of the branches. On some areas of the coral head these encrustations completely cover the spaces between branch tips and eliminate light penetration to the deeper interstices. This coral reveals little or no change with respect to the fauna encrusting the inner branches; however, very small quantities of filamentous algae and no algal tubes are present in these areas. Coral heads in the fourth group are from shallow (2--8 ft) areas exposed to increased surge conditions. Much of the encrusting material is *Porolithon*, a coralline alga. The outer portions of the branches are more heavily encrusted, often to the point where interstices between branches are nearly filled in. Relatively small amounts of filamentous algae are to be found in this environment and as a result fewer (0--3) algal tubes are present.

**ALGAE:** The algal tubes of *A. clypeatus* are constructed of seven species of algae, each of a different genus (Table II). The most abundant alga represented is *Acrochaetium*, which accounts for approximately 97% of the algae present. The percentages of the
<table>
<thead>
<tr>
<th>PHYLA</th>
<th>GENERA</th>
<th>RELATIVE ABUNDANCE IN SAMPLE</th>
<th>USE</th>
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</thead>
<tbody>
<tr>
<td>Phaeophyta</td>
<td>Sphacelaria</td>
<td>&lt;1%</td>
<td>Tube construction and food</td>
</tr>
<tr>
<td>Rhodophyta</td>
<td>Acrochaetium</td>
<td>~97%</td>
<td>Tube construction and food</td>
</tr>
<tr>
<td></td>
<td>Ceramium</td>
<td>~1%</td>
<td>Tube construction</td>
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<tr>
<td></td>
<td>Falkenbergia</td>
<td>&lt;1%</td>
<td>Tube construction</td>
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<tr>
<td></td>
<td>Goniotrichum</td>
<td>&lt;1%</td>
<td>Tube construction</td>
</tr>
<tr>
<td>Cyanophyta</td>
<td>Lyngbya</td>
<td>&lt;1%</td>
<td>Tube construction and food</td>
</tr>
<tr>
<td></td>
<td>Microcoleus</td>
<td>&lt;1%</td>
<td>Tube construction</td>
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seven species of algae which make up the tubes remain relatively constant between the deep and shallow collection sites. The amount of algae, however, does vary with depth. This is shown by a comparison of the number of adult A. clypeatus that inhabit shallow water coral heads as opposed to deep water coral heads. The mean number of shrimps per coral head in shallow water is 3.10 while in deep water the mean number is 6.60 (based on 20 coral heads from each site).

The species of filamentous algae are more abundant in portions of the habitat that are shielded from herbivorous fishes. Jones (1968) has shown that five of the seven species of algae present in algal tubes are ingested by fishes of the Acanthurus, Zebrasoma, and Naso genera, and that Acrochaetium accounts for an abundant proportion of the algae ingested by certain members of the genus Zebrasoma. The effect of algal ingestion by these fishes is shown by a comparison of the amount of Acrochaetium present inside and outside the coral head. Algal patches within the coral head may exceed 5 cm² in area while patches on the exposed periphery rarely exceed an area of 2 cm². Similarly, the mean length of the algal filaments is greater for shielded areas (7 mm) as opposed to peripheral areas (2 mm). The other species of filamentous algae were not observed in patches but were physically entangled in abundant Acrochaetium filaments.

The growth rate (mean filament length increase / 24 hrs) of Acrochaetium in the laboratory is approximately 0.8 mm / filament / 24 hrs. This growth rate may represent a maximum since the algal
samples measured were isolated from all macroscopic herbivores.

Utilization of Algae

Filamentous algae fulfill two basic requirements with respect to the survival of *A. clypeatus*, those of food, and of material utilized in tube construction.

Inspection of the contents of the esophagus and cardiac portion of the stomach revealed that these species of filamentous algae, each representing a different genus, were utilized as food (Table II). The gut of individual shrimps contained an abundance (95-100%) of a single species of alga (*Acrochaetium* or *Sphacelaria*) and small amounts (0-5%) of a second species of alga (*Lyngbya*). There were no apparent distinctions between shrimps which fed predominantly on *Acrochaetium* and those which fed on *Sphacelaria*.

The ability of *A. clypeatus* to utilize filamentous algae in construction of shelter appears to be an important factor with respect to the successful occupancy of dead coral heads. The amount of algae utilized in tube construction is dependent upon two factors, the size of the shrimp and the amount of algae present in the habitat. The curvilinear regression line (Fig. 5) indicates that the amount of algae increased exponentially with the shrimp's size (carapace length). For example, a small shrimp (3.5 mm) may utilize 0.32 gm (wet weight) of algae while a shrimp double that size may utilize nearly 12 times more algae. Large variations in the amount of algae utilized suggest that algae may be a limiting factor in some circumstances.
FIGURE 5. RELATIONSHIP OF ALGAL TUBE WET WEIGHT TO CARAPACE LENGTH IN A. CLYPEATUS, INDICATED BY CURVILINEAR REGRESSION LINE

$\log_{10} Y = 0.3059X + 0.4378$  
$N = 116$  
$P < 0.001$  
$r^2 = 59.3\%$
Spatial Relationships

Spatial relationships between individuals in a population of *A. clupeatus* continually change. Adult shrimps were studied because they represent a more stable element of the total population, they occupy well established tubes within the coral heads, and they do not exhibit the large seasonal changes in numbers as do young shrimps (Fig. 6).

The amount of habitat space available to adult shrimps increases with coral head size. The specific density of the shrimps, however, varies inversely with coral size (Fig. 4). The regression line ($\hat{Y} = 0.2596X + 2.084$) indicates that the ratio of increase in number of shrimps / $1000 \text{ cm}^3$ of estimated coral volume is 0.26:1.0. These data suggest that large coral heads contain more shrimps than do small coral heads, and shrimps which occupy large coral heads may be spaced out to a greater extent in the habitat. Similar conclusions can be drawn from a regression of number of pairs of shrimps on coral size (Fig. 7). The above relationships indicate that habitat space is not a limiting factor with respect to the number of shrimps able to survive in a given coral head.

A comparison of the sizes of shrimps and the coral heads from which they were collected (Fig. 8) reveals that shrimp size varies independently of coral size. This is to be expected, since shrimps increase in size with the passage of time and the presence of an adequate food supply. Conversely, dead coral heads would not be expected to change in size over long periods of time.

The algal tubes constructed by *A. clupeatus* appear to be variable in most aspects. Two of these aspects, however, which relate to
FIGURE 6. TOTAL VARIATION IN NUMBERS OF JUVENILE (CARAPACE LENGTH UP TO 3 mm) AND ADULT (CARAPACE LENGTH GREATER THAN 3 mm) A. CLYPEATUS IN INDIVIDUAL CORAL HEADS OVER A PERIOD OF 15 MONTHS. N = 125 CORAL HEADS. DATA NOT AVAILABLE FOR DECEMBER, 1968, AND MARCH, 1969.
FIGURE 7. RELATIONSHIP OF NUMBER OF PAIRS OF *A. CLYPEATUS* TO ESTIMATED VOLUME OF *P. MEANDRINA* CORAL HEADS. INDICATED BY REGRESSION LINE

\[ \hat{Y} = 0.1142X + 1.1615 \quad N = 120 \text{ PAIRS OF SHRIMPS} \quad P < .001 \quad r^2 = 55\% . \]

DOTTED LINE SHOWS RELATIONSHIP BETWEEN SPECIFIC DENSITY OF PAIRS OF SHRIMPS AND ESTIMATED CORAL VOLUME. THE 95% CONFIDENCE LIMITS ARE SHOWN BY THE DASHED LINES.
Figure 8. Relationship of carapace length of A. Clypeatus to estimated volume of P. Meandrina coral heads. The solid vertical lines represent the range of carapace lengths for each group of coral volumes. The rectangles superimposed on the vertical lines represent two standard errors of the mean, and the horizontal line that cuts through each rectangle indicates the mean carapace length for each group of coral volumes.
LEGEND:
- RANGE
- MEAN
- 2 STANDARD ERRORS OF THE MEAN

SHRIMP SIZE (CARAPACE LENGTH, mm)

ESTIMATED VOLUME OF CORAL HEAD (cm$^3$ x 10$^3$)
space utilization in the habitat, remain relatively constant. Most tubes are constructed in the interstices of the coral head that occur midway between the tips and bases of the branches. Algal tubes in this position are protected, to some degree, against predation as well as tube damage by herbivorous fishes. Once established, the tubes are continually increased in length and randomly branched. Unlike *Alpheus frontalis*, which constructs tubes with an enlarged chamber at one end (Cowles, 1913; Schmitt, 1931, 1965), *A. clypeatus* tubes remain relatively uniform in diameter throughout the entire length. The tube diameter, however, increases with shrimp size as shown by the regression line ($\hat{Y} = 1.39X + 6.12$) (Fig. 9).

**Population Structure**

**Occurrence of Size Classes**

The 13 monthly samples of shrimps, taken over a 15 month period, provide a basis for the interpretation of the structure of *A. clypeatus* populations. Size-frequency histograms of each monthly sample suggest that the population is bimodally distributed and this is confirmed with the use of probability paper (Harding, 1949). The two size means, taken directly from the probability paper, and plotted with respect to time of year, remain well separated. The mean size of the larger shrimps is always greater than 4.5 mm (carapace length) while the mean size of smaller shrimps never exceeds 3.0 mm (carapace length) (Fig. 10).

The intermediate size class is more difficult to represent because the shrimps appear to be transient. That is, shrimps in this size class may be present in areas of the coral head where
FIGURE 9. RELATIONSHIP OF ALGAL TUBE OUTSIDE DIAMETER TO CARAPACE LENGTH IN A. CLYPEATUS. INDICATED BY THE REGRESSION LINE $\hat{y} = 1.39x + 6.12$. THE 95% CONFIDENCE LIMITS ARE SHOWN BY THE DASHED LINES. N = 162 P < .001 $r^2 = 72\%$
FIGURE 10. MONTHLY PROBABILITY MEANS FOR THE ADULT (UPPER CURVE) AND JUVENILE (LOWER CURVE) CLASSES WITHIN THE POPULATION. CUMULATIVE PERCENTAGES OF EACH SHRIMP'S CARAPACE LENGTH IN EACH MONTHLY SAMPLE WERE PLOTTED ON PROBABILITY PAPER AND THE MEAN LENGTHS WERE READ ON THE ABSCISSA ACCORDING TO THE METHOD OF HARDING (1949). SAMPLE SIZES ARE SHOWN ACROSS THE TOP OF THE GRAPH. DASHED LINES REPRESENT MISSING DATA.
either adult or juvenile shrimps normally occur. Also algal tubes
constructed by the intermediate shrimps often correspond very closely
in size and shape to those constructed by adult and juvenile shrimps.

Carapace measurements of shrimps in the monthly samples indicate
the presence of intermediate sized shrimps; however, these data are
not sufficient to establish a valid size class. Two other sources
of information suggest the presence of an intermediate size class
and allow arbitrary size limits (carapace length) to be set. First,
the probability paper analyses graphically indicate the intermediate
size class but only for the winter and spring months of the year
(November through May). Secondly, the plot of the two size means
(Fig. 10) and the probability analyses suggest that the size of the
shrimps which make up the intermediate class should be greater than
3.0 mm and less than 4.5 mm (carapace length). On this basis each
monthly sample is separated into three size classes: (1) juveniles,
0--3.0 mm (carapace length, (3) intermediates, 3.5--4.0 mm (carapace
length) and (3) adults, 4.5--7.5 mm (carapace length). Figure 11
shows the percent composition of each size class for each of the
monthly collections.

Seasonal Variation in Size Classes

The data reveal several variations that occur within the three
size classes of the population. The most obvious change is the
increase in number of juvenile shrimps that appear on the coral
heads throughout the months of June, July, and August. The data
for the juvenile size class in Figure 10, 11, and 12 show the
increase in number of juvenile shrimps and the effect this has on
FIGURE 11. MONTHLY PERCENT COMPOSITION OF THE THREE SIZE CLASSES OF SHRIMPS WITHIN THE POPULATION. DASHED LINES REPRESENT MISSING DATA. SIZES REPRESENT CARAPACE LENGTHS.
Figure 12. Monthly comparison of the mean number of algal tubes constructed by adult shrimps to the mean number algal tubes constructed by juvenile shrimps per coral head. Dashed lines represent missing data.
the population structure. For example, there is a decrease in the mean size of juvenile shrimps (Fig. 10) that is most pronounced in the summer months. This decrease in mean size is probably brought about by the influx of younger individuals recently settled from the plankton. Further evidence is given by the change in percent composition of the juvenile class within the population (Fig. 11). The population consists of only 10--15% juveniles for the winter months. With the approach of spring and summer, however, there is a continuous increase until the juvenile shrimps represent nearly half (45%) of the total population. A more direct representation of the summer peak in the juvenile size class can be shown by a plot of the mean number of algal tubes per coral head, constructed by juvenile shrimps, for each month (Fig. 12). The algal tubes of juvenile shrimps have a characteristic size and location on the coral head and can be distinguished from algal tubes of adult shrimps. Again the results show a greater number of juvenile algal tubes, and hence juvenile shrimps, for the summer months.

The intermediate size class, when represented as a percent of the total population, is most conspicuous in the winter and spring of the year (Fig. 11). Shrimps within this size range constitute 28--33% of the population in January and February, then decline to a minimum of 5% in June.

The adult class of shrimps appears to be the most stable with respect to seasonal variation in numbers. The small increase in mean size (\( \sim 0.75 \text{ mm} \)) which occurs from February to August (Fig. 10) probably represents growth since there are no other larger size classes in the population that can filter into the adult class and
cause an increase in mean size. When plotted as a percent of the total population (Fig. 11), the adult size class shows a yearly variation (30%) nearly equivalent to that of the juvenile class (35%). It must be remembered, however, that when percentages are used a variation in one portion of the population will cause another portion of the same population, which does not vary, to mirror the effect. In this case, the large seasonal variation in numbers of juvenile shrimps is responsible for the characteristics of the adult size curve (Fig. 11). Further evidence for the relative stability of the adult size class is shown by a plot of the mean number of algal tubes, constructed by adult shrimps, that occur in the coral heads each month (Fig. 12).

**Location of Size Classes in the Coral Head and Growth of Shrimps**

The smallest shrimps in the coral heads have carapace lengths of 1.0–1.5 mm. The carapace lengths of 27 larvae of *A. clupeatus*, which had completed five molts after hatching, averaged 0.75 mm. This suggests that shrimps with carapace lengths of 1.0–1.5 mm have recently settled from the plankton and may represent the first postlarval form.

Almost without exception the juvenile shrimps occupy a more peripheral position on the coral head than do adult shrimps. Juvenile shrimps are able to utilize the relatively small amount of filamentous algae present on the branch tips of the coral head and thus gain a foothold. Often the algal tubes of the small shrimps are associated with a larger algal thallus or coral crevice which may afford protection immediately upon settlement. Generally the algal tubes of the juvenile shrimps are constructed such that the
longitudinal axis of the tube corresponds to that of the coral branch. Construction of the tube then proceeds in a direction toward the center of the coral head.

Juvenile shrimps appear to be sexually immature until a carapace length greater than 3.0 mm is attained (Fig. 13). Field data reveal, however, that male-female pair formation can occur in shrimps with carapace lengths as small as 2.0 mm. This suggests that pair formation may occur soon after settlement of the post-larvae. Laboratory studies of pair formation confirmed the occurrence of sexually immature pairs (p. 84).

Data shown in Figures 11 and 12 suggest that the transition from recently settled juvenile shrimps to intermediate shrimps may take 3–5 months. That is, the length of time that elapses between summer (June, July, and August) postlarval settlement (Fig. 12) and the early winter (November) increase of the percent composition values for the intermediate size class (Fig. 11). Throughout this period the shrimps' carapace length increases to 3.5–4.0 mm, the algal tubes show an increase in length and number of branches, and pair formation occurs. Data from monthly population samples indicate 50% (Fig. 14) of the shrimps in the intermediate size class are members of male-female pairs while 9% of the juvenile shrimps and 93% of the adult shrimps are pair members. With completion of pair formation intermediate shrimps are equivalent to adult shrimps in all but two aspects: (1) size (carapace length) and (2) position of the algal tube within the coral head.

Unlike intermediate shrimps, which are found in both peripheral and central locations within the coral head, adult shrimps generally
FIGURE 13. RELATIONSHIP OF NUMBER OF EGGS CARRIED TO CARAPACE LENGTH IN FEMALE A. CLYPEATUS. THE REGRESSION LINE IS REPRESENTED BY
\[ \hat{Y} = 77.3 x -271.4. \] THE 95% CONFIDENCE LIMITS ARE SHOWN BY THE DASHED LINES. N = 115 P < .001 \( r^2 = 45.8\%. \)
occupy the more central portions of the coral heads. Once this central location is attained the algal tubes are often constructed with an orientation that is perpendicular rather than parallel to the longitudinal axis of the coral branches. This change in orientation allows further expansion of the algal tubes without displacement from the central location.

The smallest values for the mean size of shrimps in the adult size class (Fig. 10) appear in the months of January and February. Similarly, the highest values for the percent composition of intermediate shrimps (Fig. 11) are found in January and February. These data suggest that the greatest number of intermediate shrimps are present in the population and may enter the adult size class at this time. The increase in mean size of adult shrimps (Fig. 10) and decrease in percent composition of intermediate shrimps (Fig. 11) after February give further evidence of the seasonal transfer of intermediate shrimps into the adult size class. It appears then, that juvenile shrimps, which settle on coral heads throughout the summer (June, July, and August), can complete the transition to adult shrimps by late winter (February), a period of 6-8 months.

Reproductive Potential

**Breeding**

In the present study breeding is defined as the percentage of ovigerous female shrimps present in the population at any given time (Reese, 1968). To more clearly represent breeding activity a distinction is made between sexually mature and immature female shrimps based on the data shown in Figure 13. Female shrimps with
carapace lengths less than 3.5 mm are considered to be sexually immature.

Populations of *A. clupeatus* do not exhibit any periods of greatly increased or decreased breeding activity throughout the year (Fig. 15). Rather the sexually mature shrimps appear to breed continuously, since a mean of 89% (arithmetical mean of the upper curve shown in Fig. 15) of the female shrimps are ovigerous at any given time of the year. If all the female shrimps, sexually mature or not, are taken into account, the mean value is reduced to 64% (arithmetical mean of the lower curve shown in Fig. 15).

**Fecundity**

The number of eggs carried by female shrimps varies greatly. Shrimps of the same size may carry between 6 and 325 eggs. Generally, the number of eggs increases with respect to size (Fig. 13) (Lindberg, 1955). The regression coefficient for the line in Figure 13 indicates that an increase of 77.3 eggs accompanies each 1.0 mm increase in carapace length after sexual maturity is reached. It is of interest to note that egg diameter (0.5 mm) at the time of laying remains very nearly the same for both large and small female shrimps. These data indicate that the number of eggs a given female shrimp can carry is related to the shrimp's size.

A second factor which affects the variability of the number of eggs carried by female shrimps is egg growth. Data on egg dimensions (0.5 x 0.5 mm--0.6 x 1.0 mm) indicate that a volume increase of the egg of approximately 100% occurs between the time of laying
FIGURE 15. PERCENTAGE OF OVIGEROUS FEMALE SHRIMPS WHICH OCCUR IN MONTHLY SAMPLES. CLOSED CIRCLES (●) REPRESENT PERCENTAGES FOR SEXUALLY MATURE FEMALE SHRIMPS AND OPEN CIRCLES (○) REPRESENT PERCENTAGES FOR THE TOTAL NUMBER OF FEMALE SHRIMPS. THE TOTAL NUMBER OF FEMALE SHRIMPS, ON WHICH THE PERCENTAGES ARE BASED, ARE SHOWN ACROSS THE TOP OF THE GRAPH.
The diagram shows two line graphs with the following data:

- **% Ovigerous Females**:
  - Solid line with data points: 100, 90, 80, 70, 60, 50
  - Dashed line with data points: 100, 90, 80, 70, 60, 50

- **Sample Size**:
  - Data points: 17, 20, 0, 44, 26, 0, 18, 46, 66, 103, 86, 51, 42, 26, 26

The graphs are plotted against the months of 1968 and 1969, with the x-axis labeled as **Time (Months)**.
and before it hatches. The increase in egg volume renders the pleopods and pleuron portion of the abdominal segments less effective in egg protection and those eggs attached to the outside edges and tips of the pleopods are subject to increased environmental abrasion and possible destruction.

**Influence of Eggs on Intermolt Period**

Measurements of 89 intermolt periods of 49 intermediate and adult shrimps (34 of which were sexually paired) reveal a mean value of 30.4 days and a range of 13 to 61 days. In female shrimps it appears that the length of the intermolt period is governed by the presence of eggs, because the exoskeleton is never cast off before the eggs have hatched. Further evidence of molt inhibition in ovigerous females is shown by the rapidity with which the molt process takes place after the eggs have hatched. Generally, ecdysis follows within 24 hours of hatching and, in some cases (30%, N = 11 pairs of shrimps), new eggs are laid within this period. Thus it seems that adult female shrimps can undergo the physiological changes antecedent to the molt process and produce a new batch of eggs within the 30.4 day mean intermolt period.

A consideration of the three factors (year around breeding, fecundity, and intermolt period) which pertain to the reproductive potential inherent in *A. clupeatus* suggests that high reproductive rates are adaptively significant for species which have planktonic larval stages in their life cycle.
 Predation

Field observations suggest that fish probably are the major predators on alpheid shrimps. Often the removal of a coral head from the substratum results in the exposure of shrimps which occupy crevices in the substratum. The exposed shrimps are invariably consumed by fish within a few seconds unless rapid escape movements carry the shrimps to effective shelter.

Of 40 individuals of *A. olypeatus* released on the reef flat without algal tubes, 90% were immediately consumed by reef fishes and 10% survived. The four shrimps which survived did so by rapid escape movements which carried them into a coral crevice in the substratum. In contrast, the release of shrimps in 20 intact algal tubes resulted in 95% survival of the shrimps. Those shrimps which were preyed upon (5%) abandoned their algal tubes as they drifted over the reef flat. Such experiments, although carried out in highly artificial situations that probably arise only rarely in nature, demonstrate the significance of cover in the reduction of predation.

The coral head habitat of *A. olypeatus* probably offers efficient protection from the larger reef fishes which cannot penetrate between the coral branches. Certain fishes, however, are met with in the coral heads and those which belong to three families (Muraenidae, Cirrhitidae, and Scorpaenidae) are the most abundant. The sizes (total length) of the fishes vary from 20--30 mm for the scorpaenids and cirrhitids to 150--180 mm for the muraenids. The largest assemblage of fishes found associated with a coral head consisted of a pair of cirrhitids, a muraenid, and 7 scorpaenids.

An inspection of the stomach contents of 23 fishes (7 muraenids,
4 cirrhitids, and 12 scorpaenids) revealed crustacean remains. Nine (39%) (2 cirrhitids and 7 scorpaenids) of the stomachs contained the remains of alpheid shrimps, but specific identification was not possible. An alpheid carapace (3.5 mm) found in the gut of a scorpaenid (25 mm) is probably close to the upper size limit of prey for these fishes.

Although the presence of *A. clypeatus* is not demonstrated in the gut contents of fishes commonly found in the same habitat, the ability of the fishes to prey on alpheid shrimps is evident.

**Mechanism of Sound Production**

Observations on the snapping claw of *A. clypeatus* reveal that the sound is associated with a rapid closure of the dactylus against the fixed finger of the propodus. The critical factor in sound production is the speed with which the movable dactylus strikes the propodus. The "suction pads" ("oval discs" of Coutière, 1899; Verrill, 1922; Johnson *et al.*, 1947; Knowlton and Moulton, 1963; "adhesive plaques" of Banner and Banner, 1966b) on the opposed surfaces of the dactylus and propodus above the articulation (when the dactylus is extended maximally) apparently act as a latch which holds the dactylus in place against increased muscle tension. A further increase in muscle tension overcomes the restraint of the suction pads and the dactylus closes rapidly and forcefully against the propodus.

The suction pads consist of a thin, transparent, gelatinous-like material which covers the opposed surfaces of the dactylus and propodus. The gelatinous-like material exhibits a morphology
which is similar to a suction cup. That is, the material is soft and flexible, circular in shape and with a slight concavity because the central portion of the pad is lower. The presence of a suction seal between the dactylus and propodus is demonstrated by the resistance to closure of the dactylus even in the detached snapping claws.

The significance of the suction pads in sound production is clearly demonstrated by the complete inability of *A. clypeatus* to produce any characteristic snapping sounds after disruption of the suction pad surfaces (24 shrimps used, 12 male and 12 female). Upon stimulation the experimental shrimps exhibit claw movements which position the dactylus against the suction pad of the propodus. The inability of the suction pads to hold the dactylus in the open position is evidenced by the rapidly repeated attempts of the shrimps to "cock" the claw. The shrimps with disrupted suction pad surfaces are capable of apparently normal sound production after completion of a single molt.

The dactylus of the large chela has on its inner surface a knob-like projection that fits into a socket of the propodus when the dactylus is in the closed position. The plunger-socket mechanism is generally thought to produce a jet of water that accompanies rapid closure of the chela but is not directly responsible for sound production (Knowlton and Moulton, 1963). More recently Castro (1964) has suggested the noise is produced by the rapid entrance of the plunger into the socket.

The results of the plunger ablation experiment reveal that *A. clypeatus* is capable of sound production when the plunger is
removed although the intensity of the sound is decreased. Of 20 shrimps in which the plunger was removed only six were capable of sound production. The other 14 shrimps made no attempt to snap even when exposed to stimuli which previously released snapping.

Agonistic Behavioral Patterns

Agonistic interactions shown by two shrimps of the same sex reveal the presence of three characteristic phases or levels of intensity that generally follow a regular sequence. The three phases are: (1) antennal contact, (2) chelae contact, and (3) contact with physical damage. Hazlett and Winn (1962) have reported a similar agonistic sequence for Alpheus armillatus, A. peasei, and Synalpheus hemphilli.

Observations on two adult (carapace length 4.5 mm or more) male shrimps in the chamber reveal no conclusive evidence for the use of chemical or visual cues for orientation to one another. Upon introduction into the test chamber, the two shrimps begin immediate locomotory movements. Neither shrimp appears to be aware of the other's presence until some type of tactile stimulation is received. Effective stimulation is produced either by direct contact with the second shrimp or by water currents which result from the shrimps' locomotion. Once actual contact is established between the two shrimps a brief period of mutual exploration by use of the antennae ensues. Initially the antennae may touch any part of the other shrimp's body but immediately after this initial contact the antennae of both shrimps are brought into contact. It appears that this period of antennal contact, when the antennae of both
shrimps are rapidly tapped and rubbed against each other (Fig. 16 A), provides enough information transfer to decide which of the two shrimps will be dominant. Antennal contact is maintained at irregular intervals throughout the period of agonistic interactions but in no case is there a reversal of dominance after the initial antennal contact (N = 27 pairs of shrimps).

Immediately after the exchange of tactile stimulation through the antennae the shrimps orient directly to one another such that the anterior portions of the chelae of one shrimp are brought into contact with the anterior portions of the second shrimp's chelae (Fig. 16 B). Once the chelae-contact orientation is established the dominant shrimp, by use of the pleopods and third, fourth, and fifth pairs of pereiopods, begins to push the subordinate shrimp backward. Throughout the period of chela contact both shrimps appear to act in the maintenance of the orientation, although, if the orientation is disrupted (i.e. an escape movement, such as rapid flexion of the abdomen and telson, exhibited by one of the shrimps) the dominant shrimp generally re-establishes the orientation (Fig. 17 A). The shrimps often exhibit what are thought to be "intension movements" (Wynne-Edwards, 1962; Hinde, 1966) while engaged in the chela contact phase of an agonistic interaction. The shrimps show movements in which the chelae are spread laterally, the abdomen is extended fully and raised above the substratum, and the dactyli of the chelae are extended (Fig. 16 A, B). This behavior is similar to that shown by shrimps immediately prior to snapping and therefore may be considered an intention to snap and serves the function of threat. In the confined space of the experimental chamber the only
FIGURE 16. ORIENTATION OF SHRIMPS ENGAGED IN THE ANTENNAL CONTACT (A) AND CHELAE CONTACT (B) PHASES OF AN AGONISTIC ENCOUNTER. DOMINANT SHRIMP INDICATED BY STIPPLING. (TRACED FROM PHOTOGRAPHS)
FIGURE 17. ORIENTATION OF SHRIMPS, (A) WHILE THE DOMINANT INDIVIDUAL RE-ESTABLISHES CHELA-CONTACT, (B) AFTER UNSUCCESSFUL ESCAPE MOVEMENTS, AND (C) ENGAGED IN A HIGHLY AGGRESSIVE ENCOUNTER WITH THE VENTRAL BODY SURFACES OPPOSED. DOMINANT SHRIMP INDICATED BY STIPPLING. (TRACED FROM PHOTOGRAPHS)
observable reaction, on the part of the subordinate shrimp, to threat behavior is to itself show threat. In larger aquaria, however, this threat behavior releases escape movements in the subordinate shrimp.

The relatively constant orientation exhibited by the shrimps throughout the antennal and chela contact phases of agonistic behavior suggests that some type of communication passes between combatants. Such communication may transfer information on sex, size, and readiness to compete of both individuals and may be transmitted through the tactile hairs which are present on the antenna and anterior portions of the chelae (Warden, Jenkins, and Warner, 1934; Cohen and Dijkgraaf, 1961; Green, 1961; Lockwood, 1967).

With continued contact in the experimental chamber, the shrimps enter the third and most destructive phase of aggressive interaction. One or both shrimps may exhibit a higher level of aggressiveness with an increase in the number of snaps directed toward the opponent. Concurrently the chela contact behavior changes from simple contact to an actual grasp of the opponent's appendages. Often the first appendage-grasp movements are the grasping, by the small chela of one shrimp, of the opponent's small chela or long setae located anteriorly on the large chela. Generally the original chela-to-chela orientation is maintained in the early stages of appendage-grasp movements but is soon lost when either shrimp exhibits escape movements, that consist of rapid flexions of the abdomen and telson. The escape movements do not always result in a separation of the combatants. In those cases where the shrimps remain together the orientation between them is usually altered and
allows further agonistic behavior (Fig. 17 B). The large chela, if not grasped by the opponent, is oriented toward or makes direct contact with part of the opponent's body or appendages.

The greatest amount of physical damage is inflicted when the shrimps attain an orientation in which the ventral body surfaces are opposed (Fig. 17 B, C). Shrimps oriented to one another in this way exhibit rapid sequences of activity in which the opponent's appendages are grasped, escape movements are shown, and the large chela is snapped. The extent of damage inflicted upon combatants engaged in agonistic encounters varies from light damage (loss of one or more minor appendages such as the antennae, second, third, fourth pereiopods, and pleopods) to extreme damage (loss of all appendages and portions of the exoskeleton fractured) and death.

Observations on 27 agonistic encounters between shrimps of the same sex show that physical damage is inflicted upon an opponent in at least three ways: (1) smaller appendages (antennae, second-fifth pereiopods, and pleopods) may be grasped by the opponent's large or small chela and removed (autotomy, Bliss, 1960), (2) smaller appendages may be sheared off by the action of the opponents' chelae, and (3) nearly all appendages may be removed and fractures produced in the exoskeleton by direct blows of the opponents' large chela (Fig. 18, 19). Observations made with the aid of motion picture photography reveal that the effectiveness of the large chela depends primarily on the distance between the chelae and the opponent. The large chela has little effect when fired at an opponent that is more than 5 mm away. In this case, the recipient
FIGURE 18. PHOTOGRAPH OF A MALE A. CLYPEATUS (CARAPACE LENGTH 5.0 mm) WHICH SHOWS THE EXTENT OF DAMAGE SUSTAINED WITH PROLONGED AGONISTIC ENCOUNTERS UNDER ARTIFICIAL CONFINEMENT IN THE LABORATORY.
FIGURE 19. PHOTOGRAPH OF THE LARGE CHELA (LENGTH 3.5 mm) OF _A. CLYPEATUS_ WHICH SHOWS A CIRCULAR FRACTURE PRODUCED BY THE DIRECT BLOW OF AN OPPONENT'S LARGE CHELA.
of such a blow is displaced slightly (Fig. 20) by the jet of water produced with rapid closure of the large chela. Reception of the water jet elicits responses (pereiopod movement and/or escape movements) on an irregular basis (43%, \( N = 69 \) observations). With a decrease in the distance between opponents the effectiveness of the large chela is more pronounced. When the two shrimps are engaged in an intense agonistic encounter (Fig. 17 B, C), movements which orient the anterior portion of the large chela against the body of the opponent are observed (Fig. 21). These orientation movements are followed immediately by the rapid closure of the chela with production of the characteristic sound and water jet. The recipient of a direct blow generally releases any hold on the opponent and remains nearly motionless for a short time (1--5 sec.). Continued agonistic interactions lead to the death of the subordinate shrimp in the majority of cases (92%, \( N = 27 \) pairs of shrimps).

Observations on 12 agonistic encounters between juvenile shrimps of the same sex (carapace length 3.0 mm or less) reveal behavioral patterns previously described for the adults. The only observable difference appears to be in the antennal contact phase where antennal contact is more vigorous and prolonged than in adult shrimps.

Length measurements of the large chela and body in 48 female and 56 male shrimps, which represent the normal size range of the population sampled, show that juvenile shrimps are equally prepared for agonistic interactions, with shrimps of similar size, as are adult shrimps. A linear regression of claw length on body length
FIGURE 20. SERIES OF CONSECUTIVE 16 MM MOTION PICTURE FRAMES WHICH SHOWS THE EFFECT OF THE JET OF WATER PRODUCED WITH RAPID CLOSURE OF THE LARGE CHEL.
DURATION OF SERIES .062 SEC.
FIGURE 21. SERIES OF CONSECUTIVE 16 MM MOTION PICTURE FRAMES WHICH SHOWS THE RAPID ORIENTATION AND CLOSURE OF THE LARGE CHELAE AGAINST THE BODY OF AN OPPONENT. DURATION OF SERIES .125 SEC.
(Fig. 22) suggests that the ratio between the claw and body measurements remains nearly stable throughout the growth period. The regression coefficient calculated for male shrimps ($b = 0.7094$) and female shrimps ($b = 0.3329$) indicates that male claw growth, relative to body growth, is more than double ($2.13 \times$) that of the female. Sarojini (1962) obtained similar data from specimens of *Alpheus malabaricus*. These data agree with observations on well established, mature, sexual pairs of shrimps in which the majority of males have a smaller body but larger snapping claw than the females ($77\%, N = 48$ pairs).

**Tube Construction**

One of the most important aspects of successful occupancy by *A. clupeatus* in coral head habitats is the ability of the shrimps to discriminate and utilize specific algae (Table II) which live within the habitat. The results of algal discrimination by *A. clupeatus* in a simple Y-maze suggest that specific algae are selected more often regardless of previous experience. Groups of shrimps exposed to various genera of algae (Table III) for periods of 56 days, or deprived of algae for 30 days, select tube algae, which are normally used for tube construction, in the majority of cases. For example, shrimp held without algae for 30 days choose tube algae in 100\% of the trials ($N = 30$) even though some trials ($N = 20$) include green or brown algae as alternate choices. Exposure of algae-deprived shrimp to maze choices which do not include tube algae reveal that 13\% ($N = 4$) of the shrimps choose green algae and 87\% ($N = 26$) either do not move from the start position in the Y-maze ($N = 25$)
FIGURE 22. THE RELATIONSHIP OF SNAPING CLAW LENGTH TO BODY LENGTH IN MALE AND FEMALE A. CLYPEATUS. FOR MALE SHRIMPS THE REGRESSION LINE IS REPRESENTED BY $Y = 0.7094X - 9.62$, $N = 56$, $P < .001$, $r^2 = 93.0\%$. FOR FEMALE SHRIMPS THE REGRESSION LINE IS REPRESENTED BY $Y = 0.3329X - 7.36$, $N = 48$, $P < .001$, $r^2 = 90.2\%$. 
or choose the side which contains no algae (N = 1).

### TABLE III. GENERA OF ALGAE USED FOR CONDITIONING PERIODS AND FOR Y-MAZE CHOICES

<table>
<thead>
<tr>
<th>SAMPLE DESIGNATION</th>
<th>PHYLA IN SAMPLE</th>
<th>GENERA</th>
<th>RELATIVE ABUNDANCE IN SAMPLE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Red Algae (Tube Algae)</td>
<td>See Table II</td>
<td>Bryopsis</td>
<td>100%</td>
</tr>
<tr>
<td>Green Alga</td>
<td>Chlorophyta</td>
<td>Ectocarpus</td>
<td>~98%</td>
</tr>
<tr>
<td>Brown Algae</td>
<td>Chlorophyta</td>
<td>Derbesia</td>
<td>~1%</td>
</tr>
<tr>
<td>Brown Algae</td>
<td>Phaeophyta</td>
<td>Ectocarpus</td>
<td>~98%</td>
</tr>
<tr>
<td>Brown Algae</td>
<td>Rhodophyta</td>
<td>Phytolalia</td>
<td>~1%</td>
</tr>
</tbody>
</table>

Groups of shrimps exposed to brown and to green algae for 56 days choose tube algae in the majority of trials when it is presented as one of the choices (95%, 57%, N = 21, 21). If tube algae is not present, however, then the majority of shrimps remain at the release point of the maze and do not make a choice (47%, 90%, N = 43, 42). Control shrimps, exposed to tube algae for 56 days, choose this same algae in the majority of the maze choices (93%, N = 71) and no algae for the remainder of the choices.

The ability to construct tube-like shelters from filamentous algae is not widespread among members of the family Alpheidae. To my knowledge, Richters, 1880, cited in Balss (1956), DeMan (1888), Coutière (1899), Cowles (1913), Banner (1953), and Fishelson (1966) mention only five alpheids which inhabit tubes constructed of algae: *A. alpestris* Coutière, *A. bucephalus* Coutière, *A. pachychirus* Stimpson, *A. brevipes* Stimpson, and *A. frontalis* H. Milne Edwards.
The most important appendages, with respect to algal tube construction, are the chelate second pereiopods in which the carpus is subdivided into five secondary articles. These appendages perform nearly all the manipulation of algal filaments associated with tube construction and maintenance. Fishelson (1966), however, mentions that specimens of *A. frontalis* use their maxillipeds in tube construction. The relatively small diameter, length, and high degree of flexibility allow the second pereiopods to easily penetrate the walls of the tube and grasp algal filaments. In no case (*N* = 35) was tube construction observed in either male or female shrimps after ablation of the second pereiopods. If, however, the appendages are replaced with subsequent molts, tube construction is again possible (*N* = 35). The first pair of pereiopods, which carry the larger chelae, may be important in the initial stages of tube construction, although *A. clupeatus* is capable of normal tube construction when the first pereiopods are ablated (*N* = 8).

Laboratory observations on the behavioral patterns involved in tube construction indicate that the shrimps use the second pereiopods almost exclusively. In the initial stages of tube construction algal filaments are collected with these appendages into loosely organized groups. The second pereiopods then readily penetrate between the loose filaments, grasp any free ends of these filaments, and pull them partially back through the same group. This appendage activity crudely weaves the filaments together into a relatively uniform and strong mat (Fig. 23). Once mat formation is begun actual tube construction generally follows either of two procedures. The more commonly observed method (77%, *N* = 87) under laboratory conditions
FIGURE 23. DIAGRAMMATIC SKETCH OF THE METHOD USED BY *A. GLYPEATUS* TO WEAVE ALGAL FILAMENTS. (A) FRESHLY COLLECTED, LOOSELY ORGANIZED FILAMENTS OF ALGAE. (B) CHELATE SECOND PERIOPods PENETRATE BETWEEN FILAMENTS AND PULL LOOSE ENDS BACK INTO GROUP. (C) FINISHED MAT.
involves the initial production of a relatively large and flat algal mat. Once the mat is of sufficient size the shrimps pull and weave the edges together and so form the mat into a short tube (Fig. 24 A). Further construction efforts result in increased tube length by the placement of algal filaments uniformly around each end of the tube. The second procedure in tube construction is exhibited by 23% of the shrimps (N = 87) and eliminates the production of a flat algal mat. The shrimps, in this case, appear to form a small tube with the first bit of algal mat which is produced. After the initial tube is constructed elongation takes place in the manner described above. Algal tubes constructed in this way are generally smaller in diameter and conform more closely to the body size of the inhabitants.

The third type of tube construction is exhibited by _A. clypeatus_ when relatively large clumps of filamentous algae are present in the immediate environment. The shrimps penetrate into the algal clumps by use of the chelae on the first pereiopods. The chelae, which are held close together directly in front of the shrimp, are pushed a short way into the clump and spread apart slightly. The movement spreads the algal filaments and allows the shrimp to enter a short way into the clump. With repeated similar movements the shrimp is able to penetrate any portion of the algal clump as well as hollow out a central chamber. After establishment of the central chamber any excess algae are slowly utilized in tube construction.

Observations on the ability of _A. clypeatus_ to construct tubes of different genera of algae, which are not present in the normal habitat, suggest that the shrimps can adapt to abnormal situations. All shrimps exposed to the brown filamentous alga _Ectocarpus_ are
FIGURE 24. ALGAL TUBES OF A. CLIPEATUS CONSTRUCTED
PRIMARILY OF (A) ACROCHAETIUM AND (B) ECTOCARPUS.
able to construct tubes of this material \((N = 18)\) but the tubes break apart easily upon mechanical disturbance. *Ectocarpus* appears to be a very brittle alga and although the shrimps handle it easily, the filaments break into lengths too small for tube construction (Fig. 24 B). Only 6\% \((N = 18)\) of the shrimps exposed to the green alga, *Bryopsis* are able to construct tubes. The one tube constructed (Fig. 25) reveals that *A. clypeatus* can construct tubes of this alga but is probably limited by the relatively large dimensions of a single thallus.

**Pair Formation**

From previous results (Fig. 13, 14, and 22) it is evident that relatively small (carapace length 2.5--3.5 mm) individuals of *A. clypeatus* are capable of sexual pair formation, egg production, and agonistic intraspecific interactions. Since small shrimps may be sexually mature (if carapace length exceeds 3.0 mm) and exhibit well developed agonistic behavior a study of them was undertaken to determine, as closely as possible, the behavioral mechanisms involved in pair formation.

Laboratory observations on the interactions of 120 (65 males and 55 females) previously unpaired shrimps (carapace length 1.5--3.5 mm) revealed the formation of 20 heterosexual pairs. Eight of the 20 pairs formed contained sexually immature shrimps (carapace length <3.0 mm). Of those shrimps which did not form pairs, 25 (14 males and 11 females) were killed, 21 (10 males and 11 females) did not possess algal tubes, and 34 (21 males and 13 females) did possess algal tubes. Observations on shrimps in test
FIGURE 25. ALGAL TUBE OF *A. CLYPEATUS* CONSTRUCTED PRIMARILY OF *BRYOPSIS*.
chambers with prepared algae revealed that 41% (N = 24) of the individuals had formed pairs while 31% (N = 96) of the shrimps with algal tubes had formed pairs. Although the results suggest that the percentage of shrimps involved in pair formation is slightly higher when algal tubes are not present, it must be pointed out that in this case, no paired shrimps were observed until the shrimps had constructed tubes from the prepared algae.

No evidence of pair formation was observed in groups of shrimps placed in test chambers without algae. Thus, pair formation in *A. clupeatus* appears to take place only in the presence of constructed algal tubes.

Continuous algal tube construction appears to be one of the most significant aspects of pair formation in *A. clupeatus*. That is, shrimps which continually increase the length of their tubes also increase the probability of contact with the tubes of other shrimps. Observations on eight shrimps that were placed in a test chamber in their original tubes show continuous tube construction (Fig. 26) and ultimately, pair formation when tube construction by one shrimp led to contact with the tube of another shrimp of opposite sex. Once contact is established between two tubes the shrimps may react to each other in a number of ways. The interactions exhibited by the shrimps may vary from simple antennal contact to a prolonged encounter which results in the death of one shrimp. The intensities of such encounters are usually determined by the size and sex of each shrimp. For example, in encounters between shrimps of the same sex, the larger of the two shrimps is nearly always dominant over the smaller (91%, N = 65). The smaller shrimp, in this case,
FIGURE 26. RELATIVE GROWTH OF EIGHT ALGAL TUBES OF *A. clypeatus* OVER A PERIOD OF 29 DAYS AND THE ESTABLISHMENT OF ONE PAIR OF SHRIMPS. S, DESIGNATES THE POSITION OF EACH SHRIMP. (A) START, (B) 6 DAYS, (C) 13 DAYS, (D) 29 DAYS. (TRACED FROM PHOTOGRAPHS)
FIGURE 26. (Continued) RELATIVE GROWTH OF EIGHT ALGAL TUBES OF *A. CLYPEATUS* OVER A PERIOD OF 29 DAYS AND THE ESTABLISHMENT OF ONE PAIR OF SHRIMPS. S, DESIGNATES THE POSITION OF EACH SHRIMP. (A) START, (B) 6 DAYS, (C) 13 DAYS, (D) 29 DAYS. (TRACED FROM PHOTOGRAPHS)
is either driven from its tube or killed and the empty tube utilized by the dominant shrimp. Rarely (one observation), in encounters between shrimps of the same sex, were the shrimps equally matched with neither dominant over the other. In this case, although intense agonistic interactions arose, each shrimp was able to maintain ownership of its tube and soon began construction which oriented the tube away from the opponent's tube. Heterosexual encounters are generally less intense than encounters between two shrimps of the same sex and involve relatively brief periods of interaction which may lead to pair formation or the establishment of dominance in the larger individual. Behavioral patterns elicited by heterosexual encounters are similar to those patterns described as the early phases of agonistic behavior. Encounters which involve antennal and chela contact are relatively common although snap production is generally reduced, and in some cases is absent. With the successful completion of pair formation, behavioral patterns equivalent to the advanced phases of an agonistic interaction are never exhibited.

The Influence of Algae on Agonistic Behavior

Increases in levels of activity and proportionate increases in agonistic interactions invariably result when two or more shrimps are placed together in a test chamber. Observations on groups of two to four shrimps suggest that three factors, the sex of shrimps in the group, the presence or absence of algae, and the number of shrimps in the group, are the primary regulators of agonistic behavior.

The number of snaps produced when two or more shrimps interact
can be taken as a measure of agonistic behavior. The few snaps produced by isolated shrimps (Fig. 27) suggest that this activity does not happen spontaneously in any regular or repetitive fashion. Therefore any significant changes in this activity are attributable to changes in the shrimp's immediate environment.

Experimental evidence gained from sound recordings of heterosexual pairs of shrimps and groups of two and four shrimps of the same sex shows that the presence of algae significantly reduces the number of snaps produced \( (P < .002, \text{ Wilcoxon Rank Correlation, in Sokal and Rohlf, 1969}) \) (Figs. 28, 29, 30). Although isolated shrimps produce fewer snaps there is some evidence that indicates the presence or absence of algae may have an affect on the snap production. Isolated male shrimps do not show a significant \( (P > .10) \) change in this respect; however, isolated female shrimps do exhibit a significant \( (P < .002) \) reduction in the number of snaps produced when algae are present (Fig. 28).

The presence of algae significantly reduces snap production in all cases where two or more shrimps are present. Since snapping can be attributed primarily to agonistic interactions, then the presence of algae must also reduce the number of agonistic encounters. Death may result from such encounters and any mechanism which acts to reduce contact between the shrimps may increase survival.

Experiments that involve survival of individual shrimps, two shrimps of the same sex, and groups of three shrimps that include a heterosexual pair of shrimps and a third shrimp of either sex, suggest that survival is equally good with or without algae. The high survival rate of individual shrimps \( (95.3 - 100\%) \) (Fig. 31)
FIGURE 27. NUMBER OF SNAPS PRODUCED BY A SINGLE MALE *A. CLYPEATUS* OVER A PERIOD OF 72 HOURS. LIGHT SOURCE ADJUSTED TO NATURAL DAY LENGTH. UPPER GRAPH WITH ALGAE PRESENT AND LOWER GRAPH WITH ALGAE ABSENT. (REDRAWN FROM MILLIAMMETER RECORDS)
LEGEND:

- RANGE
- MEAN
- 2 STANDARD ERRORS OF THE MEAN

NUMBER OF SNAPS/hr

WITH ALGAE   WITHOUT ALGAE
FIGURE 30. NUMBER OF SNAPS PRODUCED BY FOUR MALE A. CLYPEATUS OVER A PERIOD OF 72 HOURS. LIGHT SOURCE ADJUSTED TO NATURAL DAY LENGTH. UPPER GRAPH WITHOUT ALGAE AND LOWER GRAPH WITH ALGAE. THE NUMBER OF SNAPS / HOUR EXCEEDS, BY MORE THAN FOUR TIMES, THE NUMBER OF SNAPS / HOUR PRODUCED BY A SINGLE MALE A. CLYPEATUS (FIG. 27). (REDRAWN FROM MILLIAMMETER RECORDS)
4 males without algae

4 males with algae

NUMBER OF SNAPS

TIME (HOURS)
indicates that starvation in the absence of algae is not a significant cause of death. Shrimp mortality observed in the other experiments can then be taken as a measure of agonistic behavior. Two shrimps of the same sex survive equally well with or without algae (males 54.5-54.5%, females 63.5-60%) (Fig. 31). In groups of three shrimps survival remains nearly constant whether or not algae are present, even though the groups contained different sexual combinations (two females and one male 63.5-63.3% survival, two males and one female 66.5-63.5 survival) (Fig. 32). Generally in groups of three shrimps, agonistic encounters involve individuals of the same sex and result in the death of one. Thus, approximately 2/3 of the shrimps in these groups survive.

The results of the short duration experiments in which the presence of algae was shown to reduce the frequency of snapping and hence agonistic behavior and of the longer duration experiments in which the presence of algae did not markedly affect survival are compared in the Discussion (p. 126).

Heterosexual pairs of shrimps do exhibit increased survival in the presence of algae. Previously non-mated shrimps reveal an increase in survival of 15% while mated shrimps show a 28.5% increase (Fig. 33). It is also evident that aggressive interactions between members of heterosexual pairs more often result in the death of the female.
FIGURE 31. EFFECT OF THE PRESENCE OR ABSENCE OF ALGAE ON THE SURVIVAL OF SINGLE AND TWO SHRIMPS OF THE SAME SEX. DURATION OF EXPERIMENTS 25 DAYS. EXPERIMENTAL CONDITIONS ARE SHOWN ON THE ABSCISSA. SAMPLE SIZES ARE SHOWN ACROSS THE TOP OF THE GRAPH.
FIGURE 32. EFFECT OF THE PRESENCE OR ABSENCE OF ALGAE ON THE SURVIVAL OF GROUPS OF THREE SHRIMPS. EACH GROUP CONSISTS OF A SEXUAL PAIR PLUS AN EXTRA MALE OR FEMALE. DURATION OF EXPERIMENTS 25 DAYS. EXPERIMENTAL CONDITIONS ARE SHOWN ON THE ABSCISSA. SAMPLE SIZES ARE SHOWN ACROSS THE TOP OF THE GRAPH.
GROUP OF THREE SHRIMPS

SAMPLE SIZE (GROUPS)

<table>
<thead>
<tr>
<th>21</th>
<th>20</th>
<th>20</th>
<th>21</th>
</tr>
</thead>
</table>

% SURVIVAL

- MALE
- FEMALE

WITH ALGAE

WITHOUT ALGAE
FIGURE 33. EFFECT OF THE PRESENCE OR ABSENCE OF ALGAE ON THE SURVIVAL OF MATED AND NON-MATED PAIRS OF SHRIMPS. DURATION OF EXPERIMENTS 25 DAYS. EXPERIMENTAL CONDITIONS SHOWN ON THE ABSCISSA. SAMPLE SIZES ARE SHOWN ACROSS THE TOP OF THE GRAPH.
Sample size (pairs)

- Male: 21
- Female: 29
- Male and Female: 21
- Nonmated: 20

Survival rates:

- Mated with algae: 100%
- Nonmated with algae: 70%
- Mated without algae: 50%
- Nonmated without algae: 40%
DISCUSSION

Use of Cover

Crustaceans in General

The use of cover in benthic crustaceans can be easily observed in areas known to be inhabited by many hundreds of these animals. No matter if the substratum is flat sand or the highly irregular surface of a reef, few, if any, crustaceans are visible. The ability to dig, burrow, and bore into many different materials (Waterman and Chace, 1960; Lochhead, 1961; Schöne, 1961) permits the construction of shelters which generally hide their inhabitants from view. Certain semi-terrestrial crustaceans such as members of the Ocypodidae and Grapsidae families are visible along certain coastlines but these forms usually retire into shelters at the approach of danger (Alcock, 1902; Dembowski, 1926; MacGinitie and MacGinitie, 1949; Beer, 1959; Crane, 1967; Macnae, 1968). Often hermit crabs make up a large portion of the visible crustacean fauna. These animals represent a special case, however, since their shelter is carried throughout life and affords protection in a variety of environments (Reese, 1969). A few examples of the construction and/or use of shelter have been shown for various crustaceans, these include; amphipods (Schmitt, 1931; Nicol, 1960; and Croker, 1967), shrimps (MacGinitie, 1937; and Allen, 1960), lobsters (Mc Intosh, 1920; Lindberg, 1955; Fielder, 1965a; Dybern and Høisaeter, 1965), crayfish (Tack, 1941; Bovbjerg, 1953, 1956), crabs (Dembowska, 1926; Høtt, 1948; Bovbjerg, 1960; Harreid and Gifford, 1963; Jeffries, 1966; Shinn, 1968), and stomatopods (Hazlett and Winn, 1962; Moulton, 1964; Dingle and Caldwell, 1969).
Also many symbiotic relationships provide shelter (Dales, 1957, 1966; Castro, 1966; Cheng, 1967; Patton, 1967). Extensive reviews of earlier ecological crustacean literature are given by Ortmann (1898-1901), and Balss (1927, 1956).

**Alpheid Shrimps**

Decapod shrimps of the superfamily Alpheoida comprise the largest group, as regards the number of species, within the Caridea. The relative degree of success of these animals is shown by their world-wide distribution in tropical and temperate waters (Johnson et al., 1947; Knudsen, Alford, and Ealing, 1948; Dobrin, 1949).

Often these shrimps are present in such great numbers that the characteristic snapping sound they produce forms the greatest component of underwater ambient noise (Hulburt, 1943; Loye and Proudfoot, 1946; Johnson, et al., 1947; Everest, Young, and Johnson, 1948; Johnson, 1948; Moulton, 1958; Albers, 1960; Knowlton, 1960; Dumontier, 1963a; Knowlton and Moulton, 1963; Fish, 1964; Tavolga, 1965). A second indication of the success of alpheid shrimps is shown by their ability to adapt to a great variety of habitats.

Various species of alpheid shrimps commonly live in areas where the substratum consists of mud, sand, coral, shells, rocks or any combination of these types (Brooks and Herrick, 1891; Ortmann, 1898-1901; Verrill, 1922; Darby, 1934; MacGinitie, 1935; Banner, 1953, 1957, 1958; Chace, 1955; Macnab, 1957, 1968; Rangarajan, 1957; Buchanan, 1958; Stevenson, 1958; Macnab and Kalk, 1962; Ricketts and Calvin, 1962; Knowlton and Moulton, 1963; Banner and Banner, 1964, 1966a, 1966b, 1967, 1968a and 1968b); Lewinson and Holthuis, 1964;
Crosnier and Forest, 1966; Shinn, 1968; Banner and Smalley, 1969). Others, found in similar habitats but not in shelters of sand, rocks, coral, etc., utilize algae as it occurs naturally (Schmitt, 1921; MacGinitie, 1937; MacGinitie and MacGinitie, 1949; Pope, 1949) or modify the algae into specialized shelters (Richters, 1880, cited in Balss, 1956; De Man, 1888; Coutière, 1899; Cowles, 1913; Taylor, 1950; and Fishelson, 1966). These shrimps are also known to live in association with organisms from other phyla. Such associations provide cover and increased protection from predation. Sponges, for example, generally contain a series of canals which can be inhabited by alpheid shrimps (Couch, 1861; Good, 1878; Packard, 1881; Herrick, 1888; Coutière, 1910; Mc Clendon, 1911; Hay and Shore, 1915-1916; Schmitt, 1931, 1965; Pearse, 1932a, 1932b, 1950; Arndt, 1933; Green, 1961; Hazlett, 1962). Similarly, other species of alpheid shrimps have established associations with crinoids (Coutière, 1909; Potts, 1915; Patton, 1967), tunicates (Hewatt, 1937; Lebour, 1938), and gobioid fishes (Inther, 1958a, 1958b; Herald, 1961; Magnus, 1967; and Harada, 1969).

Significance of Shelter

Previous workers have shown that crustaceans that occupy shelters may benefit from at least four functions provided by these shelters; (1) reduced predation, (2) territorial behavior and the related activities of pair formation, (3) increase feeding potential, and (4) a means of range extension (Nicol, 1960; Herreid and Gifford, 1963; Macnae, 1968). The present study has revealed similar functions provided by algal tube construction by A. clypeatus.
The Significance of Algal Tube Construction in Habitat Selection

The guild concept of Root (1967) seems particularly relevant to the fauna associated with coral heads. The environmental resources of the coral head habitat are utilized by a number of characteristic species that include shrimps, crabs, fishes, and micro-inhabitants. It seems that these species could be considered members of an all inclusive "coral head habitat guild." Animals which utilize specific resources within the designated guild, such as shelter, could be assigned to the "shelter-use guild." Members of the shelter-use guild could then be further grouped into the "crevice-preference guild" and "tube-preference guild." Animals which have been assigned to different guilds can then be compared ecologically with respect to the environmental variable on which "guild membership" is based. Hopefully an accumulation of this type of data would produce a clearer picture of the niche requirements for different species (Reese, 1969).

One of the most important aspects of tube construction by *A. clupeatus* is that it allows occupancy in a part of the habitat which is not utilized by other species of alpheid shrimps. This portion of the habitat is generally devoid of the types of shelter utilized by the other species and thus offers reduced competition for space (Milne, 1961; DeBach, 1966). For the purpose of this paper, the term competition will be used as defined by Birch, 1957, cited in Klomp (1961, p. 90), "Competition occurs when a number of animals (of different species) utilize common resources the supply of which is short." Extensive field observations reveal no other organisms within the coral head habitat which utilize filamentous
algae in quantities equal to those of *A. clupeatus*. Perhaps this apparent lack of competition for algae and space in a specific portion of the environment is a primary factor in the establishment of *A. clupeatus*. Macfadyen (1963) suggests that the existence of an animal within a specific area may be a result of such a lack of competition.

Behavioral adaptations shown by *A. clupeatus* act to further reduce intraspecific competition for hard substratum. For example, well established algal tube complexes are attached to coral branches only at certain places. Thus portions of the algal tubes are suspended in the water between the branches. Tubes suspended in this manner increase the amount of substratum available to the shrimps, algae, and micro-inhabitants of the algae without a significant reduction in the coral branch substratum.

Allee, Emerson, Park, Park, and Schmidt (1949) discuss the relationship between the ability of a population to physically condition the substratum and the density of that population. They have suggested that both the rate and the extent of this conditioning are proportional to the population density. It seems that *A. clupeatus*, which conditions the substratum extensively through algal manipulation, may produce environmental conditions which would favor increased densities. Field collections have shown that *A. clupeatus* is, in fact, consistently found in greater numbers than other alpheid species inhabiting coral heads. The more apparent conditions that may lead to higher densities include a continuous food supply provided by the growth of algae within the tube complex.
and decreased inter- and intraspecific interactions that result from residence in the algal tubes. Connell (1961), in his work with barnacles, has also shown that decreased interspecific competition increases the success of species that normally occupy the same habitat.

Field observations have revealed that various fishes, which commonly associate with coral reefs, are the primary predators on alpheid shrimps. Hiatt and Strasburg (1960) studied the feeding habits of fishes of the Marshall Islands and found alpheid shrimps in the stomachs of many species of fishes. Similarly, Randall (1967) reports alpheid shrimps in the stomachs of fishes from the West Indies more often than any other group of shrimps. Certain fishes which occur in tide pools along the California coast are also known to prey upon these shrimps (Mitchell, 1953).

Several factors determine the relative degree of predation that a given alpheid species will be subjected to. Klopfer (1962) has suggested that behavioral mechanisms play an important role in the ability of a prey to escape from its predator or reduce the chances of being detected by its predator. It seems that the behavioral mechanisms that allow *A. clypeatus* to construct algal tubes do play a significant role in the reduction of predation. Well established algal tubes provide physical barriers against certain predators by their location within the coral head. The coral branches efficiently exclude larger predators and herbivorous fishes that may damage the tubes. The wall of the tube itself may protect the shrimps from smaller predators that are able to enter the coral heads. The walls of the tube also act as a visual barrier. That
is, the shape and movements of the shrimps are masked to potential predators. Field observations supporting this hypothesis show that in artificial situations, where shrimps and tubes are removed from the coral head, 95% of the shrimps in tubes survived while only 10% of those without tubes survived.

Klopfer (1969) pointed out the importance of habitat selection and substratum matching as ways in which species may effectively reduce predation. *A. clupeatus* is apparently able to survive wherever sufficient quantities of filamentous algae occur. Where the algae are found without shrimps it appears that predation or some other factor has influenced their distribution. Such a distribution may result from the differential predation on shrimps of more exposed habitats as compared to those in more protected habitats. Further decreases in predation may result from the degree to which the algal tubes match the substratum. Predatory fishes that have the morphological capability of reaching the algal tubes, for example the long snouted *Forcipiger longirostris*, may not react to them because of their resemblance to the natural substratum.

Habitat selection by *A. clupeatus* apparently has evolved in response to the interactions of three factors: (1) competition for natural resources, (2) predation, and (3) the ability to construct specialized shelters. The most significant of the three factors may be competition for natural resources. In this respect *A. clupeatus* differs significantly from all other alpheid shrimps (with the exception of *A. brevipes*, *A. bucephalus*, *A. pachychirus*, and *A. frontalis*) that normally inhabit coral heads, by its ability to
utilize more exposed surfaces within the coral head. Observations on the coral head habitat reveal that these other alpheid species occupy shelters requiring little or no modification. Such shelters include crevices in the coral, canals within sponges, and the spaces produced by the growth of several types of macroscopic algae. These observations also reveal that the shelters are usually 100% occupied. Complete usage of available shelter suggests that space for these species is at a premium; consequently, competition for space would be intense. Since *A. clypeatus* does not utilize habitat space similar to that of other alpheid shrimps, it is not subjected to such rigorous interspecific competition for space. Such behavioral adaptation would certainly influence the shrimps' chances of survival and thus provide material for natural selection (Tinbergen, 1951; Hinde, 1966).

The chemical sensitivity of crustaceans plays a significant role in their ability to detect both food and shelter (Warden, et al., 1934; Davenport, 1955; Nicol, 1960; Barber, 1961; Hazlett, 1962; Fielder, 1965a, 1965b; Marler and Hamilton, 1966). The results of Y-maze tests show that *A. clypeatus* is capable of orienting chemically to the algae normally used for tube construction. The results also suggest that such chemical discrimination may be a significant factor in substratum selection during settlement.

Interspecific competition for algae within the coral head appears to be of little significance. Although many of the alpheid species appear to be herbivores or omnivores no evidence of competition for algae was obtained. Intraspecific competition for algae is highly significant, however, and the amount of utilizable algae present may
become a limiting factor with respect to the population density.

**The Significance of Algal Tube Construction to Spatial Relationships**

The floral characteristics of a given environment may be highly significant with respect to the habitats it provides for various organisms (Nicol, 1960; Marler and Hamilton, 1966; Frank, 1968). The presence of sufficient quantities of filamentous algae is essential to the persistence of *A. clupeatus* in a given habitat. The relative abundance of such algae appears to be a most significant factor affecting the specific density attainable by the shrimps.

Field observations have shown that the major physical components (hard substratum, dead *P. meandrina* coral heads) of the deeper habitat are stable. Such environmental stability is often reflected in the associated fauna and flora and results in the formation of characteristic communities (Shelford, Weese, Rice, Rasmussen, and MacLean, 1935; Thorson, 1957; Buchanan, 1958; Newell, Imbrie, Purdy, and Thurber, 1959). The growth of filamentous algae in such communities is a result of the interactions of many factors. The more important factors, as mentioned by Zaneveld (1969), include competition with other species of algae and invertebrates for space and light and the effects of grazing animals. Backus (1964, 1966, 1967) discusses the effects of fish grazing on the abundance and distribution of organisms living on the coral substratum and attributes the general lack of organisms on exposed coral surfaces to this phenomenon. Other workers, such as Wismer and Swanson (1935), Jones (1950), Dawson (1966), and Neushul (1967), have pointed out that the environmental influence of light, water movement, depth, and
temperature are equally important with respect to specific communities.

The results have shown that the deep habitat supports approximately twice the number of individuals of *A. clypeatus* as does the shallow habitat. The growth of the calcareous alga, *Porolithon*, in habitats exposed to strong water movements, exceeds that of most other species of algae (Dawson, 1966). Such a growth differential may result in the utilization of available space by *Porolithon* at the expense of other algal species. Further reduction in the amount of space and light available is brought about by the continual coalescence of the coral head affected by the growth of calcareous algae. Coral heads in deeper water, however, are subjected to reduced water movements and light intensities, both of which may enhance the survival of filamentous algae. The shrimps' algal tubes consist primarily of red algae (Table II) which are capable of efficient light absorption in deeper water (Dawson, 1966).

Further evidence which indicates that the specific density of *A. clypeatus* may be related to the supply of filamentous algae can be shown by a comparison of the number of shrimps to the size of the coral head they inhabit (Fig. 4). Larger coral heads contain more shrimps than do smaller coral heads; however, results show that for every unit increase in the number of shrimps there is a four-fold increase in the estimated coral volume. This relationship indicates that space is not a limiting factor. It seems that the larger coral heads do provide space, in terms of a suitable substratum, sufficient for the support of shrimp densities greater than those shown by the results, but apparently there are insufficient algae to allow a four-
fold increase in the shrimp population.

The spatial distribution of the shrimps within the coral head is characterized by continual change. The settlement of young individuals, with subsequent construction of new algal tubes, the continued tube construction and pair formation of the intermediate shrimps, and the continued tube construction of adult shrimps all contribute to this overall pattern of change. Field and laboratory studies suggest that the three size classes of shrimps generally occupy specific areas within the coral head, although with the growth of juvenile and intermediate shrimps, the algal tubes are found more and more proximal in the coral head. Shrimp growth and increased use of algae also affect the spatial relationships between algal tubes within a coral head and ultimately determine the number of individuals a given coral head can support.

The ability of a species to spread out over the available habitat is highly significant in its continued success (Lorenz, 1966). The mechanisms involved in the spacing of animal species are numerous and generally result in efficient ways to match the numbers of individuals to the food supply while retaining the adaptively significant genetic characteristics of that species. In animals with sufficiently developed sensory capabilities, agonistic intra-specific interactions are extremely important. For example, Allee, et al., (1949), Lack (1954), Bovbjerg (1959, 1960, 1964), Klopfer (1962), Wynne-Edwards (1962, 1964, 1965), and Fielder (1965a) have discussed examples, with special reference to the concept of territoriality, which illustrate that such agonistic interactions
result in the dispersal and specific density of individuals within the population.

The algal tubes constructed by *A. clypeatus* appear to represent relatively compact and completely functional territories. The results have shown that the juvenile shrimps, presumably recent arrivals from the plankton, begin construction of algal tubes on or near the coral branch tips. The shrimps continue to increase the size of their tubes, and orient them toward the center of the coral head, for approximately 3--5 months. Throughout this period the juvenile and intermediate shrimps suffer a higher mortality than do adult shrimps as a result of their relatively exposed positions and through the chance contact with tubes of conspecific shrimps. Such intraspecific interactions further reduce the number of shrimps present, through agonistic encounters, when between members of the same sex. If the interaction involves members of opposite sexes, however, pairs may form. Although pair formation does take place with sexually immature individuals (Fig. 14), the greatest proportion of pair formations originates in the intermediate size class. This suggests that tube construction, initiated when the juvenile shrimps settle on the coral head, may reach a point where the probability of contact with another tube is greatly increased. Shrimps in the intermediate size class, which successfully complete pair formation, appear identical with adult shrimps in all aspects except body size and tube size. Established adults probably engage in territorial conflicts as a result of tube contact with other adults, since tube construction is a continuous process.

Such a system of continued tube construction, in which contacts
with conspecific shrimps regularly happen, is an efficient means of spacing the shrimps in the habitat and helps provide homeostatic control of specific density. The inherent agonistic capacity displayed by *A. clypeatus*, and by the alpheid shrimps in general, also forms an important part of this population control system. Efficiency of this system is indicated further by the absence of algal losses. Shrimps that have gained possession of other shrimps' tubes through agonistic interactions incorporate these tubes into their own tube complex. It appears that in a system of this type selection would favor shrimps with increased tube construction capabilities and relatively high levels of agonistic behavior.

Sound Production and Agonistic Behavior

The Production and Significance of Sound in Alpheid Shrimps

Sound production, one of the most conspicuous characteristics of alpheid shrimps, always accompanies agonistic interactions of these shrimps (Hazlett and Winn, 1962). It seems, however, that this ability to produce relatively intense sounds stimulated many workers to attempt to explain the mechanism of sound production rather than its behavioral implications.

Several of the early hypotheses erroneously attributed the sound to movements of the uropods (Lovett, 1886) to a rapid extension of the dactylus on the large claw (Heller, 1863, and Pesta, 1918, cited in Volz, 1938; Kent, 1877; Wood-Mason, 1878), and to the rapid flick of the carpo-propodal joint of the large claw (Miner, 1950). Alcock (1902) felt the sound was produced either by the forcible penetration into or extraction of the plunger on the dactylus from
the propodal socket. Both Volz (1938) and Castro (1964) have suggested the importance of the rapid entrance of this plunger into the propodal socket, although Hazlett and Winn (1962) and the present study indicate that sound production is still possible after ablation of the plunger and portions of the dactylus.

More commonly, the sound was thought to be produced by the rapid closure of the large claw (Goode, 1878; Wilson, 1903; Schmitt, 1921, 1931, 1965; Knudsen, et al., 1948; Dobrin, 1949; Pope, 1949; Moulton, 1959) and several workers have described the closure mechanism (Brooks and Herrick, 1891; Coutière, 1899; Verrill, 1922; Volz, 1938; Johnson, et al., 1947; Dumortier, 1963a; Knowlton and Moulton, 1963).

The significance of sound production, especially in marine invertebrates, is difficult to ascertain. Problems encountered in investigations of this type are compounded by disagreement among researchers as to the exact nature of sound reception (Carthy, 1958; Frings and Frings, 1958; Frings, 1964; Cohen and Dijkgraaf, 1961) and to the general lack of proof for sound communication between marine crustaceans (Frings and Frings, 1964; Tavolga, 1965). Frings and Frings (1966) have stressed the need for increased behavioral and electrophysiological studies to help clarify the relationships between receptors and responses. Such studies could provide the basis for a more accurate and complete definition of sound communication among aquatic invertebrates.

The significance of sound production in alpheid shrimps has not been adequately demonstrated. Although it is generally agreed that the large claw is used in agonistic encounters (Brooks and Herrick,
1891; Johnson, et al., 1947; Pope, 1949; Moulton, 1957; Knowlton, 1960; Hazlett and Winn, 1962) and, in some species, for food capture (MacGinitie, 1937; MacGinitie and MacGinitie, 1949; Given, 1958, Marshall and Orr, 1960), the importance of the associated sound remains obscure. Graphic recordings of the frequency of sounds produced by A. clupeatus have indicated that sound production is directly proportional to the frequency of agonistic encounters between the shrimps. The lack of any observable temporal patterns in the snaps produced by groups of shrimps and by individual shrimps as well as the reduction in number of snaps when the shrimps are isolated physically but not acoustically suggests that sound by itself may be of little or no importance but that the water jet produced is functionally important.

It appears that Schmitt (1931) and Volz (1938) were the first to state that the water jet may be the most important aspect of rapid claw closure. Similarly Johnson, et al. (1947), Balss (1956), Dumortier (1963a) and Tavolga (1965) mentioned the lack of evidence for the function of sound and suggest that the water jet may be of greater significance. Observations on A. clupeatus further support the functional importance of the water jet. For example, the actively maintained chela orientation between two individuals engaged in an agonistic encounter (Figs. 16, 17) suggests that some advantage may be gained when the anterior portion of the large claw is positioned against the opponent. Such a position would not appear relevant in sound production yet would be most efficient for the release of an anteriorly directed jet of water or a direct blow by the dactylus.
The Significance of Sound Production in Other Marine Animals

Behavioral studies on certain species of fishes have indicated that sound production may be significant in mating and reproductive rituals (Tavolga, 1958; Drown, 1961; Bull, 1961; Schevill, Backus, and Hersey, 1962) as well as intraspecific recognition, territorial defense, and escape from predators (Moulton, 1958, 1964; Winn, 1964). Similar studies on various crustaceans, apart from the alpheid shrimps, have revealed several examples of sound production related to specific behavioral patterns. Work with crabs of the Oxystomata and Brachygnatha subsections suggests that sounds are important with respect to reproduction, territory defense, and ritualized aggression. Such sounds are generally categorized as threats of protests (Alcock, 1892; Balss, 1921; Burkenroad, 1947; Guinot-Dumortier and Dumortier, 1960; Schevill et al., 1962; Wynne-Edwards, 1962; Dumortier, 1963b; Fish, 1964; Reese, 1964; Hughes, 1966). Salmon and Stout (1962) suggest that sounds may have more significance at night in the absence of visual signals. Studies of sound production in the Macrurans, Pandalus and Palinurus, show that the sounds occur during agonistic encounters and may be of a threat or protest nature (Meibius, 1867; Parker, 1878a, 1878b; Dijkgraaf, 1955; Lindberg, 1955; Moulton, 1957, 1958, 1959; Cohen and Dijkgraaf, 1961; Schevill, et al., 1962).

Factors Which Influence Agonistic Behavior

RITUALIZED COMPONENTS: The results show that agonistic interactions between two shrimps of the same sex generally become more destructive with continued contact. The orientation and level of
intensity exhibited by two shrimps in the early stages of an agonistic encounter, however, suggest the presence of ritualized components in the behavior. For the purposes of this paper, the term ritualized will be used as defined by Crane (1967, p. 54) "... ceremonial encounters replace injury-producing use of weapons, while the advantages of aggression are maintained." Movements which initiate and maintain antennal and chela contact and possibly the use of water jets may be ritualized to the extent that injury rarely occurs. The use of water jets may be similar to the "tail fighting" behavior of certain species of cichlid fishes (Lorenz, 1966; Baerends and Blokyl, 1963; Eible-Elbesfeldt, 1961).

SENSORY PERCEPTION: Sensory setae on the antennae and pereiopods are capable of perception in several modalities (Warden, et al., 1934; George, 1961; Green, 1961; Laverack, 1962a, 1962b, 1963a, 1963b, 1964; Wynne-Edwards, 1962; Bullock and Horridge, 1965; Lockwood, 1967). Any position which allows contact between the setae of opposed shrimps theoretically could be advantageous for information transfer. The large claw of A. clypeatus has a concentration of setae on the anterior portion (Fig. 19) which could function in the collection of information when oriented against an opponent. A similar function seems applicable to the antennae. Antennal contact has been described for several other crustaceans also (Warden, et al., 1954; Dougis, 1946; Lindberg, 1955; Bovbjerg, 1956; Schone, 1961; Reese, 1962; Wynne-Edwards, 1962; Penn and Fitzpatrick, 1963; D. E. Bowers, 1964; Johnson, 1969). It is possible that antennal and/or pereiopod contact may provide information on the sex, size, and the general level of aggressiveness of an opponent and thus could determine dominancy.
SIZE AND SEX: Both size and sex appear to be the most significant factors in the determination of the dominant individual and the ultimate outcome of an agonistic interaction in a variety of species of crustaceans (Volz, 1938; Bovbjerg, 1953, 1956; Lowe, 1956; Olsen, 1958; Reese, 1961, 1964; Hazlett and Winn, 1962; D. E. Bowers, 1964; Fielder, 1965a; Hughes, 1966; Hazlett, 1968; Dingle and Caldwell, 1969). The results of agonistic encounters in *A. clypeatus* suggest that males are generally more aggressive than females. In encounters between two individuals of the same sex, size is the most important aspect and the larger of the two combatants dominates the smaller.

The ritualized components are most adaptive when the opponents are unevenly matched. For example, encounters between shrimps of the same sex but with significant size differences may result in the immediate retreat of the smaller. Retreat by the smaller shrimp then becomes a step toward population dispersal and any reduction in physical damage sustained in such aggressive encounters would be of adaptive significance (Reese, 1962; Wynne-Edwards, 1965). It is of interest to note that size plays little, if any, role in heterosexual aggressive interactions. Both large males paired with small females and small males paired with larger females have been observed.

The Influence of Agonistic Behavior on Dispersal

Physical damage and death (Figs. 18, 19) commonly result from aggressive interactions between shrimps held in small containers (Brooks and Herrick, 1891; Darby, 1934; Volz, 1938; Hazlett and Winn, 1962). It is difficult to believe that agonistic interactions which occur in the natural habitat would be as detrimental as those
observed in the laboratory. Since intraspecific agonistic encounters often lead to dispersal (Tinbergen, 1951; Bovbjerg, 1959, 1960, 1964; Elbl-Eibesfeldt, 1961; Reese, 1962, 1964, 1969; Wynne-Edwards, 1962, 1964, 1965), it seems that any behavioral mechanism which prolongs an agonistic encounter would be detrimental and selected against. Presumably, the initial ritualized portions of an agonistic encounter allow sufficient communication between the opponents to establish the dominant shrimp and allow the subordinate shrimp to retreat unharmed.

Prolonged agonistic encounters are more likely to occur between shrimps of the same sex and of equal size regardless of whether they are adult, intermediate, or juvenile shrimps. The results show that agonistic interactions of juvenile shrimps are very similar to those of adult shrimps. This is to be expected since tube construction and pair formation occur soon after settlement of the juveniles from the plankton. Hence, the significance of prolonged agonistic encounters between shrimps in all size classes is apparent from the standpoint of a homeostatic density regulation mechanism (Wynne-Edwards, 1962, 1964, 1965).

The Influence of Algae on Agonistic Behavior

The results show that the presence of algae generally reduces agonistic behavior, as measured by the number of snaps produced, between two shrimps of opposite sex, two shrimps of the same sex, and between groups of four shrimps of the same sex (Figs. 28, 29, 30). In a second series of experiments agonistic behavior is measured by the survival of the shrimps involved. The results suggest that the
presence of algae does not influence survival between two shrimps of the same sex or groups of three shrimps which consist of two shrimps of the same sex plus a third shrimp of the opposite sex (Figs. 31, 32). The presence of algae does, however, enhance survival of heterosexual pairs of shrimps (Fig. 33).

The results indicate that the presence of algae for tube construction allows increased densities of *A. clypeatus* within the habitat. Not only does the construction of tubes permit efficient use of habitat space but the walls of the tubes act as definite borders to the territory. Further, *A. clypeatus* appears to be herbivorous and is able to obtain its nutritional requirements from the algae used for tube construction (Table II). Observations made throughout the present study indicate that the shrimps occupy their algal tubes continuously unless displaced as a result of intraspecific agonistic interactions. In short, the algal tubes seem to be complete life-support systems for shrimps that are established within the habitat.

The differential effect of algae on the survival of two shrimps of the same sex and two shrimps of opposite sex indicates the high degree of intolerance that exists between individuals of the same sex. Although sufficient algae are present in the test chamber two shrimps of the same sex engage in agonistic encounters until one of the shrimps is killed (Fig. 31). In groups of three shrimps one of the two shrimps of the same sex is generally killed and the two shrimps which remain survive as a viable heterosexual pair. Similar observations have been reported by Brooks and Herrick (1891),
Disagreement between the sound recording data (Fig. 28) and the percent survival data (Fig. 31) may be a result of the large difference in durations of the two experiments. The sound recordings were taken for a period of 72 hours and may only represent an initial decrease in agonistic behavior with the presence of sufficient algae in the test chamber. The percent survival data, however, were calculated from experiments which were carried out for 25 days.

Breeding

Where temperatures in the marine environment are relatively stable, breeding activities of invertebrates have been shown to be both continuous and seasonal (Orton, 1920; Stephenson, 1934; Boolootian, Giese, Formanfarmaian, and Tucker, 1959; Giese, 1959; Goodbody, 1965; Reese, 1968). Invertebrates which appear to breed throughout the year often show seasonal peaks in these activities which coincide with periods of higher temperature (Giese, 1959). The results of the present study indicate that populations of A. clypeatus breed continuously and do not show definite seasonal variations in their breeding activity (Fig. 15).

The inhabitance of algal tubes by A. clypeatus appears to be one of the most important factors with respect to continuous breeding. In well established pairs of shrimps the algal tube not only supports the pair-bond between the shrimps but also provides a continuous source of food.
Survival of Larvae

Although temperature has little effect on the breeding activity of sexually mature individuals of *A. clypeatus*, it appears to influence the survival and settlement of the juvenile shrimps. The greatest number of juvenile shrimps are present throughout the warmer months of the year (Fig. 11, 12). Templeman (1936) showed that a reduction of both temperature and salinity would increase the length of time required by lobster larvae to reach the bottom living stage. He further postulated that increases in the length of the free swimming larval period greatly reduce the chances of survival to the bottom living stage. Similar environmental parameters may affect the number of *A. clypeatus* larvae which survive the planktonic period of their life cycle.

Bathen (1968) showed that temperature and salinity of the surface water in Kaneohe Bay fluctuates on a seasonal basis. The highest values occur in summer (May--August) and the lowest values in winter (November--December). Perhaps the winter decline in temperature and salinity prolongs the free swimming period of *A. clypeatus* larvae and subsequently reduces their numbers through increased predation. Marshall and Orr (1955) demonstrated that predation by planktonic animals on copepods could reduce the number of copepods in a given area significantly. A second alternative with respect to larval survival may be the availability of food for the larvae. Boolootian, et al. (1959) suggested that breeding cycles may be adapted to the availability of food for the larval stages. In *A. clypeatus*, however, no similar adaptation is apparent and larvae are released in equal numbers throughout the year. Larvae, which
are released at a time when the water contains sufficient food for their survival, are most likely to attain the bottom living stage.

The significance of temperature, salinity, food and predation have been implied as controlling factors in the survival of *A. clypeatus* larvae, but definitive studies have not been done.
SUMMARY AND CONCLUSIONS

Tube Construction

1. *Alpheus clypeatus*, although morphologically similar to other species of *Alpheus*, differs from them in several behavioral aspects. The ability to construct tubes of filamentous algae appears to be the most significant behavioral difference.

2. Tube construction is accomplished entirely by use of the chelate, second pereiopods. Experimental animals from which these appendages had been removed were not capable of tube construction.

Ecology and Population Control

1. The food of *A. clypeatus* consists primarily of the red alga *Acrochaetium* and the brown alga *Sphacelaria*.

2. The filamentous red alga *Acrochaetium* is used predominantly for the construction of algal tubes.

3. Dead and encrusted heads of *P. meandrina* provide the greatest amount of habitat space for *A. clypeatus*.

4. No seasonal cycle occurs in the breeding activity of *A. clypeatus*. A high percentage of sexually mature females are found to be ovigerous at any given time throughout the year.

5. Because a greater number of juvenile shrimps occur on the coral heads in the summer months, it seems likely that the survival of larvae is greatest under summer conditions.

6. The most significant adaptive advantage associated with tube construction and inhabitance is thought to be the reduction of inter- and intraspecific competition for space in the habitat.
7. The decrease in specific density of _A. clypeatus_ with increased coral head size suggests that the amount of algae present rather than space is a limiting factor.

8. Continuous construction of algal tubes ultimately results in pair formation and serves as a homeostatic control mechanism of specific density through intraspecific competition for algae.

**Agonistic Behavior**

1. Intraspecific agonistic behavior generally occurs in three levels of intensity: (1) antennal contact, (2) chela contact, and (3) contact with physical damage. The first two levels, which include tactile stimulation, pushing the opponent by use of the pereiopods and pleopods, and the rapid closure of the large claw with the production of a water jet and snipping sound, are thought to be ritualized components in agonistic behavior.

2. Prolonged agonistic encounters may result in physical damage or death of the combatants.

3. The large chela is used as a weapon in agonistic behavior. Orientation of the large chela against an opponent suggests that the jet of water or direct blow of the dactylus, rather than sound, is the more significant aspect of rapid claw closure.

4. Males engage in agonistic encounters more often than females and agonistic encounters between members of heterosexual pairs of shrimps more often results in the death of the female.
5. Size is a significant factor with respect to dominancy in most agonistic encounters. The larger combatant becomes dominant in the majority of encounters between two shrimps of the same sex. Pair formation may occur regardless of the size differences between male and female shrimps.

6. The presence of algae significantly reduces the number of snaps produced by individual shrimps (except females), two shrimps of opposite sex, and groups of two and four shrimps of the same sex, for a period of 72 hours.

7. In laboratory experiments of 25 days duration the presence of algae increased survival of heterosexual pairs of shrimps but had no significant effect on the survival of two shrimps of the same sex or individually isolated shrimps.

Adaptive Significance of Algal Tube Construction

The adaptive significance of algal tube construction and of the associated behavioral patterns is that it permits _A. clypeatus_ to utilize the dead coral head habitat to the greatest advantage. The algal tubes increase the exploitable surface area of the coral head, provide the basis for a territorial social system which allows a higher specific population density, and in addition, three species of algae that are present in the tube are utilized as food.
LITERATURE CITED


______. 1968a. Three new species of the genus Alpheus (Decapoda, Alpheidae) from The International Indian Ocean Expedition. Crustaceana, 15:141-148. A correction for this paper has been published by the authors. Crustaceana, 16:207.


Knowlton, R. E. 1960. The biology of the snapping shrimps Alpheus (Crangon) and Synalpheus, with particular attention to the structure and function of the snapping claw and the sounds produced by the claw. Bowdoin College, Brunswick, Maine, Thesis, pp. i-iii, i-134.


Neushul, M. 1967. Studies of subtidal marine vegetation in

Organism communities and bottom facies, Great Bahama Bank.

Pitman and Sons Ltd., London. 707 pp.


Odum, H. T., and E. P. Odum. 1955. Trophic structure and pro-
ductivity of a windward coral reef community on Ehiwetok


Ortmann, A. E. 1898-1901. Crustacea. In Dr. H. G. Bronn's Klassen

Orton, J. H. 1920. Sea-Temperature, breeding and distribution of

Packard, A. S. 1881. Notes on the early larval stages of the

Parker, T. J. 1878a. Remarks upon the stridulating organ of the

———. 1878b. Notes on the stridulating organ of Palinurus

3:1228-1244.

Pearse, A. S. 1932a. Observations on the parasites and commensals
found associated with crustaceans and fishes at Dry Tortugas,

———. 1932b. Inhabitants of certain sponges at Dry Tortugas.

———. 1950. Notes on the inhabitants of certain sponges at

Penn, G. H., and J. F. Fitzpatrick. 1963. Interspecific competition
between two sympatric species of dwarf crawfishes. Ecology,
44:793-797.
146.


