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SPACING MECHANISMS IN A HERMIT CRAB POPULATION

by

Elaine Kay Snyder-Conn

A Dissertation Submitted to the Faculty of the
DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY

In Partial Fulfillment of the Requirements
For the Degree of

DOCTOR OF PHILOSOPHY
WITH A MAJOR IN ZOOLOGY

In the Graduate College

THE UNIVERSITY OF ARIZONA

1977
I hereby recommend that this dissertation prepared under my direction by Elaine Kay Snyder-Conn entitled Spacing Mechanisms in a Hermit Crab Population be accepted as fulfilling the dissertation requirement of the degree of Doctor of Philosophy.

Elaine Kay Snyder-Conn 10 June 77
Dissertation Director Date

After inspection of the final copy of the dissertation, the following members of the Final Examination Committee concur in its approval and recommend its acceptance:

Elaine Kay Snyder-Conn 10 June 77
Robert Y. Hardman May 27, 1977
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*This approval and acceptance is contingent on the candidate's adequate performance and defense of this dissertation at the final oral examination. The inclusion of this sheet bound into the library copy of the dissertation is evidence of satisfactory performance at the final examination.
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ACKNOWLEDGMENTS

Foremost, I thank Dr. Elisabeth Stull and Dr. Donald Thomson for encouraging me in this study, for conferring creative and useful advice, and for their thorough attention to manuscripts evolving from this study. Dr. Peter Pickens aided in the identification of hermit crabs species and also assisted in the experimental design of some of the rhythm studies. Dr. Ronald Pulliam also provided assistance in the experimental design and statistical treatment of the results, as well as providing able criticism of the manuscript. Mr. John Skeoch of the Villa School assisted in many of the experiments described in the final chapter. Dr. Robert Hoshaw gave valuable time in reading this manuscript. Dr. Brian Hazlett and Dr. Ernst Reese graciously supplied unpublished data and ideas, in addition to stimulating my greater interest in the biology of hermit crabs. Numerous other researchers contributed unpublished observations to Chapter 3, including Drs. Richard Vance, William Grant, Jr., Elliot Norse, and Eldon Ball. In addition, Dr. Ball has contributed many research ideas to this study. Dr. Robert Kuehl suggested several of the statistical procedures followed in this study. Lastly, I would especially like to thank my husband, Mr. Jeffery Conn, for his aid in both research and writing phases of this study, and forbearance throughout this study.
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The aims of this study are (1) to describe the pattern of spacing of a population of the hermit crab, *Clibanarius digueti*; (2) to determine mechanisms which regulate its spatial patterns under natural conditions and under laboratory conditions; and (3) to ascertain the adaptive value of the spatial strategy.

At Puerto Peñasco, Sonora, Mexico, field observations indicate that *C. digueti* exhibits a rhythmical pattern of cluster formation during the tidal cycle. Clusters of up to 700 individuals assemble both above and below boulders and in crevices. Throughout low tide, most hermit crabs remain inactive and in physical contact with each other. At the beginning of flood tide and near the end of ebb tide, the hermit crabs disperse on upper boulder and other surfaces and feed. When water depths become greater than 0.7 m, the hermit crabs refuge under boulders and in crevices, remaining loosely spaced. The sites of refuging and clustering may differ, and the cluster site may be on a boulder adjacent to the refuge site.

Thirteen monthly transects on two different substrates, boulder and shell-hash beachrock, are utilized to detail clustering trends. In both habitats, highly significant degrees of clustering are demonstrated. The degree of clustering \( (s^2/\bar{x}) \) varied as a function of the relative abundance of *C. digueti*. However, similar degrees of clustering between and within habitats and with time are demonstrated using Morisita's
Index, a measure independent of numerical abundance. The transect data are interpreted as indications that the clustering of *C. digueti* is independent of substrate heterogeneity or seasonal variation.

Tidal rhythms of activity, skototaxis, phototaxis, and gregariousness are demonstrated under constant laboratory conditions of temperature, light, and water depth. Except for the high tide response, a high degree of correspondence occurs between the rhythms in the laboratory and in nature under conditions of shallow water depth. Experimental evidence suggests that the predicted high tide response, based on laboratory behavior, may be altered by responses to currents, to the absence of light, and/or to increasing water depth. A model incorporating both rhythmic and environmentally induced behavior is developed to predict the different phases of spacing behavior of *C. digueti*.

To determine the adaptive significance of clustering in *C. digueti*, resistance to desiccation, shell exchange, mating, predator avoidance, shell cleaning, resistance to current, and resistance to cold are examined. The results of field observations and experiments indicate that aggregation may improve survivorship under conditions of desiccation and cold. Where refuges are lacking, clusters may also enable *C. digueti* to resist strong currents. In habitats where hermit crabs remain damp or wet at low tide, clustering may also promote shell exchanges.

The spectrum of interacting rhythmic and environmental responses permits a versatility of spacing behavior in *C. digueti*, thereby adapting this species to a wide variety of habitats in the Gulf of California.
The propensity to regularly cluster at Puerto Peñasco may be associated with multiple advantages secured during exposure at low tide.
CHAPTER 1

INTRODUCTION

Presentation of the Problem

Rhythmic clustering and dispersal among hermit crabs is of common occurrence (Hazlett, 1966a; Reese, 1969). Yet the phenomenon is not well-understood, either in terms of mechanisms which effect clustering and dispersal, or in terms of adaptive values of the two alternating behaviors. In this study, the aggregation and dispersal of Clibanarius digueti, a small, intertidal hermit crab of the Gulf of California, is investigated. This endeavor follows that of Snyder (1972) and represents a considerable diversification in both field and laboratory techniques and results.

Preparatory to the presentation of my research, the problem of spacing is first considered generally (this chapter), then with regard to crustaceans (Chapter 2), and finally with respect to hermit crabs (Chapter 3). In Chapter 4, the mechanisms of aggregation and dispersal are investigated. Results from this chapter suggest that components of innate behavior rather than responses to substrate heterogeneity or seasonal progression account for aggregation and dispersal of C. digueti. Both rhythmic and environmentally induced rhythmic behavior are studied. A synthesis of these responses is presented by means of a flow diagram model at the conclusion of Chapter 4. In the final chapter, Chapter 5, the adaptive significance of clustering is considered. Seven hypotheses
are tested. The result is compared to that suggested by the relationships between the degree of clumping and density based on transect data and also with data of Hazlett (1966a).

**Theoretical Aspects of Spacing**

A regular or uniform distribution in space may be advantageous to a population for many reasons: to avoid predation, to partition sparse resources, to decrease predisposition toward disease and parasitism, and to reduce conspicuousness to predators (Wolfenbarger, 1946; Elton, 1949; Wynne-Edwards, 1962; Lorenz, 1963; Tinbergen, Impekoven, and Franck, 1967; Alexander, 1974). Contrariwise, locally dense populations and even massive clusters of hundreds to millions of individuals may occur among certain species. Under what conditions do these aggregations occur?

Viewed strictly in terms of resource availability, one would predict that when essential resources are uniformly distributed and predictable in their appearance, dispersion would evolve. In the case where these resources were defendable by one individual or a pair of individuals, territoriality would be likely to develop. If not defendable, the resources might be apportioned through a dominance hierarchy. Non-random distribution of one or more essential resources would, in contrast, predictably lead to a clumped distribution (Brown and Orians, 1970).

Another important determinant of spacing is the bioenergetics of the organism. The home range of an individual is a function not only of resource availability, but also of the total daily expenditure of energy, type of diet, and mobility of the organism (McNab, 1963). Metabolism is, of course, affected by climatic and seasonal conditions, as well as local
nutrient and water patterns. These desiderata dictate that herbivores and saprobes are most likely to maintain locally dense populations for long periods of time. However, those species with very short generation times, low mobility, and high fecundities will also exhibit clumped distributions. Even within highly populated areas, there may exist a random spacing of animals if the area is productive and if individuals do not compete directly for food, e.g., suspension feeders (Connell, 1963). There may exist a uniform spacing if the population is so dense that individuals compete directly for food or body space, e.g., deposit feeders (Pielou, 1960; Connell, 1963). In a heterogeneous habitat containing homogeneous portions of suitable habitat, animals may form aggregations in which, however, regular spacing occurs. In such cases, elaborate social behavior typically evolves (McNab, 1963).

The pattern of spacing adopted by a population must also be contoured to the size of the population in relation to reproductive success and enemy avoidance. At very low densities, aggregation may be requisite for adequate sexual production of young, especially if the species is not highly mobile. Too, at very low densities, the chance of encounter by a predator, parasite, or pathogen may be minimized by clustering, particularly if a large search area is involved relative to the mobility and density of the enemy (Brock and Riffenburgh, 1960; Cheke, 1974; Burdon and Chilvers, 1976). However, at moderate densities, both reproductive and predator avoidance advantages may cease and spacing out tends to be beneficial (Laing, 1938; Pimentel, Nagel, and Madden, 1963; Murdie and Hassell, 1973).
At very high densities, the saturation densities of Holling (1965, 1966), the predation rate becomes independent of the prey density and solely a function of hunger and satiation level of the predator. At such densities, aggregation may be advantageous to survival, if the inter-aggregation distance is substantially greater than that expected between randomly spaced individuals. Aggregations may then be likened to islands relative to the rate of colonization (predation), while uniformly distributed individuals may be likened to readily accessible "stepping stones," providing the required nourishment in transit for dispersal of the natural enemy. Thus, at high densities, the predation rate becomes a function of the cluster size, distance from the natural enemy, the mobility of the enemy and its sensory capabilities.

When mixed aggregations of two or more species yield a high total density, the survival of both species may be increased. This effect results when predation is apportioned between species and the total predation per species is thereby reduced. Holling (1965) argues that, for edible species which form large, mixed aggregations, convergence of appearance and, hence, mimicry may evolve. In Mullerian mimicry, involving two non-palatable prey, no large critical density is required in order to be favored, although increased advantage may accrue with increases in group size by the same mechanism or by reinforcement of learned avoidances. In Batesian mimicry, involving one edible prey and a non-palatable model, the survival of the edible species is enhanced with the presence of greater proportions of the inedible species, which reinforces learned avoidance of the aggregation by the predator. No
advantage appears to be available to the non-palatable species in this association, however. In other instances, aggregations of mixed species may, through combined visual, audible, or olfactory stimulation, increase their conspicuousness in order to be better serviced as by pollinators (Platt, Hill, and Clark, 1974).

The attack strategy of the natural enemy may also partially dictate the pattern of spacing which is most judicious for the prey. If the predator is insatiable, as in the type 1 predation response of Holling (1965, 1966), random distribution at most densities would seem to favor survival. In contrast, ambush predators, which become satiated following predation on one food item, may be best avoided by aggregating (Taylor, 1976b). Likewise, prey species may show increased survival if by aggregating they reduce the number of territories of potential predators which are occupied. This hypothesis is suggested by the results of Stimson (1970), who found more algal biomass within territories of the limpet _Lottia_ than outside, owing to the limpet's exclusion of competitors. In yet other cases, concealed clumps within a heterogeneous environment may disrupt the associative learning of some predators, as demonstrated experimentally using meal worms and wasps by Taylor (1976a). In the case of parasites or parasitoids, mutual interference may be greater for randomly spaced than clumped hosts at low densities and, in such cases, clustering may also be adaptive.

The above considerations suggest the optimal strategies of distribution but cannot, in most instances, serve as the proximal causes of aggregation. What are the immediate causes of aggregation? Stavn
(1971) categorizes five stochastic mechanisms which may bring about contagion:

1. Vectoral pattern, stemming from physico-chemical gradients in temperature, light, humidity, nutrients, salinity, etc.

2. Stochastic-vectoral pattern, resulting from mass transport of materials due to environmental energy gradients, such as wind or water currents.

3. Reproductive pattern, as a consequence of eggs being laid in bunches and the young remaining in the same area.

4. Social patterns, in which aggregations of organisms in herds are induced by gregarious responses.

5. Coactive patterns, as an effect of competition between populations or species [or adjacent individuals according to Pielou (1960) and Connell (1963)].

Predator-induced patterns should, perhaps, be included in the coactive patterns. Selective predators may almost totally eliminate a population in areas where they overlap in range with a preferred prey. The remaining areas in which the prey survive and reproduce may, thus, be "refuge" zones in which the growth and reproductive capacity may be suboptimal (Connell, 1970). Another, more indirect, modus operandus of predators is to alter the coactive pattern by reducing the density and competition between similar species.

Contagious distributions are manifested in varying degrees of organization, including: patches, stratifications, clusters and swarms, schools, and migrations. The mechanisms of formation and also the
adaptive value of these types of aggregations vary and are discussed in detail in Chapter 2. While patches may result from physical concentration via vectoral or stochastic-vectoral mechanisms, other forms of aggregation appear to be more complex, relating to reproductive patterns, behavioral responses, and/or coactive patterns. The resultant pattern of distribution often reflects the causal mechanisms, as may the shape of the aggregation. Often, the maintenance of relatively constant individual distances signifies intraspecific communication of a highly developed nature. The distance may be dictated by a threshold beyond which aggression occurs (Moynihan, 1960; Brown and Orians, 1970). Alternatively, some individuals may assume close physical contact within aggregations and no threshold appears to exist.

Patterns between aggregations may also vary. A "mobile group space" corresponding to individual distance may effect a regular spacing between some aggregations (Brown and Orians, 1970). In addition, numerous other patterns between aggregations exist (Chanut, 1975), most of which also depend on the stochastic mechanisms regulating the spacing of individuals.

Whatever the mechanisms and the resultant patterns, the contagious distribution must be of survival value in order to be sustained, since an energy expenditure is involved in the formation of clumps. The advantages may be for the individual, for the group, or for both (Hamilton, 1964, 1971; Williams, 1964; Brown and Orians, 1970, Alexander, 1974). Mutual benefit to all individuals of a group may be inferred when aggregations serve as environmental buffers, altering the microhabitat or
microclimate surrounding the aggregation (Klopfer and Hailman, 1967), or
when aggregations function as cooperative units in alert or defense
against competitors or predators (Trivers, 1971) or minimize the chance
of detection (Brock and Riffenburgh, 1960; Vine, 1971). Reciprocal
advantage is also derived when aggregations act in concert in the harvest
or capture of food or other resources or when individuals aid by sympa-
thetic induction in the feeding, growth, orientation, or learning of
other individuals (Allee, 1931, 1938; Tinbergen, 1965; Klopfer and
Hailman, 1967).

Alternatively, decoy behavior or issuance of an alarm by one
individual in some circumstances may be slightly disadvantageous to that
individual, but highly advantageous to survival of the group (but see
Charnov and Krebs, 1975; Owens and Goss-Custard, 1976). Predictably,
such altruism would usually involve reciprocation (Trivers, 1971) or kin
selfishly use the group for protective cover to the detriment of marginal
group members would appear to involve individual advantage and group
disadvantage (Vine, 1971). However, Pulliam (1973) shows that the mutual
alert of the group may outweigh the disadvantages incurred by peripheral
members. The overall fitness of the successful selfish individuals in
terms of increased alertness and mobility may also promote the survival
of the species.

The optimum pattern of spacing may be aggregation at certain
times and dispersal at other times, often according to some synchronous
pattern. This is frequently the case when breeding occurs on a
circannual or seasonal basis. Too, the advantage of clumped distribution to the eggs and young is often reversed with growth, whereupon dispersal becomes adaptive. Similarly, seasonal changes in the abundance of food and in the metabolic demands of the organism may lead to temporally altered distributional patterns. On a daily basis, synchronous aggregation may occur, depending on the behavioral regimen of the population or species.

"Refuging," the rhythmical dispersal of groups of animals from a fixed point in space and their subsequent return, is a frequently observed phenomenon (Elton, 1949; Hamilton et al., 1967; Hamilton and Watt, 1970). Such is often the case with hibernating, nesting, or roosting species. Refuging results when the central return places are in short supply and provide advantages unavailable to nomadic individuals. The advantage may consist of shelter, a place of food storage, or a watering place. Conceivably, it may also be a place previously unassailed by predators or resilient to physical damage. Radial dispersal allows the individuals which refuge to forage outside the core area in the "arena" of undepleted resources. The individuals which disperse the furthest reap increased resources which, therefore, compensates for the greater energy expenditure.

In summary, the pattern of spacing adopted by a particular species or population must be proximally related to one or more of a variety of causal mechanisms and ultimately to one or more adaptive functions. Among some of the possible determinants of spacing are resource availability, bioenergetics of the organism, population size, predator
population size and attack strategy, and relationships with other species. A consideration of these determinants may permit prediction of the optimal pattern of distribution. The mechanisms by which the species distributes itself may involve either passive or active behavior. Active selection may be attuned to environmental gradients or to other individuals, including conspecifics and/or non-related co-occurring species.

Synopsis of the Research Approach

The theoretical aspects discussed above indicate the need for a multilateral approach to the problem of clustering in *Clibanarius digueti*. First, the possible mechanisms of clustering require analysis. Secondly, the possible functions of clustering require examination. These separate analyses appear in Chapters 4 and 5, respectively. The formulation of hypotheses examined in these chapters is largely based on studies of contagion in other crustaceans and among other hermit crab species. These studies are reviewed in Chapters 2 and 3, respectively. Hypotheses were also generated in the course of observations of *C. digueti* and its environment and incorporated in Chapters 4 and 5.
CHAPTER 2

PATTERNS OF AGGREGATION AMONG MARINE CRUSTACEA

Introduction

Contagious distributions are manifested in at least five distinct but related phenomena: patches, swarms and clusters, schools, migratory assemblages, and stratifications. The phenomena of patches, schools, migratory assemblages, and stratifications are briefly considered below. Subsequently, the phenomenon of swarms and clusters is reviewed in detail. It is of interest to examine aggregations of this sort in depth, since clusters of hermit crabs fall within the scope of this category. However, the phenomenon of clustering of marine hermit crabs is omitted from this discussion and presented in Chapter 3.

Patches

Although the term has been applied in diverse fashions (Cushing, 1962), patches may be said to result from either physical concentration or from individual responses to one or more environmental variables. Near the sea surface, patches may occur in wave cusps (Cubit, 1969), or Langmuir spirals (Stavn, 1971). Within the water column and in the benthos, populations may become affiliated with small-scale "physical inhomogeneities" (Cassie, 1959, 1963), or large-scale current and water mass systems (Barnes and Marshall, 1951; Wilson, 1958; Bary, 1959; Fager and McGowan, 1963; Banse, 1964).
Concentration may also occur at discontinuity layers (Russell, 1927; Lance, 1962; Cassie, 1963; Banse, 1964; Harder, 1968), in temperature inversions, and in other gradients (Friedrich, 1961; Lance, 1962; Banse, 1964; Grindley, 1964; Boyd, 1973). Large populations may also develop passively by growth and retention in areas of upwelling or other water movement (Bainbridge, 1963; Cushing and Tungate, 1963). Avoidance, for example, of low oxygen content (Russell, 1927; Loesch, 1960; Banse, 1964; May, 1973; Newman and Pollock, 1974) may also induce aggregations, as may toxic substances (Hardy, 1936; Bainbridge, 1961; Marlowe and Miller, 1975). However, aggregation of mysids in areas of high ammonia is also known (Bainbridge, 1953).

In many of the instances above, patches result from the combination of behavioral responses and physically concentrating mechanisms. Thus, an important manifestation of patches is their shape, which is often closely related to that of one or more environmental variables. Consequently, patches typically occur in discrete layers corresponding to hydrographic layers (Banse, 1964; Bainbridge, 1963) or bands corresponding to areas of convergence and divergence (Stavn, 1971). However, in the case of benthic patches, such patterns are less easily discerned due to the mosaic of substrates and frequent topographical diversity. Thus, habitat selection may play an important role in patch formation of epibenthic plankton (Sale, McWilliam, and Anderson, 1976).

Within patches, individuals may come into close physical proximity. Concomitantly, communication may occur. However, the functional significance of these interactions is usually small. More often, the
function of such aggregation lies in advantages secured by each individual, such as an increased food supply within certain layers (Boyd, 1973; Biggs and Wetzel, 1968) or "neutral buoyancy" (Stavn, 1971).

Schools

Schools, by definition, involve mutual attraction between members. Often, both species and size specificity is observed within schools of crustaceans (Steven, 1961; Clutter, 1967, 1969; Emery, 1968). As in fish, schools of crustaceans show concerted, often parallel, movement. Frequently, a constant distance between individuals is also maintained (Steven, 1961; Zelickman, 1974). Thus, schools of crustaceans may be highly organized and may result directly from optomotor and vibrotactile attraction rather than taxes in responses to environmental gradients (Clutter, 1967, 1969). Such benefits as improved location and capture of prey and/or enhanced confusion or avoidance of predators are possible functions of schooling in fishes (Brock and Riffenburgh, 1960; Breder, 1967; Cushing and Harden-Jones, 1968). These hypotheses have also been applied to schools of crustaceans (Emery, 1968; Zelickman, 1974). In the case of some crustaceans, schooling may also facilitate mating (Mauchline, 1960).

Among benthic crustaceans, cases of schooling behavior frequently involve the formation of queues. An interesting case is that of the shore isopods *Megaligia exotica* (Ondo and Mori, in Ricketts and Calvin, 1968, p. 488). These rock lice travel in queues toward the tideline each morning and return in late afternoon. The isopods tend to sort into groups according to size, with younger isopods preceding older ones in
the march shoreward. Most interestingly, the isopod queues proceed along preestablished pathways on these daily feeding sojourns.

Both juvenile and adult lobsters may form queues. In *Panulirus interruptus*, adult "schools" involve groups of several dozen individuals (Lindberg, 1955). Apparently, foraging may occur in such schools at night. This form of aggregation may, thus, be of value in food procurement. In groups, Lindberg found that individuals with their antennules removed were stimulated to forage, an activity curtailed in isolation. Such groups may sometimes originate by mutual attraction to a food source, but may also depend on interaction between individuals.

In *Panulirus argus*, queuing activity is apparently "irresistible when one lobster passes the den of another" (Berrill, 1975). This behavior may be preparatory for the large-scale migrations in queues which characterize the spiny lobster (Herrnkind and Cummings, 1964; Herrnkind, 1969, 1970; Herrnkind and McLean, 1971; Bill and Herrnkind, 1976). These migrations occur in the fall subsequent to intense storms. In contrast to their usual diurnal seclusiveness, "trains" or columns of up to several hundred mature (but non-gravid) individuals move over open areas in parallel queues for many miles over complex terrain and through difficult currents. The direction which is pursued is characteristics for the given locality. Initial visual orientation of the lobsters is followed by physical contact of the antennae or antennules so that each individual protects the abdomen of the preceding lobster. However, loss of the antennae or antennules does not alter the queuing, nor does
blinding. When approached, lobsters will crowd together, sometimes circling in covered-wagon fashion, to ward off a potential predator.

Unfortunately, the extent of the migrations and the destination of the lobsters has yet to be discovered. Herrnkind (1970) calculated that some of these lobsters, brought into the laboratory, queued for five weeks and moved the equivalent distance in captivity of 833 km. In nature, at least some of the migrating lobsters pile onto rock jetties near shore. In the queue, lobsters eat only briefly and enter shelters rarely. An environmentally induced neurohormonal change is believed to elicit migration. In the laboratory, a change of diet, from molluscs to fish, induces some migratory behavior (Herrnkind, 1970). In nature, an increase of biomass or decrease of temperature might effect similar metabolic changes. The adaptive value of these migrations is unknown. However, the formation of queues does reduce drag (Bill and Herrnkind, 1976).

Migratory Assemblages

Schools may facilitate migrations, as in isopods and lobsters. However, in most cases, migratory assemblages may be regarded as a distinct type of grouping in which periodic, directional movements often result in contagion without synchronous parallel movement and the maintenance of constant individual distances. Exemplary cases are those of vertically migrating crustaceans (reviewed by Russell, 1927; Kikuchi, 1930; Cushing, 1951; Bainbridge, 1961; and McLaren, 1963). However, vertical migrators do not always form congregations. At night, some species merely spread out from their daytime depth (Foxton, 1970a);
others migrate as discrete layers (Russell, 1927; Foxton, 1970a; Zalkina, 1970; Roe, 1974); in others, a mixture of the two patterns occurs (Brusca, 1967). Vertical migrators may, however, form aggregations en masse at one very specific depth, as in the case of euphausiid young just below the surface film at night (Mauchline and Fisher, 1969).

Some deep sea sonic layers may also constitute dense aggregations of euphausiids (Hersey and Moore, 1948; Tucker, 1951; Johnson et al., 1956; Bary, 1958; Dietz, 1962) or sergestid shrimp (Dietz, 1962; Clarke, 1966). These layers tend to exhibit vertical migrations (Tucker, 1951; Johnson et al., 1956; Dietz, 1962; Boden and Kampa, 1967; Dickson, 1972) and assume the distribution of patches or schools (Kanwisher and Volkmann, 1955; Dietz, 1962).

Four principal mechanisms have been proposed to account for the synchronous vertical migratory behavior of planktonic and nektonic crustaceans: 1) the reversible tropisms of Loeb (reviewed by Esterly, 1919, pp. 7-9, and Loeb, 1918; Kikuchi, 1930; Cushing, 1951), 2) optimum light intensities (Rose, 1925; Russell, 1927; Cushing, 1951; Enright and Hamner, 1967; Kerfoot, 1970), 3) endogenous rhythmicity (Esterly, 1917, 1919; Welsh, Chace, and Nunnemacher, 1937; Waterman et al., 1939; Hardy and Bainbridge, 1954; Harris, 1963; Enright and Hamner, 1967; Hoese et al., 1968; Rudjakov, 1970), and 4) dual optimum temperature control (Moore, 1952). Most correlational data (Clarke, 1933, 1934; Bogorov, 1946; Tucker, 1951; Lewis, 1954; Mauchline, 1960; Backus, Clark, and Wing, 1965; Boden and Kampa, 1967; Hoese et al., 1968; Jansson and Kihlander, 1968; Kerfoot, 1970; Dickson, 1972; Jones, Peacock, and
Phillips, 1973; Hure and Scotto di Carlo, 1974) and most experimental data (Hardy and Paton, 1947; Harris, 1953; Harris and Wolfe, 1955; Enright and Hamner, 1967) support the hypothesis that planktonic organisms seek an optimal light level, or isolume, resulting in diurnal vertical migration.

However, Clarke (1930, 1932) demonstrated that, in freshwater *Daphnia*, the rate of change of light intensity rather than the absolute intensity governs migration. Verheijen (1960) also cast doubts on the validity of many experimental studies by demonstrating a generalized "trapping effect" of artificial light, independent of intensity. The optimum light mechanism is also difficult to invoke in explanations of: 1) midnight sinking (Welsh et al., 1937; Bainbridge, 1961), 2) migrations below the photic zone (Waterman et al., 1939), 3) cases of reverse migrators (Hersey and Moore, 1948; Bainbridge, 1961; Brusca, 1967; Enright and Hamner, 1967; Baker, 1970; Roe, 1972a, 1972b, 1974; Hure and Scotto di Carlo, 1974), 4) different species-typical responses to moonlight and cloudiness (Hardy and Gunther, 1935; Moore, 1949; Moore et al., 1953; Moore and O'Berry, 1957; Herman, 1963; Mauchline and Fisher, 1969; Donaldson, 1975), and 5) predawn rises (Cushing, 1951).

It is important to realize that the mechanisms of reversible tropisms, optimal light intensities, endogenous rhythmicity, and dual temperature control are not mutually exclusive. Further, the presence of one mechanism does not warrant the tacit assumption that other mechanisms are precluded; all or several mechanisms may act in concert in some species. Thus, a crustacean could exhibit an automatic, precisely timed, reversible response to light, as suggested by Hardy and Bainbridge (1954).
Indeed, both responses to light and an endogenous rhythm are involved in the behavior of the shrimp *Penaeus duorarum*. Fuss and Ogren (1966) demonstrated that light was the most significant inhibitory factor in the diel periodicity. Adults were only active in intensities of less than .0176 lumens/m$^2$. However, they also found a positive correlation between temperature and nocturnal activity. In addition, however, the shrimp exhibit a persistent rhythm of diel activity under constant light (Fuss and Ogren, 1966; Hughes, 1968). The transition between light and dark and food both act as Zeitgebers (timers) of this rhythm (Hughes, 1968).

The functional significance of vertical migrations constitutes yet a second aspect of "the planktonic puzzle No. 1" (Hardy, 1956). Although widespread, vertical migrations are not ubiquitous. They seem, however, to be especially prominent in the Crustacea. Thus, while Marlowe and Miller (1975) report migrations in only 10% of all planktonic species examined, both Brinton (1967) and Baker (1970) state that 50% of the euphausiids which they examined were migratory. Of 31 species of euphausiids surveyed, Mauchline and Fisher (1969) found evidence of vertical migration in all but four species. Esterly (1912) found that 16 of 19 copepod species off southern California migrated, and Roe (1972b) reported that the majority of the calanoid copepods in his study migrated. However, Roe (1974) found that less than half of the copepods, amphipods, euphausiids, and ostracods were migratory.

The participation of large nektonic forms in vertical migration seems to be as great or greater than that of planktonic species. All sergestid shrimp examined by Donaldson (1975) were migratory. Of 12
penaeid and 6 caridean species examined, Foxton (1970a,b) found all but one species to migrate.

Few comparative studies of migrant versus non-migrant species have been made. Brinton (1967) found that migratory euphausiids were generalists with respect to their diet. With one exception, he found that migrators were morphologically adapted for sweeping or straining food, while non-migratory species possess limbs for selective feeding.

Migratory euphausiids were larger in size in the study of Baker (1970), constituting 46% of the numbers and about 64% of the biomass in his study. Bogorov (1958) also concluded that the smaller non-migratory species contribute little biomass to the plankton. He estimated that about 3/4 of the zooplankton biomass is migratory. This effect is so pronounced that Bogorov refers to abundant, large migratory species as "mass species." Also consistent with the feeding hypothesis is the finding that species occupying the deepest depths by day conduct the most extensive migrations (Moore, 1949; Moore et al., 1953; Moore and O'Berry, 1957; Moore and Bauer, 1960). Since these species are farthest removed from productive surface layers, this behavior concords well with the hypothesis that vertical migration may involve a feeding function.

Vertical migration may also play a role in the reproductive functions of some species. Ripe female *Calanus finmarchicus* and *C. helgolandicus* tend to migrate higher in the water and more extensively than unripe females or males (Marshall and Orr, 1960). Sexually mature opossum shrimp, *Neomysis americana*, undergo migration closely associated with breeding periods in May-June and October, but do not migrate
significantly at other times (Herman, 1963). Among tidal migrants, such as the amphipods *Atylus swammerdami* and *Bathyporeia pelagica*, females in the surf are mostly gravid (Fincham, 1970a). In the case of both these species, a semilunar rhythm was imposed on the pattern of vertical migration.

These pooled observations suggest that vertical migration toward the surface frequently involves feeding or reproductive functions. There is as yet no support for the contention of Wynne-Edwards (1962) that vertical migrations occur for the purpose of epideictic display. The photophores of many crustaceans would seem to adapt most species for such display at depth (Brinton, 1967).

What is the rationale for returning to great depths during vertical migrations? Speculations seem to have proliferated in inverse proportion to the available data on this topic. The following hypotheses have been promulgated in regard to downward migration: 1) predator avoidance, 2) horizontal dispersal into new feeding grounds by different currents at different depths (Hardy and Gunther, 1935; Hardy, 1956), 3) horizontal dispersal to facilitate genetic recombination and polytypy (David, 1961), 4) animal exclusion of zooplankton by phytoplankton during the day (Hardy and Gunther, 1935; Hardy, 1936; Bainbridge, 1953), 5) avoidance of the lethal effects of sunlight (Bainbridge, 1961; Marshall and Orr, 1955; Friedrich, 1961), 6) energy bonus by feeding more efficiently in warmer waters and by assimilating more for growth at colder temperatures (McLaren, 1963), 7) cultivating the maximal sustainable yield by withdrawal during the period of photosynthesis (Hardy and
Gunther, 1935; Conover, 1968; Petipa and Makarova, 1969), and 8) enhanced biotic accommodation of migrating species (Baker, 1970; Zalkina, 1970; Roe, 1974).

None of the proposed advantages of vertical migration are consistently supported. However, many of the above functions are mutually compatible. It is, thus, likely that multiple functions may be served by vertical migrations. Harris (1963) maintains, in contrast, that vertical migrations are mere consequences of utilizing light to regulate depth. Rudjakov (1970) posits instead that vertical migrations are relict phenomena. Despite these opposing suggestions, the preeminence of vertical migrations among diverse crustacean groups strongly argues for their widespread adaptability.

In addition to vertical migratory assemblages, other types of migratory assemblages are also common among marine crustaceans. Many migrations are associated with or are in response to environmental variation, including: seasonal migrations (Rathbun, 1918; Russell, 1927; Panning, 1938; Bogorov, 1946, 1958; Lloyd and Yonge, 1947; Moore et al., 1953; Lindberg, 1955; Marshall and Orr, 1955; Verwey, 1958; Pike and Williamson, 1959; Moore and Bauer, 1960; Bainbridge, 1961; Banse, 1964; Allen, 1966; Rebach, 1968, 1974; Ricketts and Calvin, 1968; Fish, 1970; Cooper and Uzmann, 1971; Naylor, Atkinson, and Williams, 1971; Rodriguez and Naylor, 1972; Atkinson and Parsons, 1973; Fotheringham, 1975), tidal migrations (Forster, 1951; Edwards, 1958; Verwey, 1958; Enright, 1961, 1962, 1963; Efford, 1965; Morgan, 1965, 1967; Allen, 1966; Hughes, 1969, 1972; Cubit, 1969; Jones and Naylor, 1970; Naylor et al., 1971;
Preece, 1971; Rodriguez and Naylor, 1972; Venema and Creutzberg, 1973), lunar migrations (Watkin, 1939; Sutcliffe, 1956; Gifford, 1962; Warner, 1967; Fish, 1970; Preece, 1971; Enright, 1972; Klapow, 1972), and horizontal diurnal migrations (Watkin, 1941; Hammer, Smyth, and Mulford, 1968; MacNae, 1968; Herrnkind, 1972; Rodriguez and Naylor, 1972). In many cases, these rhythms are related to feeding or reproductive functions. However, in the case of intertidal crustaceans, migrations may be requisite to maintain an intertidal position. Endogenous rhythms, responses to changing light, responses to changing pressure, and responses to tidal action may play important roles in the migration of these species (Wieser, 1956; Enright, 1961, 1962, 1963; Digby, 1961, 1967; Morgan, 1965; Fincham, 1970a,b; Jones and Naylor, 1970; Preece, 1971).

Stratifications

Stratifications involve the physical or behavioral segregation of individuals within a species according to ontogenetic development, sex, or brood. Such segregation may produce positive contagion according to the different physical and/or chemical preferenda of different segments of a population. Most frequently, this stratification is vertical, whether in the water column, in the intertidal zone, or in the sub-stratum.

Size stratification is especially noticeable among planktonic and nektonic Crustacea (Russell, 1927; Kikuchi, 1930; Einarsson, 1945; Cushing, 1951; Marshall and Orr, 1955, 1960; Mauchline, 1960; Mauchline and Fisher, 1969; Baker, 1970; Roe, 1972a,b,c,d). However, size stratification is also common among benthic species (Powell and Nickerson,
1965; Allen, 1966; Harris, 1972; Powell, 1974), and among semi-
terrestrial species (Milne and Milne, 1946; MacNae and Kalk, 1962;

With respect to size, juveniles are often distributed in more
shallow layers than adults. Such stratification may be quite refined.
Sulkin (1975) found that the four zoeal stages and the megalopa stages of
*Leptodius floridanus* and *Panopeus herbstii* all assumed different vertical
distributions, each succeeding stage being successively deeper.
Mauchline (1960) likewise demonstrated a progressive increase in depth
with size of the euphausiid *Meganyctiphanes norvegica*. Even small inter-
stitial copepods may exhibit this pattern of stratification (Harris,
1972). In addition to vertical stratification by size, size stratifica-
tion may be due to segregation of activity periods (Crane, 1941a; Rice,
1961; Barrass, 1963a; Temple and Fischer, 1965; Allen, 1966; Hughes,
1966).

Vertical stratification according to sex or sexual development is
also typical of marine crustaceans (Lindberg, 1955; Pike and Williamson,
1959; Marshall and Orr, 1960; Pereyra, 1966; Allen, 1966; Fincham, 1970a;
Foxton, 1970a,b; Baker, 1970; Omori, 1974; Klaasen, 1975). Sexual
stratification may also occur according to habitat type (Forster, 1951;
Wieser, 1956; Allen, 1966; Jones et al., 1973) or activity pattern
(Watkin, 1941).

The mechanisms by which crustaceans accomplish stratification are
basically unknown. In the case of schooling species, differences in
swimming rates and visual stimulation may segregate individuals of
different sizes (Clutter, 1969). Similar explanations may be employed to explain differences in the extents of vertical migration. However, these may also be related to the different fat contents of females, males, and juveniles, as suggested by Sushkina (in Banse, 1964, p. 98) and Rudjakov (1970). Yet another plausible explanation is that of Cushing (1951). He relates the occupation of different depths to the fact that adults are more sensitive to light than young. This seems to be the case in adult *Penaeus duorarum*, which Fuss and Ogren (1966) report to be more sensitive to light than young. All of these hypotheses warrant further experimental evaluation before a general acceptance is feasible.

The proximal significance of stratification may be the fulfillment of different nutritional or physiological requirements (Marshall and Orr, 1955; Allen, 1966). However, the ultimate function of stratification is probably more closely related to reduction of competition and/or cannibalism within a species (Thorson, 1964; Anderson, 1971; Salmon and Horch, 1972), or aiding in dispersal (Sulkin, 1975). Anderson (1971) has also proposed that sexual stratification may aid in conservation of energy, otherwise spent in untimely copulatory pursuits.

**Swarms and Clusters**

Swarms and their benthic counterpart, clusters, represent aggregations which are intermediate in their organization between patches and schools. Environmental variables may represent important cues in swarm and cluster formation. However, swarms and clusters differ from patches in that they are maintained primarily by the attractive forces between individuals (Bainbridge, 1963; Cassie, 1963). Therefore, the resultant
shape of swarms and clusters often deviates from that of hydrographic or topographic features which are present. Within the water column, individuals typically occupy spheres (Bainbridge, 1963; Banse, 1964), while benthic clusters frequently consist of circular or oblong heaps. Like schools, a constant individual distance may be maintained, particularly among colonies. Unlike schools, coordinated, directional movement, and hence continuous intraspecific responses, are not manifested.

Since the clusters of hermit crabs clearly fit into the category of swarms and clusters, these forms of aggregations will be reviewed in depth in the following discussion. Particular attention is given to mechanisms and functions of swarms and clusters.

Swarms

Among planktonic and nektonic Crustacea, swarms, in which "clouds" of aggregated, interacting individuals appear within a discrete area, are especially common to copepods, mysids, and euphausiids (Bainbridge, 1963). Cushing (1951), Bainbridge (1952), and Marshall and Orr (1955) discuss numerous instances of spontaneous surface swarming in the copepod Calanus finmarchicus. Their swarming is in contradiction to the usual diurnal migratory or subsurface distribution.

However, swarms are not always irregular in occurrence nor are they necessarily surface phenomena. Emery (1968) observed the copepods Acartia spinata, A. tonsa, and Oithona nana to regularly form compact swarms along edges of Thallasia beds. Here they maintained position in surge and against currents in densities estimated at 110,000 copepods/m³ and seemed to be quite stable. The mechanisms involved in swarming of
copepods are unknown. Perhaps pheromones are involved, as they seem to be utilized to evince mating encounters (Katona, 1973; Griffiths and Frost, 1976). Vision is probably also important since many species are elaborately appareled (Wynne-Edwards, 1962) and occasionally swarms of copepods may school spontaneously (Emery, 1968).

Cases of euphausiid swarms are reviewed by Komaki (1967). He concludes that they result from the approach of cold, offshore water masses. However, he also observes that such swarms are composed of mature individuals and may facilitate mating. Mauchline and Fisher (1969) distinguish between regular seasonal swarms, breeding swarms, and irregular swarms. Cases such as the mass stranding of millions of the euphausiid Meganyctiphanes norvegica appear to have resulted from an irregular swarm as a result of a population explosion combined with local tide and wind conditions, rather than cold temperatures (Cox, 1975). However, an unusual shallow water swarm of Thysanoessa longicaudata involving mature males and females with spermatophores (Forsyth and Jones, 1966) apparently results from wind and cold water conditions.

Hardy and Gunther (1935) observed the krill Euphausia superba in dense swarms between 183 m and 1/3 km in diameter. The swarms were fairly evenly separated from one another by gaps greater than 1/3 km. They also noted that, within a swarm, there were separate shoals of different-sized individuals. Hardy and Gunther recorded one shoal which formed a "red cloud" about one meter wide near the surface. This swarm varied from dumbbell to spherical in shape, but when the dumbbell appeared to split, the individuals regrouped and again behaved in
superorganism fashion. Enormous congregations of nototheniid fish collected and fed on the krill, as did the blue and fin whales, the crabeater seal, the Weddell seal, and the emperor penguin. Evidence of different size groupings was also obtained from the organization of krill in the stomachs of whales.

Similar observations have been made by Marr (1962), who studied swarm periodicity and found swarms of E. superba to be of quite common occurrence between 0-5 meters after nightfall. During the day, this zone appeared to be largely deserted, but net avoidance made distribution difficult to assay. Swarms seemed, however, to be most numerous between 40-80 m during the day. The swarms displayed no regular rhythmical movement, however. Marr further noted that each swarm was composed of similarly sized individuals. Also, the swarms appeared to be formed by nauplii or metanauplii and to remain cohesive throughout the lives of the participating individuals.

Swarms also seem to occur among planktonic amphipods, although they have not apparently been reported as such. MacGinitie and MacGinitie (1949) note that windrows formed on the beach give clear evidence of swarming. These windrows may alternately be composed of Paramisto libellula, Melita formoso, or Anonyx nugax. The windrows washed ashore during storms are sometimes 8 cm deep, 40 cm wide, and several kilometers in length. Other evidence of swarming among amphipods comes from stomach contents of bearded seals, which consist almost entirely of amphipods.

Swarming among stomatopods may occur in several life stages. The initial larval stages of the stomatopod Gonodactylus bredini swarm in the
cavity occupied and defended by the female (Dingle, 1969). These swarms are apparently maintained by a combination of both thigmotactic and negatively phototactic responses. In the pelagic stage IV, the positive thigmotaxis disappears and the larvae become positively phototactic. While Dingle did not mention whether these larvae also swarm, Schmitt (1965) reports that pelagic swarms of stomatopod larvae off the west end of Cuba gave the sea an appearance of a thick soup.

Swarming of the adult stomatopod Oratosquilla investigatoris in the Gulf of Aden and the western Indian Ocean was studied briefly by Losse and Merrett (1971). They observed swarms of this usually benthic species in shallow, inshore waters as well as over deep water. The swarms appeared on the surface from mid-afternoon through the night and sometimes until early morning. The most extensive swarm was approximately 56 km in length. Participants included individuals 6-37 mm in cephalothorax length and, at least in subsurface swarms, females were numerically dominant. Since swarms were observed in only one of three years, Losse and Merrett intimate a population explosion. A considerable impact was exerted on both bait and free swimming fish by this capable predator which was, in turn, subjected to high predation by large fish.

Oceanic swarms of the portunid crab Charybdis edwardsi also occur in the surface waters of the extreme western Indian Ocean. Losse (1969) states that these occur during the southeast-northeast intermonsoon and the early northeast monsoon period from October through December as a result of offshore migrations and subsequent congregation. The surface swarms are organized to the extent that they are mainly crepuscular and
nocturnal. At other times, the swarms apparently occur at depth. No ovigerous females were observed. During the swarms, nighttime activity was high and the crabs fed voraciously on dorado, mackerel, sardines, and myctophid fish and were, in turn, preyed upon by tuna, marlin, and sharks. Losse (1969) hypothesizes that the swarms involved a voracious feeding phase followed by a spawning period.

Mature portunid crabs, Polybius henslovi, although sometimes benthic in habit, also form surface swarms over deep water (Allen, 1968). Individuals of both sexes actively maintain distances of about 1-3 meters from one another and do not feed. Since eggs are laid at a later time, Allen proposes a mating function of this swarm. However, swarms previously reported of this species were often composed almost exclusively of males and were associated with sardine shoals. Thus, P. henslovi may also swarm for feeding purposes.

The red, purple, and blue swimming crab Euphylax dovii forms vast surface swarms in the early morning (Garth, 1948). According to Garth (1946, 1948), these "periscopic-eyed swimmers" occur in the greatest numbers during the seasonal invasion of the warm El Niño current off Panama, and seem to be an indicator of this current. No behavioral notes on the crabs were taken, but there was evidence of heavy predation by gulls and boobies.

In the case of pinnotherid crabs, short-lived copulatory swarms are formed. These swarms occur when the pea crabs abandon their hosts and swarm together in large numbers in the water (Hartnoll, 1971). Pinnotheres maculatus and Fabia subquadrata, which parasitize bivalves,
are particularly interesting in that the females are precociously inseminated (Pearce, 1962, 1964). The males, which spend a longer time in the water, are apparently preyed upon to such an extent that few are found in hosts subsequent to swarming.

A number of anomuran crustaceans exhibit strong tendencies to swarm. Along West Africa, a promontory and a bay have been dubbed, respectively, Cabo dos Camaraós and Rio dos Camaraós, after the nuptial swarming of the estuarine ghost shrimp *Callianassa turnerana* (Schmitt, 1965). This species apparently produces prodigious swarms at three-year intervals during the evening and night for periods ranging from three hours to ten days in August. All work is suspended by native tribes at this time, who fish and feast on this delicacy. So numerous are the ghost shrimp that baskets dipped into the whitened estuaries are retrieved full to the brim.

Galatheid crabs form spectacular masses, often resulting in huge windrows along the beaches of California and Baja California (Boyd, 1967; Haig, Hopkins, and Scanland, 1970). In one case in the Gulf of California, a windrow was about one meter deep, three meters wide, and five to seven kilometers long. Although little investigated, the swarms may result from the presence of low oxygen, phytoplankton blooms, or warm countercurrents (Radovich, 1961; Boyd, 1967; Longhurst, 1968). Radovich (1961) found that the partially demersal "pelagic red crab" forms masses on the surface several meters wide which are transported by warm-water currents and wash ashore. At other times, mid-water and bottom samples yield large numbers.
Longhurst (1968) reviewed many cases of mass occurrences of galatheid crabs and concluded that they often occur in highly eutrophic areas. He found that *Munida gregaria* and *Pleuroncodes planipes* tend to concentrate in surface waters as juveniles and young adults to graze upon diatom blooms, while *M. subrugosa, Cervimunida johni*, and *P. monodon* concentrate on the continental shelf, often in waters low in oxygen. However, despite these indications that these mass occurrences may be patch phenomena, Boyd (1967) found that red crabs may swarm on the surface throughout the year. He collected many more in night samples, suggesting less than a passive accumulation of *P. planipes*. Since the breeding period occurs during the winter, however, a breeding function does not appear to be of primary importance, although *in situ* breeding in some oceanic populations does occur (Longhurst and Seibert, 1971).

The aggregations of *Emerita analoga*, a mole crab, may provisionally be classed as swarms in that a degree of interaction as well as cohesion is evidenced. According to Efford (1965), the swarms are usually coherent for many days and also show size segregation. He postulates that the swarms function in the location of mates and in predator avoidance. However, Cubit (1969) argues that the aggregations result from stochastic-vectoral processes, and not from any gregarious tendencies.

Prawns also show a propensity to swarm. Wheeler (1937), after a year-round study of *Anchistioides antiquensis*, suggested that the direct action of moonlight or an internal rhythm controlled its nightly swarming pattern. Prawns maintained in captivity for two years exhibited a
molting rhythm with marked increases between lunar days 18-22. Wheeler and Brown (1936) had originally linked swarming to worm abundance, but Wheeler (1937) could not substantiate that correlation. Nearshore swarms of *Spirontocaris marmoratus*, consisting of 100-150 individuals, were observed by MacKay (1945). Since this species usually is found in deeper water, a breeding function may be involved in these aggregations.

Swarming in the deep-water layers has proven very difficult to investigate. In the deep meso- and bathypelagic zones, dominated by carnivores, only small, widely spaced swarms have been documented. For these swarms, a copulatory function is suggested (Omori, 1974). However, Omori reports evidence of swarms in a number of epipelagic and upper mesopelagic shrimps, notably *Sergestes similis*, *Sergestia lucens*, *Acetes* spp., and *Peisos petrunkevitchi*. The position, zone, and density of these swarms seems to change incessantly. Those detected by echo sounding of sonic scattering layers must consist of at least 9 individuals/m$^3$ in order to be detected. Omori indicates that several species may be as dense as 20 per m$^3$.

In Suruga Bay, large numbers of *Sergestia lucens* swarm and also form shoals by size group (Omori, 1974). Early postlarvae are separate from adolescents and adults, which usually form offshore swarms. Omori observed that the size and density of postlarval swarms were the greatest. Adult swarming climaxed in summer prior to and during breeding. Visual cues seemed important, since these swarms dispersed during the darker periods of the night.
Both the mechanisms which maintain the integrity of swarms of crustaceans and the adaptive values of swarming behavior remain obscure, as indicated in the above discussion. The fact that there is frequently a correlation between species which swarm and abundance (Barnes and Marshall, 1951; Wiebe, 1970; Fasham, Angel, and Roe, 1974) suggests that mechanisms other than vectoral or stochastic-vectoral ones are in operation. Tonolli and Tonolli (1958), examining freshwater distributions, observed that parthenogenetic species of cladocerans and rotifers were randomly distributed, whereas sexually reproducing species remained clustered. They hypothesized that these "patches" (quite likely swarms) maintained the genetic integrity within each population. Such an argument could easily be applied in the case of marine swarms, but, of course, requires testing. Bainbridge (1963) proposed that swarms or "actively engendered aggregations" have four possible raisons d'être: they may be natural by-products of animal exclusion, i.e., by phytoplankton toxins; they may result from feeding migrations into dense plant areas; they may subserve breeding; and/or they may be epideictic. All of these hypotheses require further testing. Ducruet (1973) has demonstrated that gammarid amphipods may show attraction between individuals regardless of the state of sexual maturity, suggesting functions other than reproductive in these species.

Clusters

Clusters represent the benthic counterpart of swarms and, thus, consist of aggregations at relatively stationary sites. Two sorts of clusters should first be distinguished: clusters composed of sedentary
individuals with highly limited mobility and clusters formed of potentially motile individuals. In the case of sedentary individuals, which reproduce sexually, clusters serve principally to insure the accessibility of mates. Mutual protection and location of suitable habitat may be subsidiary functions (Meadows and Campbell, 1972). In the case of "contact species," such as the barnacles Balanus hameri, which grow in tree-like form from an older basal individual, or in the case of Chelonobia patula, epizoic on blue crabs, and Lepas anatifera, Pollicipes cornucopiae, P. polymerus, and Scalpellum spp., with isolated or island-like habitats, gregarious settlement may primarily be an adaptation to highly circumscribed spatial requirements (Crisp, 1961; Barnes and Reese, 1960).

Within the crustaceans, the best studied instances of sedentary clusters are among the barnacles. Both physical attributes of the habitat and gregarious behavior are involved in the settling and attachment of larval barnacles. A gregarious response is elicited when physical contact is made between the larva and a previously settled conspecific (Knight-Jones and Stevenson, 1950; Knight-Jones, 1953; Barnes and Reese, 1960; Crisp, 1961; Crisp and Meadows, 1962, 1963). This response seems to be toward a species-specific chemical factor, termed arthropodin, which is sensed only when physical contact is made. In many species, contact with a conspecific incites a cyprid larva to further exploration of the immediate area, and the cyprid frequently settles a few millimeters from that individual. The territory immediately adjacent
to the attached conspecific is thus avoided, although a site quite close to a competitor may be selected (Crisp, 1961).

In addition to gregarious responses, certain attributes of the substrate are selected by the barnacle cyprid. Most barnacles are rugophilic, settling in grooves and concavities (Moore, 1935; Moore and Kitching, 1939; Pomerat and Weiss, 1946; Barnes, Crisp, and Powell, 1951; Crisp and Barnes, 1954; Skerman, 1958; Barnes and Reese, 1960; Connell, 1961). Highly fibrous surfaces may, however, inhibit settlement (Barnes and Powell, 1950). One exception noted by McDougall (1943) is *Balanus eburneus*, which selects smooth over rough substrates. Subsequently, however, individuals on rough substrates become more firmly attached and tend to show enhanced survivorship.

Shaded substrates are much preferred to lit substrates by barnacle cyprids (Visscher, 1928; McDougall, 1943; Gregg, 1945; Pomerat and Weiss, 1946; Skerman, 1958; Thorson, 1964), as are substrates of a dark color (Pomerat and Reiner, 1942; McDougall, 1943; Gregg, 1945). However, the mechanisms and functions of selection of a dark background are not understood. Since less preferred habitats near preferred habitats are settled after the latter are densely populated, the analysis of settling preferences may be complicated (Crisp and Barnes, 1954).

Another important physical factor influencing settlement is current. Many species require currents of a certain range in order to attach. Current direction also influences orientation, which is usually downstream prior to attachment (Moore, 1935; Smith, 1946; Crisp, 1953; Crisp and Stubbings, 1957). Using rotating discs, Smith (1946) found
that water velocity limits attachment between 0.5-0.9 knots for *Balanus amphitrite*, between 0.4-0.7 knots for *B. eburneus*, and to greater than 1.1 knots for *B. improvisus*. The physical attributes of the water mass may also influence settlement (Wilson, 1958). Also, a thin surface film may favor settlement (Knight-Jones, 1953), but thick films of microorganisms are inimical to attachment (Pomerat and Reiner, 1942).

The settlement of barnacle cyprids seems to be timed in order to maximize chances of locating a suitable substrate. Prior to settling, cyprids exhibit diurnal migratory behavior (Visscher and Luce, 1928), which may be correlated with becoming photonegative and avoidance of strong light during the day (Thorson, 1964). In some species, there is a rhythm of settling in which daylight hours are preferred unless the water is artificially illuminated at night (Weiss, 1947). A tidal component may also be involved. Visscher and Luce (1928) noted a greater number of larvae on incoming and high tides and McDougall (1943) found settlement to occur at high water for *B. eburneus*. Weiss (1947), on the other hand, found greatest settling of *B. improvisus* during low tide. Thus far, lunar rhythms have not been documented in barnacle larvae (Crisp and Davies, 1955).

Once attachment occurs, barnacles are more or less fixed to their chosen sites. There is often a high mortality in densely settled areas due to lateral flattening, undercutting, and smothering. In species such as *B. balanoides*, dense concentrations lead to the formation of hummocks, which are quite vulnerable to peeling off during adverse sea conditions (Connell, 1961a). However, rotation may take place during growth in
response to prevailing light and current (Moore, 1935; Crisp, 1953; Crisp and Davies, 1955; Crisp and Stubbings, 1957). Also, once settled, the individual can modify its shape to accommodate neighbors (Moore, 1935). Individuals of some species are even capable of slowly gliding over the substrate in response to lateral pressure and may, in this way, come to fill odd spaces (Crisp, 1960, 1961). Such limited mobility may allow adjustments to growth within a crowded barnacle population and also allow colonization of shell surfaces.

The initial patterns of distribution are later shaped not only by intra- and interspecific competition (Connell, 1961a, 1961b, 1972, 1974; Paine, 1966, 1974; Dayton, 1971), but also by predation (Connell, 1961a, 1961b, 1970, 1972, 1974; Paine, 1966, 1969; Dayton, 1971) and physiological limitations (Doty, 1957; Kensler, 1967; Connell, 1961b, 1972, 1974). In the case of intertidal species, the upper limit of distribution is frequently set by intolerance to physical factors, particularly desiccation and temperature extremes. Competitive hierarchies and predation define the lower limits of distribution. In some cases, selective predation may enable a species to exist in areas where it would otherwise be competitively excluded. In addition to biotic disturbances, physical disturbances may result in random denudation of barnacle colonies and thereby impose additional patchiness (Dayton, 1971). The overall result of these influences is that a species may be restricted to a narrow band, or "refuge" zone (Connell, 1970) where growth, reproductive capacities, and survival may be suboptimal.
Gregarious settling behavior is also manifested in the wood-boring isopod *Limnoria*. In this genus, there is evidently a local, seasonal migration of several meters prior to mating by mature individuals (Johnson, 1935). Burrows are dug by the males which initially occupy the blind end. Subsequent to copulation, the female and male reverse positions within the burrow (Menzies, 1972). Johnson and Menzies (1956) noted that the migratory swarm occurs at night and is correlated with high water temperatures. No preference is shown for settling with respect to depth, but settlement following initial random colonization becomes clumped (Menzies and Widrig, 1955), suggesting the production of a chemical attractant. Dr. F. A. McNeill (quoted in Schmitt, 1965) found *Limnoria lignorum* to be invested in wood at densities of 18-24 individuals per cm$^3$. This represents a high tolerance for crowding, considering that larger individuals may be almost a centimeter long.

Access to mates is only rarely the obvious function of an aggregation of a motile benthic species. Although a variety of mechanisms and selective values have been purported, even many spectacular cases of clustering remain largely unexplained. Crane (1947, pp. 83-84) does record the following pertinent observation: "... as in other animal groups, those crabs which are predominantly vegetarian or feeders on microorganic food live in larger groups than predacious forms." This observation corresponds to those of McNab (1963) who concluded, on the basis of bioenergetic considerations, that only "croppers" (grazers and browsers) could afford to maintain locally dense populations. However,
the positive aspects promoting clustering versus dispersal within this class of feeders remain unclear.

Instances of clustering behavior among the benthic motile Crustacea have received only scattered attention. Clusters among the many small pericarid crustaceans can easily go unnoticed. It is, therefore, not surprising that few studies involve spacing of these organisms. However, congregations are evidently widespread. Many species of amphipods, for example, build nests in clusters or live in colonies built on tubes. *Ericthonius hunterii* forms colonies of mud tubes several inches high, for instance (MacGinitie and MacGinitie, 1949). However, the degree of sociality in these amphipods has not been explored. In the marine amphipod *E. braziliensis*, tubes are so constructed that the feeding territories of individuals do not overlap (Connell, 1963). Therefore, within an established colony of this amphipod, individuals maintain a uniformly dispersed pattern of distribution. Fighting for homesites is, thus, limited. However, wanderers, especially if smaller, are driven off.

Another amphipod which clusters is the salt marsh amphipod *Orchestia palustris*. Smallwood (1905) found that this species collects under rocks as a result of contact reactions, negative phototaxis, and response to moisture. Without cover, individuals would cling to one another, but glass tubing provides sufficient contact to diminish this response. In the intertidal zone, the related amphipod *O. littorea* similarly shelters in cracks and holes by the hundreds at low tide (Murray and Hjort, 1912).
Among sand burrowing amphipods, Bowers (1964) suggests that in Orchestoidea corniculata the close packing of burrows increases the air spaces and softens the sand. Thus, individuals expend less energy than if their burrows were widely spaced. Bowers found ritualized fights for burrows, and possibly for females, in two species of this genus. Another study by Campbell (1974) reports aggregation in the burrowing amphipod Corophium volutator. Aggregation of this species stems in part from selection of fine sand substrates. However, intraspecific recognition is also involved, since grouped animals show a much more pronounced tendency to burrow. Campbell suggests that this gregarious tendency aids in sexual reproduction, protects individuals from predation, and produces aggregations in more favorable environments.

Among large brachyuran crabs, some impressive clustering behavior is known. The heaps formed by the spider crab Maja squinado are particularly remarkable. Carlisle (1957) reported that one such heap, located in June in Plymouth waters, was composed of about 60 individuals and was located only one meter below the low spring tide level. The heap remained stationary with the crabs on the bottom clinging to an isolated rock. By July, twenty additional crabs had joined. According to Carlisle, the heap consisted of molting and copulating crabs. In the center of the heap were located soft crabs, a few molting each day. By August, six to eight pairs could be observed mating at one time. Members of the heap began to disperse by mid-September.

Stevčić (1971) noted that heaps of M. squinado also occurred in shallow waters (less than 5-10 m) in the Adriatic Sea.
laboratory studies of the dominance structure, Stevčić observed that the "dominant" crabs invariably occupied outer positions. The primary function of heaping, thus, seems to be protection of molting individuals. Baal (1953) observed that crabs in heaps were relatively secure from predation by octopuses, in contrast to other motile species. Sexual access to newly molted females (Carlisle, 1957) may not be critical, since mating can apparently occur when both sexes are hard (Hartnoll, 1965; Stevčić, 1971). However, the degree of reproductive success may be increased by such aggregations.

The Tanner crab *Chionoecetes tanneri*, a giant, commercial spider crab, also clusters, but under quite different circumstances (Pereyra, 1966). Males and females remain vertically segregated from April through September, but in winter males congregate in the zone of abundance of females (about 640 m). During this period of intermixing, females, which are three times as numerous as males, release maturated eggs and ovulate anew. Thus, winter clusters may enhance the necessarily polygamous breeding. Dispersal at other times may increase the effective feeding area.

The small, mud-burrowing crab *Goneplax rhomboides* (Family Goneplacidae) lives in underwater colonies (Rice and Chapman, 1971; Atkinson, 1974a,b). In this species, territorial defense and ritualized male combats have been observed (Atkinson, 1974b). The horizontal tunnels are rather complex with 1-6 openings (Atkinson, 1974b) and are frequently clumped in their distribution (Atkinson, 1974a).
There is also evidence suggesting clustering of other marine brachyuran crabs. For example, Garth (1946) records that *Ozius perlatus* lives in small colonies in favored localities in the Galapagos. About 40 individuals were removed from a single moist pocket in James Bay. Crane (1947) found that *Xanthodius sternberghii* maintains two distinct patterns of distribution. During low tide, a single male plus two to three gravid females and young usually refuge under each damp rock. When covered by water, the crabs mobilized, dispersing to open areas exposed to bright sunlight, in order to feed. Crane recorded a similar pattern for *Eurypanopeus planus*. However, in this species, only one adult male and one or two gravid females lived under one stone.

The participation of some grapsid crabs in clusters, particularly in the supralittoral and shore habitats, is well-known to beachcombers and naturalists. In the supralittoral, the lined shore crab, *Pachygrapsus crassipes*, clusters in crevices and fissures by day, dispersing at night in order to forage (Hiatt, 1948; Bovbjerg, 1960). Crabs of the same species which live in tidepools, in contrast, actively forage in the day and do not aggregate (Bovbjerg, 1960). In tidepools, only one crab occupies each crack, and aggression occurs during close encounters between two crabs. In the laboratory, Bovbjerg was able to demonstrate that submergence accounts for this altered behavior. He postulated that occupation of the supralittoral enables escape from marine predators and that behavioral differences have evolved which enable aggregation in the few suitable crevices and at the same time help conserve moisture. Although no pheromones are yet implicated in their aggregative behavior,
the molting pheromone, crustecdysone, is known to be involved in sexual attraction (Kittredge, Terry, and Takahashi, 1971).

There are also scattered mentions of clustering behavior in several grapsid relatives. For example, Garth (1948) notes the "swarms" of Grapsus over rocks at sea level, notwithstanding some cannibalism. Steinbeck and Ricketts (1941) report many comical escapades aimed at catching Grapsus grapsus, or "Sally Lightfoot." Their stories reinforce the idea of cohesive escape movements by hordes of this species. Crane (1947) calls attention to the yet unexplained, but common, phenomenon in which members of this species sun themselves on damp rocks in groups.

A number of grapsid crab species, including Sesarma sulcatum (Wright, 1967), S. meinerti (MacNae, 1968), S. smithii (MacNae, 1968), Goniopsis pulchra (Wright, 1967), and Helice crassa (Beer, 1959), form colonies and defend burrows. In the cases of S. meinerti and H. crassa, territorial display and defense are utilized, but little is known of the factors influencing cluster formation or the benefits derived.

The gregarious tendencies of semi-terrestrial ocypodid crabs appear to be quite highly developed. Although often territorial with respect to a particular burrow, the fiddler and ghost crabs, Uca and Ocypode, usually exhibit a high degree of colonialism in burrow placement. Although Pearse (1914) relegates crowding merely to individual selection of the most suitable habitat, Crane (1941b) has noted species-specific colony formation even within homogeneous habitats.

Ocypodid crabs manifest complex social behavior, which may result in colony formation and regulation, as well as in social interaction.
Display of the major cheliped by the male, sometimes accompanied by body movements and color changes (Crane, 1941a, 1941b, 1943, 1957, 1958, 1967; Salmon, 1965, 1967; Griffin, 1968; Salmon and Atsaides, 1968) are utilized in courtship and/or ritualized aggressive communication during the day. These displays are species-typical and highly stereotyped (Crane, 1941a, 1941b, 1957; Salmon and Atsaides, 1968), so that actual aggression is usually avoided.

Sound production assumes major importance when crabs cannot be seen; for example, within the burrow, amid vegetation, or at night (Burkenroad, 1947; Salmon and Stout, 1962; Salmon, 1965, 1967; Salmon and Atsaides, 1969; Salmon and Horch, 1972). Sound production is channeled most effectively through the substrate and is as important and widespread as visual display in the communication of ocypodid crabs (Burkenroad, 1947; Salmon and Stout, 1962; Salmon, 1965, 1967, 1971; Crane, 1967; Salmon and Atsaides, 1968, 1969; Horch and Salmon, 1969; Altevogt, 1970; Salmon and Horch, 1972, 1973). Both bubbling and stridulation, including rasping and rapping sounds, may be produced under different circumstances and in one or more ways: by ambulatory leg movements, rapping with the propodus, body thumping, and rubbing of stridulatory surfaces. Ocypodid crabs seem to be tuned to certain sound frequencies and species-typical patterns of production also occur, indicating the likelihood of species-typical communication by sound also.

In at least one ghost crab, Ocypode saratan, sand pyramids are constructed by males to attract females in lieu of courtship display (Linsenmair, 1967). In this species, a complex is built by adult males
consisting of a pyramid, a pathway, a vestibule, and a spiral burrow. In addition to attracting females at a distance, the pyramids, constructed at a minimum of 134 cm apart, may also function in the spacing of burrows (Linsenmair, 1967; Lighter, 1974). The size of the neighboring crab and burrow-filling by the dominant males are also determinants of spacing. Pyramid construction has also been recorded for *O. ceratopthalmus* at Eniwetok by Horch and Salmon (1969), but in this species the function is unknown. The hoods and archways constructed by males of some fiddler crabs (Crane, 1943; Linsenmair, 1967) and the hoods of some *Sesarma* burrows (MacNae, 1968) may serve similar functions or act as acoustical baffles in communication.

In addition to the manifestation of elaborate courtship and ritualized agonistic conduct of ocypodid crabs, individuals of both sexes and assorted sizes feed together, typically in close proximity to their respective burrows (Pearse, 1914; Crane, 1967). However, some species adjourn to different feeding areas. Altevogt (cited in Schöne, 1961, p. 475) reports that in *Uca marionis* individuals form a queue of 15-20 individuals. Their march carries the group to new feeding grounds. Hyman (1922) found that *U. pugilator*, after emergence and a period of excavation, formed huge aggregations which moved and fed along the water's edge. Herrnkind (1968; in Herrnkind, 1972) found these droves to be quite cohesive, due to the orientation of members within the drove to conspecifics. The movement of the aggregations, Herrnkind found, was greatly facilitated by their acute directional orientation, involving a telotaxis toward objects of optical contrast and a time-compensated
celestial orientation ability. Apparently *Uca pugnax* also wanders (Rathbun, 1918), but the extent of cohesion among individuals is unclear. Valiela et al. (1974) suggest that the prolonged excursions of male *Uca*, sometimes even into shallow water, stem from their need to feed for a longer period of time to compensate for the possession of only one utilizable cheliped in feeding.

Although some fiddler crab species occur on identical substrates in colonies of close proximity (Crane, 1941b), some fiddler crabs species do segregate on the basis of substrate preference (Teal, 1958; MacNae, 1968). Temperature tolerance may also account for some segregation (Edney, 1961; MacNae, 1968), while in yet other species competitive exclusion seems to operate. Teal (1958) found that there is a 50% reduction of burrowing activity by *U. pugilator* in the presence of *U. pugnax* or *U. minax*, while *U. minax* reduced its burrowing by 25-55% in the presence of the other two species. Likewise, Aspey (1971) recorded reduced burrow densities when both *U. pugnax* and *U. pugilator* overlap. However, *U. stenodactyla* and *U. stylifera* may apparently reduce their inter-burrow distances when mixed from 7.5 to 3.8 cm (Crane, 1941b), suggesting enhanced coexistence with mixes of these species.

Although the behavioral repertoire of ghost crabs is similar to that of fiddler crabs, there is considerable variation in feeding behavior and burrow spacing, both between and within species. Barrass (1963a,b) reports that the burrows of *Ocypode ceratophthalmus* are widely spaced, while Hughes (1966) contends that considerable plasticity in
spacing exists, depending on environmental factors. Grubb (1971) reports interconnecting burrows in this species.

With regard to the frequently observed feeding aggregations of *Ocypode*, Barrass (1963a,b) suggests that these are imposed by high tides and Hughes (1966) relegates these aggregations to both tide and limited food supply. However, Jones (1972) reports studies to the contrary. In *O. kuhlii*, Jones observed that 90% of the population aggregated in the swash zone during high tides. At night, individuals participated in a wandering phase with only intermittent feeding and no antagonistic behavior. Feeding occurred during the day. Jones postulated that since *O. kuhlii* otherwise spends most of its time in widely spaced burrows, this behavior functions to bring the population together at regular intervals, perhaps for epideictic purposes.

Clustering among species of *Uca* and *Ocypode* is so far seen to result from a combination of spatial limitations and gregarious tendencies. Yet another important aspect of clustering is the synchrony of movement and behavior. Time-compensated celestial navigation in addition to teletaxis toward objects of optical contrast enables oriented, synchronous movements in a number of ocypodid genera, including *Uca*, *Ocypode*, and *Cardisoma* (see review by Herrnkind, 1972). Activity cycles in ocypodid crabs are also present in many species, but are best documented in *Uca* (see review by Barnwell, 1968). In nature, the phasing of different activities in several species of *Uca* is evidently influenced by exogenous factors superimposed on the activity cycle (Crane, 1958). The activity cycle often contains diurnal, tidal, and (consequently)
semilunar components. Other rhythms besides activity may also be involved in the behavior of ocypodid crabs. In *U. pugnax* there is a rhythm of phototaxis (Palmer, 1964) and in *U. pugilator* a tidal rhythm of directional preference exists (Herrnkind, 1972). The synchronous behavior of fiddler crabs in complex tidal situations may be less consistent than those of predictable diurnal or tidal situations. Honegger (1973a,b) found a rather weak correspondence between the activities of *U. crenulata* to both light and tide. Turbulence at high tide seemed to inhibit high tide activity in this species in nature.

Natural periods of activity are also well known in *Ocypode* (Barrass, 1963a; Harrigan, cited in Salmon and Horch, 1972, p. 63; Hughes, 1966; Palmer, 1971; Jones, 1972). In *O. ceratophthalmus*, Jones (1972) showed an endogenous diel rhythm, with no tidal component. Likewise, Palmer (1971) demonstrated an endogenous diel rhythm with high night activity in *O. quadrata*. In *O. kuhlii*, which is active both night and day, Jones (1972) was unable to demonstrate any rhythm.

In genera related to *Uca* and *Ocypode*, there is far less known of gregarious tendencies. However, Wright (1968) reports that the ocypodid crab *Ucides occidentalis* maintains extensive and crowded colonies in which each individual occupies its own hole. The estuarine ocypodid *Hemioplax hirtipes* is also colonial but as far as Beer (1959) could ascertain, individuals live in and defend burrows dug by another species.

In southeast Asia and the East Indies, the ocypodid beach crab, *Dotilla myctiroides*, manifests gregarious tendencies, reminiscent of human military maneuvers (Schmitt, 1965). Although these crabs may
instantly burrow when threatened, individuals may be three or four deep when initially detecting danger. According to Schmitt, the countless numbers give beaches an appearance of "endless shimmering." A continuous rustling and swishing is heard when the crabs move over the surface, which Schmitt suggests gives warning of a change in movement to all members of a corps.

Hartnoll (1973) only noted one march of D. fenestrata on East African shores, which he did not apparently study. However, Hartnoll did find that small individuals, females, and young males maintain semi-permanent burrows beyond which they rarely venture. Males, after feeding in the vicinity of their burrows, wander over the intertidal, engaging in social contacts until just before flood tide, when they burrow anew. Only 50% of the population was active during a low tide period. At Mocambique, MacNae and Kalk (1962) found that, while juveniles remained feeding in dry areas of the lower midlittoral zone, adults migrated up and down the beach with the tide, burrowing just prior to flood tide.

The ocypodid crabs Heloeicus cordiformis and Hemiplax latifrons exhibit patterns of behavior perhaps homologous to those of Uca (Griffin, 1968). The crabs maintain burrows from which they emerge as the tide recedes and around which most activity, including feeding, is centered. Like Uca, these species display typical waving patterns for courtship and agonistic functions. The burrows are defended by males, which engage in combat as well as ritualized display. Aggressive wandering by individuals is also common. Even "play" is developed in H. cordiformis.
Other semi-terrestrial crabs also exhibit strong gregarious tendencies. *Gecarcinus ruricola*, the blue land crab, constructs burrows in low marsh areas. The burrows intersect one another in all directions according to Freminville (Rathbun, 1918). Following rains, *Gecarcinus* emerge from their burrows and wander up and down hills (Chace and Hobbs, 1969). *Gecarcinus quadratus* is found frequently under trunks of trees in groups of six to eight, on the other hand (Rathbun, 1918). Like many crustaceans, members of this genus exhibit diurnal rhythms of activity, with high activity at night (Bliss and Sprague, 1958; Bliss, 1960; Palmer, 1971). Abele, Robinson, and Robinson (1973) have found that at least one species produces bubbling and stridulating sounds, especially when disturbed or attacked by dummy predators. Since a brown, bitter-tasting fluid is secreted concurrent with bubbling, a warning of predators may be the principal function.

The semi-terrestrial ocypodid crabs *Cardisoma crassum* and *C. guanhumi* also live in crowded colonies of considerable size (Wright, 1967). In the case of *C. guanhumi*, burrows are apparently constructed as close together as possible without resulting in interconnections or collapse (Gifford, 1962). Pearse (1916) mentions that hordes of this species come forth at night near Santa Marta, Columbia, and walk about everywhere over the flats, even climbing trees. The extent of cohesion in these hordes was not indicated. *Cardisoma carniflex* individuals are also quite tolerant of crowding, with members both feeding and resting together (Grubb, 1971). At night, hundreds congregate to feed on the edges of solution pans.
Another parallel with the ocypodid crabs is the occurrence of male combats in *Cardisoma*. According to Herreid (1963), individuals also feed within close proximity of the burrow (two meters). Individuals are quite sensitive to sound, especially of falling fruit or leaves. Herreid found that the usually observed nocturnal activity of *Cardisoma* may be altered in the case of colonies located in the shade and remote from human activity. An endogenous rhythm of activity with nightly peaks has been revealed in one *Cardisoma guanhumi* population, in conformity with its more usual behavior (MacNae, 1968; Palmer, 1971). In some cases, *C. carniflex* constructs colonies of sand castles, resembling termitariums, up to 75 cm tall with both a top entrance and several other openings (Silas and Sankarankutty, 1960). These towers are reminiscent of the towers of *Ocypode saratan*; the function, however, is unknown.

Perhaps most spectacular of all are the curious congregations of the soldier crab, *Mictyris longicarpus*, which occur during the feeding and wandering phase (Cameron, 1966). During and after feeding, the soldier crabs assemble into armies of many hundred individuals, consisting almost entirely of males. Although cohesive forward motion is displayed, the armies are apparently without permanent leadership. Instead, larger individuals exchange places within the vanguard. After formation of this congregated stage, the armies may cover as much as 456 m and wander for up to two hours before orienting homeward and dispersing. At this time, females, who have been feeding, and males return to their burrows. Meanwhile, a certain percent of the individuals have
remained in their burrows. Some kind of apportionment of food or space resources may be involved in this latter behavior.

The intertidal sand crabs of the genus *Scopimera* also occur in quite dense, restricted aggregations (Harada and Kawanabe, 1955; Sugiyama, 1961; Silas and Sankarankutty, 1967; Fielder, 1970). *Scopimera globosa*, *S. proxima*, and *S. inflata* normally occupy semi-permanent burrows and feed in the near vicinity at low tide. Some nest hole exchanges occur, however. In situations of high density, combats may increase (Harada and Kawanabe, 1955), but the alternate feeding at the surface by different portions of the population would seem to reduce the potential number of combats (Sugiyama, 1961). The spacing of holes within the colony is often quite uniform (Harada and Kawanabe, 1955), and apparently stems from territorial behavior, including actual combats, in addition to threat displays. Following the feeding period, large males may act as "rogues," wandering from their territories and forcing feeding crabs to retreat within their burrows (Fielder, 1970). Combats may result in nest abandonment and in the formation of fugitive, loose aggregations outside the species' normal habitat (Sugiyama, 1961). Artificial increases in the density also result in evictions until the original colony size is achieved (Harada and Kawanabe, 1955). In contrast, in low density areas, each crab may extend its feeding area. Colonies artificially depleted of their numbers return rapidly to their original numbers, as a result of the invasion of new crabs.

Many anomuran crustaceans exhibit gregarious propensities similar to those of brachyuran crabs. The Alaskan king crab, *Paralithodes*
camtschatica, partake in large clusters termed "pods" (Powell and Nickerson, 1965; Powell, 1974). One such pod was studied for over 57 days. It consisted of 40-50 individuals, primarily juveniles, but also some less densely packed adults. The pod was shaped like a low pyramid and consisted of about equal numbers of males and females. All members faced outward and there was a normal size distribution of individuals. Pods such as this are believed to merge after one year into elongated "domes." The domes are formed parallel to the beach and may consist of approximately 500,000 individuals. Only the crabs on the bottom are able to probe for food. While the bulk of the dome remains intact, thousands of other crabs are scattered and feeding. Neither the functions nor the mechanisms of these clusters are understood. Powell and Nickerson (1965), however, advocate predator protection and "biological organization and control" as advantages of the behavior.

Other lithode crabs also are strongly gregarious. Lithodes antarctica form aggregations which seem to result from attraction by females of males, which firmly embrace the female. This habit is capitalized on by Chilean fishermen who use females repeatedly as "love lures" (Schmitt, 1965). A similar attraction of males to female L. maja was noted by Pike and Williamson (1959). These observations are highly suggestive of the presence of a sex pheromone.

Porcelain crabs also appear to be gregarious to a large extent, but little in specifics has been recorded. MacKay (1945) noted that 5-6 specimens of Petrolisthes cocineus are normally present under each rock in the Hawaiian intertidal zone. MacGinitie and MacGinitie (1949) state
that, in general, where species of Petrolisthes occur at all, individuals are usually quite abundant. Bovbjerg (1960) found that P. cinctipes aggregates under stones and at the bases of Mytilus beds. Observed in the laboratory, aggregation was also the rule and no tension contacts were noted. Molenock (1975) found that this species manifests ritualized behavior and defends territories during courtship. The territories consisted of a harem of 1-4 females, which occasionally "groomed" the male.

The large, long-tailed Pacific beach "crab" or "mud lobster" Thalassina anomala exhibits behavior parallel to some ocypodid crabs (Horst, in Wynne-Edwards, 1962, p. 175; Sankolli, 1963; Schmitt, 1965; MacNae, 1968). It lives in grass-covered swamp flats and raises towers to 3/4 m high. Each tower contains a rounded retiring cavity several centimeters wide. These towers are often quite dense and the underlying burrows are apparently large and ramifying with lengths many meters long. No detailed study of this species exists, unfortunately, in part because of the animal's subterranean and nocturnal habits (Sankolli, 1963; MacNae, 1968).

Clustering among marine hermit crabs is also a commonly observed phenomenon, both in nature and in the laboratory. However, this topic is deferred until the following chapter, in which it is thoroughly reviewed.

Land hermit crabs also exhibit strong gregarious tendencies, but these have so far received little attention. Chace and Hobbs (1969) found Coenobita clypeatus to be gregarious with 5-6 individuals within a square foot, and more than one dozen in congregations under stones by day. Similarly, Palmer (1971) reports groups under piles of litter and
windfalls during the day. He comments that the most common sounds in south Bimini are from hordes of this gregarious crab shuffling through leaf litter. Of C. compressus, Ball (1972) states that, during the day, great aggregations can frequently be found under ledges, in small rocky caves, under logs and driftwood, or dug into the sand. In addition to sleeping aggregations, feeding aggregations may occur. Coenobita rugosus clusters around the feces of the tortoise Gnettarda (Grubb, 1971). Massive clusters 4 feet in height may also occur annually during daytime periods of congregation; at night, individuals may scatter and initiate shell exchanges (Carpenter and Logan, 1945).

Aggregations of land hermit crabs also apparently form for the purpose of shell exchange. Radinovsky and Henderson (1974) describe the incidence of shell-exchanging aggregations of C. clypeatus. A switch between two individuals appears to trigger mass exchange. In one case, they noted 13 participants in such an aggregation. They propose that mass exchanges are one means of insuring that most crabs inhabit suitably sized shells.

Members of the genus Coenobita utilize both visual displays and sounds in communicatory behavior (Hazlett, 1966c). Also, synchronous behavior appears to be characteristic of this genus, which manifests a circadian rhythm of locomotor activity (Palmer, 1971). The fact that C. clypeatus may live eleven years or more (Chace, 1972) may allow for the extended benefits of sociality such as learning.

Lobsters also exhibit gregarious tendencies, including cover-sharing, nocturnal group foraging, queuing, and migrations (see Schools).
In some species of lobsters, coversharing is only pronounced among young. For instance, Fielder (1965) found young *Jasus lalandii* to cluster in nature, although older *Jasus* tend to be solitary. Juvenile *Panulirus argus* also commonly share cover both in beds of *Thalassia* and in the laboratory (Berrill, 1975). They are distracted from coversharing only by queuing of their cohorts. Adults of this species may also gregariously cluster in large crevices (Herrnkind, 1970). Gregariousness within the den is suggested to be effective against some predators by means of mutual warning and defense (Berrill, 1975). It may also be adaptive in areas where shelters are in short supply. In *Homarus americanus*, even young do not share shelters, except in crowded laboratory conditions (Cobb, 1971). Among burrowing lobsters, there is also sometimes a tendency to burrow in groups spaced by greater intergroup distances, as in *Nephrops norvegica* (Dybern and Høisaeter, 1965; Chapman and Rice, 1971), but random distribution is also known for this species (Atkinson, 1974a).

Visual cues (Herrnkind, 1969, 1970; Berrill, 1975) and tactile cues (Herrnkind, 1969, 1970) are very important in queuing and migration and may likewise be critical determinants of local clustering patterns. However, Herrnkind and McLean (1971) found that most lobsters, even if blinded, were able to orient directionally and home. A 20% recovery rate was realized by Creaser and Travis (1950), even when lobsters were released two miles from the homesite in 1500 m of water or behind land barriers five miles around, indicating the use of sensory modalities other than vision or tactile cues. These senses must be quite keen in
order to allow certain individuals to occupy the same hole for several consecutive years (Herrnkind and McLean, 1971).

Communicatory sounds may be important in homing and social behavior (reviewed by Moulton, 1964). These include stridulation upon impending threat or conflict (Lindberg, 1955; Moulton, 1957) and a slow rattle, when lobsters are contained in groups (Moulton, 1957). These sounds may be species-typical (Hazlett and Winn, 1962). In Homarus americanus, sounds are perceived in the low frequency range by means of substrate vibration (Cohen, 1955) and very likely by water-borne vibration also (Offutt, 1970). Both low frequency pressure waves and vibrations are also received by hair-fan organs in H. americanus (Laverack, 1962, 1963).

Chemical communication may also play a salient role in the social behavior of lobsters. There is evidence of water-borne sex pheromones in Homarus americanus (Hughes and Matthiessen, 1962; McLeese, 1970; Atema and Engstrom, 1971) and in Jasus lalandii (Rudd and Warren, 1976). The pheromone may be crustecdysone, the molting hormone, or one of its metabolic products (Kittredge and Takahashi, 1972; Rudd and Warren, 1976). However, in H. americanus, tests of crustecdysone and related ecdysones have yielded negative sexual responses, as well as defensive and aggressive responses (Atema and Gagosian, 1973; Gagosian and Atema, 1973). These sensitivities at least give promise to the possibility of chemical communication.

Among benthic shrimps, surprisingly little information exists on patterns of spacing or social behavior. However, the reef shrimp Saron
marmoratus apparently forms large feeding aggregations of several hundred individuals. Kruschwitz (1967) has found that a "gregariousness" pheromone may be responsible for the nocturnal formation of such groups, the function of which is not understood.

Summary

In this chapter, five types of contagion found among marine crustaceans are described. The results of this survey are summarized in Table 1. The order of presentation of the different types of contagion may or may not reflect an evolutionary sequence in the degree of organization. In particular, the placement of "migratory assemblages" is questionable, since so little documentation of causal mechanisms and functions is available.

The results of this review indicate that contagion may be the consequence of a variety of interacting mechanisms and is seldom the consequence of a single mechanism. Responses to physico-chemical gradients may be complicated by the presence of reversible taxes. Also, endogenous rhythms may dictate behavior either in the presence or in the absence of environmental variation. The advantages imparted by contagious distribution are not easily deciphered in most of the studies reported, although a plethora of advantages have been proposed, many of which are mutually compatible.

Experimental studies are clearly in great need in the area of crustacean aggregations. However, the diversity of mechanisms and advantages evidenced even within the crustaceans dictates that extreme
<table>
<thead>
<tr>
<th>Type of Contagion</th>
<th>Possible Mechanisms</th>
<th>Possible Advantages</th>
</tr>
</thead>
<tbody>
<tr>
<td>Patches</td>
<td>Physical Concentration or Individual Responses to Environmental Gradients</td>
<td>None or increased food; buoyancy; or physiological tolerance</td>
</tr>
<tr>
<td>Stratifications</td>
<td>Individual Responses to Environmental Gradients according to size, sex, or ontogeny; Conspecific Responses?</td>
<td>Reduction in intra-specific competition or cannibalism; reduction in energy expenditure; reduction in predation</td>
</tr>
<tr>
<td>Migratory Assemblages</td>
<td>Individual Responses to Environmental Gradients which change or may be reversed; Endogenous Rhythms; Conspecific Responses?</td>
<td>Avoidance of toxins; UV procurement of food; maintenance of position; release of larvae; predator avoidance; increased polytypy; enhanced biotic accommodation; cultivating the maximum sustainable yield</td>
</tr>
<tr>
<td>Swarms and Clusters</td>
<td>Individual Responses to Environmental Gradients; Conspecific Responses (both of the above may be rhythmic)</td>
<td>Enhanced reproductive success; maintenance of genetic integrity; eideictic display; retention of moisture (intertidal or supralittoral spp.); reduced energy expenditure in burrowing; protection of molters; reduction of predation; shell exchange (land hermit crabs); mutual warning</td>
</tr>
<tr>
<td>Schools</td>
<td>Conspecific Responses</td>
<td>Improved location and capture of prey; predator avoidance; drag reduction</td>
</tr>
</tbody>
</table>
caution be exercised in the interpretation of mechanisms of contagion. Particularly, the acceptance of a single mechanism rather than multiple, possibly redundant, mechanisms is to be avoided. Likewise, the chance of multiple advantages of contagion requires careful consideration.
CHAPTER 3

SPACING IN HERMIT CRABS

Introduction

In the case of the prevalent, but puzzling, habit of clustering among hermit crabs, an overview of the habit is clearly desirable in addition to autecological studies. A comparative survey of the spacing patterns of marine hermit crabs is, therefore, presented in this chapter. Table 2 summarizes data on the clustering habits of marine hermit crabs in nature. In addition to published sources, results from a census of prominent researchers in crustacean biology are included in the survey. The data of Table 2 reveal a widespread tendency of hermit crabs to cluster. Trends with regard to species, types of clusters, composition of clusters, and environmental variables are examined below.

Clustering Species

The marine hermit crabs fall into one superfamily, the Paguroidea, composed of two families: the Paguridae and the Diogenidae. The clustering habit appears to be more characteristic of diogenid genera, especially species of Clibanarius and Calcinus. (Table 2). In these genera, the ratios of clustering to non-clustering species are 12:1 and 5:2, respectively. In contrast, only 7 of 16 species of Pagurus (Family Paguridae) cluster. Since species of Clibanarius and Calcinus are tropically derived, while members of Pagurus typify waters of colder
Table 2. Spacing Patterns of Marine Hermit Crabs in Relation to Habitat Preference and Body Size.

<table>
<thead>
<tr>
<th>Species</th>
<th>Habitat</th>
<th>Zone</th>
<th>Body Size</th>
<th>Clumps?</th>
<th>Rhythm</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aniculus elegans</td>
<td>varied</td>
<td>SL</td>
<td>large</td>
<td>2-5+</td>
<td>-</td>
<td>Haig et al. (1970)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Ball and Haig (1974)</td>
</tr>
<tr>
<td>Calcinus californiensis</td>
<td>rocky</td>
<td>L,SL,TP</td>
<td>medium</td>
<td>yes</td>
<td>-</td>
<td>Snyder-Conn (pers. obs.)</td>
</tr>
<tr>
<td>Calcinus explorator</td>
<td>rocky</td>
<td>TP+?</td>
<td>medium</td>
<td>yes</td>
<td>-</td>
<td>Snyder-Conn (pers. obs.)</td>
</tr>
<tr>
<td>Calcinus herbstii</td>
<td>?</td>
<td>L</td>
<td>small</td>
<td>yes</td>
<td>-</td>
<td>MacKay (1945)</td>
</tr>
<tr>
<td>Calcinus laevimanus</td>
<td>broken</td>
<td>L</td>
<td>small</td>
<td>no</td>
<td>moves with tide</td>
<td>Reese (1969)</td>
</tr>
<tr>
<td></td>
<td>coral</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Hazlett (1970a)</td>
</tr>
<tr>
<td>Calcinus latens</td>
<td>rocky</td>
<td>L,SL</td>
<td>small</td>
<td>yes</td>
<td>clumps at high tide</td>
<td>Reese (1969)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Hazlett (1970a)</td>
</tr>
<tr>
<td>Calcinus obscurus</td>
<td>rocky</td>
<td>L</td>
<td>medium</td>
<td>no</td>
<td>-</td>
<td>Ball and Haig (1974)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Ball (1973)</td>
</tr>
</tbody>
</table>
Table 2. Spacing Patterns of Marine Hermit Crabs. — Continued.

<table>
<thead>
<tr>
<th>Species</th>
<th>Habitat</th>
<th>Zone</th>
<th>Body Size</th>
<th>Clumps?</th>
<th>Rhythm</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Calcinus tibicen</em></td>
<td>rocky, coral</td>
<td>L,SL</td>
<td>small</td>
<td>yes, in shallows</td>
<td>daytime clumps</td>
<td>Hazlett (1966a)</td>
</tr>
<tr>
<td><em>Clibanarius albidigitus</em></td>
<td>varied</td>
<td>L</td>
<td>small</td>
<td>yes</td>
<td>daytime clumps</td>
<td>Ball and Haig (1974), Norse (1974)</td>
</tr>
<tr>
<td><em>Clibanarius antillensis</em></td>
<td>mangrove mudflats</td>
<td>SL</td>
<td>small</td>
<td>5-10 individuals</td>
<td>daytime clumps</td>
<td>Hazlett (1966a)</td>
</tr>
<tr>
<td><em>Clibanarius africanus</em></td>
<td>mangrove sandflats</td>
<td>L</td>
<td>small</td>
<td>100+ individuals</td>
<td>low tide in heat</td>
<td>Schmitt (1926)</td>
</tr>
<tr>
<td><em>Clibanarius cooki</em></td>
<td>mangrove sandflats</td>
<td>L</td>
<td>medium?</td>
<td>100+ individuals</td>
<td>low tide in heat</td>
<td>Schmitt (1926)</td>
</tr>
<tr>
<td><em>Clibanarius corallinus</em></td>
<td>broken coral</td>
<td>L</td>
<td>small</td>
<td>yes</td>
<td>clumps at low tide</td>
<td>Reese (1969)</td>
</tr>
<tr>
<td><em>Clibanarius cubensis</em></td>
<td>mudflats, mangrove</td>
<td>L</td>
<td>medium</td>
<td>no</td>
<td>moves with tide</td>
<td>Hazlett (1966a)</td>
</tr>
<tr>
<td><em>Clibanarius digueti</em></td>
<td>rocky</td>
<td>L</td>
<td>small</td>
<td>up to 700 individuals</td>
<td>clumps at low tide</td>
<td>Snyder (1972, 1974)</td>
</tr>
<tr>
<td><em>Clibanarius erythrops</em></td>
<td>-</td>
<td>L</td>
<td>small?</td>
<td>yes</td>
<td>-</td>
<td>Mainardi and Rossi (1972)</td>
</tr>
<tr>
<td>Species</td>
<td>Habitat</td>
<td>Zone</td>
<td>Body Size</td>
<td>Clumps?</td>
<td>Rhythm</td>
<td>Source</td>
</tr>
<tr>
<td>------------------</td>
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<td>------</td>
<td>-----------</td>
<td>---------</td>
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<td>-------------------------------</td>
</tr>
<tr>
<td>Clibanarius</td>
<td>rocky, pilings</td>
<td>L</td>
<td>small</td>
<td>yes</td>
<td>semilunar (or tidal?) in lab</td>
<td>Drzewina (1907), Bouvier (1940)</td>
</tr>
<tr>
<td>misanthropus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Clibanarius</td>
<td>sandy, muddy</td>
<td>L</td>
<td>medium</td>
<td>yes, above water</td>
<td>tidal?</td>
<td>Snyder-Conn (pers. obs.)</td>
</tr>
<tr>
<td>panamensis</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Clibanarius</td>
<td>varied</td>
<td>L,TP</td>
<td>small</td>
<td>yes, in shallows</td>
<td>daytime</td>
<td>Hazlett (1966a)</td>
</tr>
<tr>
<td>tricolor</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>clumps</td>
<td>Norse (1974)</td>
</tr>
<tr>
<td>Clibanarius</td>
<td>sandy, muddy</td>
<td>L,SL</td>
<td>medium</td>
<td>sometimes</td>
<td>tidal, winter</td>
<td>Hazlett (1973)</td>
</tr>
<tr>
<td>vittatus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>clumps</td>
<td>Snyder-Conn (pers. obs.)</td>
</tr>
<tr>
<td></td>
<td>broken, coral</td>
<td>L</td>
<td>small</td>
<td>yes</td>
<td>clumps at low tide</td>
<td>Reese (1969)</td>
</tr>
<tr>
<td>Clibanarius</td>
<td>varied</td>
<td>SL</td>
<td>medium</td>
<td>no</td>
<td>-</td>
<td>Snyder-Conn (pers. obs.)</td>
</tr>
<tr>
<td>zebra</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dardanus</td>
<td>varied</td>
<td>SL</td>
<td>medium</td>
<td>no</td>
<td>-</td>
<td>Snyder-Conn (pers. obs.)</td>
</tr>
<tr>
<td>sinistripes</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Paguristes</td>
<td>rocky</td>
<td>L,SL</td>
<td>small</td>
<td>yes</td>
<td>clumps at low tide</td>
<td>Snyder-Conn (pers. obs.)</td>
</tr>
<tr>
<td>anahuacus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Paguristes</td>
<td>rocky, coral</td>
<td>SL</td>
<td>small</td>
<td>yes</td>
<td>-</td>
<td>Hazlett (1973)</td>
</tr>
<tr>
<td>anomalus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Paguristes</td>
<td>rocky</td>
<td>SL</td>
<td>medium</td>
<td>yes</td>
<td>-</td>
<td>Snyder-Conn (in press)</td>
</tr>
<tr>
<td>digueti</td>
<td></td>
<td></td>
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Table 2. Spacing Patterns of Marine Hermit Crabs. -- Continued.

<table>
<thead>
<tr>
<th>Species</th>
<th>Habitat</th>
<th>Zone</th>
<th>Body Size</th>
<th>Clumps?</th>
<th>Rhythm</th>
<th>Source</th>
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<td>-</td>
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</tr>
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<td></td>
<td></td>
<td></td>
<td>Provenzano (1959)</td>
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<td>Grant (1963)</td>
</tr>
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<td></td>
<td></td>
<td>Grant and Ulmer (1974)</td>
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<td>Schmitt (1921)</td>
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<td></td>
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<td></td>
<td>Vance (1973)</td>
</tr>
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<td>Pagurus bernhardus</td>
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<td>SL</td>
<td>medium</td>
<td>no</td>
<td>-</td>
<td>Hazlett (1968a)</td>
</tr>
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<td></td>
<td></td>
<td></td>
<td>Hazlett (1973)</td>
</tr>
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<td>Pagurus bonairensis</td>
<td>mud</td>
<td>SL</td>
<td>small</td>
<td>?contagion in field, yes in lab</td>
<td>-</td>
<td>Hazlett (1966a)</td>
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<tr>
<td>Species</td>
<td>Habitat</td>
<td>Zone</td>
<td>Body Size</td>
<td>Clumps?</td>
<td>Rhythm</td>
<td>Source</td>
</tr>
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<tr>
<td><em>Pagurus brevidactylus</em> (=<em>P. miamensis</em>)</td>
<td>rocky, reef</td>
<td>L,SL</td>
<td>small</td>
<td>yes, in shallows</td>
<td>daytime clumps</td>
<td>Hazlett (1966a)</td>
</tr>
<tr>
<td><em>Pagurus granosimanus</em></td>
<td>rocky</td>
<td>L,TP</td>
<td>medium</td>
<td>yes</td>
<td>daytime clumps, especially young</td>
<td>Ball (1968), Ball (1973), Schmitt (1921), Vance (1973)</td>
</tr>
<tr>
<td><em>Pagurus hirsutiusculus</em></td>
<td>pools with sand</td>
<td>L</td>
<td>small - medium - young, yes less, but gravid females especially</td>
<td>clump at low tide</td>
<td>Vance (1972a), Vance (1973), Kuris (1974)</td>
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<td><em>Pagurus lepidus</em></td>
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<td>TP</td>
<td>small</td>
<td>yes</td>
<td>clump at low tide</td>
<td>Snyder-Conn (pers. obs.)</td>
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<tr>
<td><em>Pagurus longicarpus</em></td>
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<td>SL</td>
<td>medium</td>
<td>sometimes</td>
<td>daytime clumps</td>
<td>Thompson (1903), Williams (1965), Norse (1974)</td>
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<td>SL</td>
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<td>medium</td>
<td>no, except in winter</td>
<td>winter clumps</td>
<td>Pike and Williamson (1959)</td>
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Table 2. Spacing Patterns of Marine Hermit Crabs. -- Continued.

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<thead>
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<th>Species</th>
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<th>Body Size</th>
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<th>Rhythm</th>
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<td>Squires (1964)</td>
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<td>Pagurus pygmaeus</td>
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<td>L</td>
<td>small</td>
<td>yes</td>
<td>daytime</td>
<td>Hazlett (1966a)</td>
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<tr>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>clumps</td>
<td></td>
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<tr>
<td>Pagurus samuelis</td>
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<td>L,TP</td>
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<td>daytime</td>
<td>Ball (1968)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>clumps</td>
<td>Ball (1973)</td>
</tr>
<tr>
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<td></td>
<td></td>
<td></td>
<td>Schmitt (1921)</td>
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<td>Petrochirus</td>
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<td>Hazlett (1973)</td>
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<tr>
<td>Pylopagurus</td>
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<td>small</td>
<td>yes</td>
<td>daytime</td>
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<td>operculatus</td>
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<td></td>
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<td>small</td>
<td>yes</td>
<td>-</td>
<td>Snyder-Conn (pers. obs.)</td>
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<td>Species</td>
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<td>Body Size</td>
<td>Clumps?</td>
<td>Rhythm</td>
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<td><em>Trizopagurus magnificus</em></td>
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<td>-</td>
<td>Ball and Haig (1974)</td>
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<td>coral</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Unidentified species</td>
<td>-</td>
<td>SL</td>
<td>-</td>
<td>yes</td>
<td>-</td>
<td>Ball (1973)</td>
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</table>

aHazlett claims that this species does not show specific clusters, but exhibits positive contagion.
latitudes (Hazlett, 1966a), habitat rather than family distinctions may, however, be more relevant.

There is a noteworthy absence of clustering in two of the most primitive genera, *Dardanus* and *Petrochirus*. Members of these genera lack the ritualized antagonistic display behavior of other species and cannibalism frequently results from the imposition of group life (Hazlett, 1966a, 1972). Hence, the presence of clustering in diverse, more advanced genera may indicate the independent evolution of the clustering habit several times.

Types of Clusters

Three types of clusters may be distinguished: regular, spontaneous, and seasonal clusters. Where protacted observations have been made, most researchers have reported evidence of one of two clustering rhythms. A tidal rhythm in which clusters occur at low tide (7 spp.) or high tide (1 sp.) and disperse during other tidal phases is common. Alternately, a diurnal rhythm with clustering during the daytime and dispersal at night applies in the case of nine species reported. The occurrences of both tidal and diurnal rhythms are easily reconcilable. Both diurnal temperature range and tidal amplitude dictate whether regular rhythms of tidal or diurnal frequency predominate in marine crustaceans (Drzewina, 1910; Barnwell, 1968; Naylor et al., 1971).

Spontaneous aggregations, although opportunistic in nature, are not uncommon in occurrence. Spontaneous aggregations often occur when hermit crabs accumulate around large decaying organisms in order to feed. I have observed *Clibanarius vittatus* to congregate on dead *Callinectes*
sapidus and C. digueti to cluster upon Octopus remains. Similarly, Grant (1974) reports spontaneous feeding aggregations of Pagurus acadianus. Another kind of spontaneous cluster may be involved in the case of small Paguristes grayi, which sometimes collect outside octopus lairs, possibly for feeding and/or for obtaining empty mollusc shells (Hazlett, 1966a). Clusters of Clibanarius digueti occurring on the tube feet of Heliaster kubinijii may have similar purposes (Snyder-Conn, pers. obs.). Seasonal clusters involving the winter aggregation of hermit crab species occur in certain species (Pike and Williamson, 1959; Fotheringham, 1975). In the case of Clibanarius vittatus, Fotheringham (1975) speculates that cold, which is easily tolerated, slows the retractile movements of the hermit crab into its shell. Hence, hibernation in deeper water may be advantageous, but both the mechanisms and benefits of aggregation at this time are yet unclear. Migration to deeper water followed by winter hibernation is also characteristic of Pagurus longicarpus, but the extent of aggregation during this time has not been reported (Rebach, 1968, 1974).

Even regular clusters may depend to some extent on exogenous factors. Schmitt (1926) observed that the clusters of Clibanarius africanus and C. cooki formed during low tide on warm, clear days. On cloudy or cool days, clusters were not evident. However, Hazlett (1966a) found the diurnal clusters of C. tricolor to be quite regular in occurrence. It would be of interest to examine the extent and regularity of hermit crab clusters over a lunar cycle in the case of species which exhibit tidal patterns of clustering.
Composition of Clusters

Size Composition

A pronounced tendency exists for small species of hermit crabs to cluster (Table 2). Of 24 small species (c.l. ≤ 10 mm), 21 species are reported to cluster. In contrast, only about half (11:12) of all medium-sized species (c.l. > 10 mm ≤ 20 mm) cluster. Large species tend to space out (3:1). Medium and larger hermit crab species which do cluster form smaller groups with 2-8 individuals each, as opposed to groups of small hermit crabs with several hundred to several thousand individuals. Smaller individuals within a species may also show an increased propensity to cluster. For example, Pagurus hirutiusculus and P. granosimanus (Vance, 1973) and Clibanarius tricolor (Hazlett, 1966a) form clusters composed mostly of young, while large adults are more likely to space out.

Species Composition

Membership of hermit crab clusters may or may not be species-specific. MacKay (1945) records several aggregations consisting largely of Clibanarius zebra together with small numbers of Calcinus herbstii, while Schmitt (1926) found that C. africanus and C. cooki mingle regularly in clusters. Hazlett (1966a) records a few C. antillensis among some groups of C. tricolor, although aggregations mostly appeared to be species-specific. It is interesting that the gregarious response which Hazlett demonstrated of Clibanarius tricolor was not species-specific. No preference was exhibited by C. tricolor for conspecifics.
over the hermit crab *Calcinus tibicen*, but the brachyuran crabs *Uca rapax* and *Mithrax verrucosus* were avoided. In most cases, depth and habitat preferences may effectively separate populations of various species and thereby minimize mixing in clusters.

**Environmental Variables**

**Depth**

Hermit crab clusters are apparently most prevalent among littoral species, although they are not uncommon in their sublittoral counterparts. Of 30 species from the littoral habitat (including tidepools), 24 species cluster; of 29 species recorded in the sublittoral habitat, only 10 species are known to cluster. (Two additional migratory species aggregate in the sublittoral habitat in the winter.) Many species occurring in both the littoral and sublittoral zones cluster only in the former habitat. This depth tendency is also corroborated in laboratory studies of sociality. Hazlett (1966b) reports that of 11 deep-water species studied individuals of most species did not cluster and, in fact, showed avoidance of other conspecifics.

**Substrate**

Of 27 species from rocky or coral substrates, 20 species cluster. A more ambivalent pattern exists on sandy and muddy substrates where 8 of 13 species aggregate. It is important to note that many sandy shore species are also large in size and sublittoral in habit. The spacing of sandy shore species may, therefore, be dependent on a combination of factors.
Summary

In this survey, the habit of clustering is revealed to be widespread among the marine hermit crabs of both the Diogenidae and Paguridae. It is prevalent in the more advanced genera, particularly the tropical genus Clibanarius. Three types of clusters occur. Regular clusters form according to tidal or diurnal cycles in nature. This type of cluster may be distinguished from spontaneous opportunistic and seasonal, hibernational types of clusters. With regard to size, smaller hermit crab species and smaller individuals within a species show the greatest propensity to form regular clusters. However, clusters may consist of a mixture of species where populations overlap. With respect to habitat, clustering is most common in littoral species and among species which occupy rocky or coral substrates. The great diversity in the occurrence of clustering species precludes any prediction as to general mechanisms or functions. A multiplicity of causes may, indeed, be the case.
CHAPTER 4

AGGREGATION AND DISPERSION IN CLIBANARIUS DIGUETI: MECHANISMS

Introduction

The tidal phasing of clustering in Clibanarius has been suggested by Schmitt (1926), Hazlett (1966a), and Reese (1969). In the case of C. digueti, Snyder (1972) also reported the formation of aggregations according to a tidal rhythm. I observed individuals to form clusters primarily on dark substrates at low tide. During ebb and flood tides, individuals dispersed. These behaviors appeared to correspond with certain tidal rhythms demonstrated under constant laboratory conditions, including those of oxygen consumption, light versus dark substrate selection (skototaxis), and gregariousness.

The aim of this chapter is to produce a model of behavior which identifies the mechanisms controlling the rhythm of aggregation and dispersal of C. digueti in nature. The initial hypothesis tested is that aggregation and dispersal stem from the tidal rhythms of behavior exhibited under constant laboratory conditions. The steps for evaluating this hypothesis are: 1) documentation of the rhythm of activity and behavior of C. digueti in nature, 2) documentation of the rhythms of activity and behavior of C. digueti under laboratory conditions, and 3) detailed comparison of the laboratory and field rhythms for correspondence.
The rhythm hypothesis alone is shown to be inadequate to explain the behavior of *C. digueti* in nature. Therefore, the latter half of this chapter is devoted to the role of environmental influences on behavior. Certain responses to environmental variation are demonstrated. When both rhythmic and environmentally induced behavior are evaluated together, an adequate model of aggregation and dispersion is rendered. This model, presented as a flow diagram, summarizes the mechanisms of aggregation and dispersal of *C. digueti*. The synthesis is probably incomplete in terms of the full behavioral repertoire of *C. digueti*, but does amply account for both laboratory and field observations of aggregation and dispersal.

**Behavior in Nature**

Sequential Diving Observations at Puerto Peñasco

With the aid of snorkeling equipment, hourly observations were made at two rock sites in the upper mid-intertidal zone of Playa Estación in Puerto Peñasco, Sonora, Mexico, in order to determine the regimen of activity of *C. digueti*. These observations covered a 28-hour period, including two tidal cycles in September 1974. During each observation, the numbers of individuals on the rock surfaces were tallied. Then the numbers of individuals beneath the rocks were counted. Clusters on adjacent rocks were also noted. At night, a diving light aided these observations. The rocks were relocated each hour by following a series of yellow tent pegs wedged under rocks, beginning in the upper intertidal zone.
Figure 1 depicts the numbers of *C. digueti* on the upper surface of one of the two tagged boulders in the study. The other tagged site, a coquina boulder, was unstable and remained relatively barren of hermit crabs. No pattern of use was noted for this boulder, although nine hermit crabs did disperse on top of this boulder during the first ebb tide. No *C. digueti* were found underneath the boulder. The behavior of the hermit crabs at the stable boulder was quite rhythmical. During stages when the water depth was between .1-.7 m in depth, the end of ebb tide and the beginning of flood tide, the hermit crabs were observed to disperse and occupy the upper surface of this and other boulders. At this time, individuals exhibited rapid antennule and maxilliped movements indicative of filter-feeding. Scavenging was also observed, although this behavior was less common than filter-feeding. Thus, *C. digueti* disperses from clusters during parts of both ebb and flood tide. It can also be seen that, during the higher low tide of the neap tide series, during the latter 12-16 hours observation period, that the hermit crabs remained dispersed on top of the boulders, covered by a shallow layer of water.

During the period of low water neap tide, when the depth fell below .7 m and eventually exposed the hermit crabs completely, only a few individuals remained on the boulder surface. Most individuals were not found near this boulder at all, either on or under it, but seemed to have migrated to a large cluster on an adjacent rock. This contrasts sharply with the behavior during high tides, when about 25 hermit crabs were found to be loosely arranged under the tagged boulder. Thus, during the
Figure 1. In Situ Pattern of Behavior of C. digueti in the Puerto Peñasco Intertidal Zone. -- The number of individuals seen on top of a tagged rock is graphed versus time and depth. The arrow during low tide indicates the period during which individuals were observed clustering on an adjacent, untagged boulder and were not found on or under the tagged boulder. During high tides, individuals were semi-dispersed under the tagged boulder.
period of observation, the sequence of behavior at Puerto Peñasco was: aggregation at cluster sites when exposed at low tide, dispersion and feeding on upper boulder surfaces during ebb and flood tides, and then refuging under boulders throughout the high tide period and until the depth was less than .7 m.

Although the data presented above represent a period of only two tidal cycles, numerous subsequent dives at Puerto Peñasco at different tidal stages have indicated the same pattern of activity throughout the year. In addition, subsequent low tide observations support the contention that the cluster site may differ from that of the refuge site. Moreover, most cluster sites appear to be quite stable in location. Observations of five tagged sites over a 22-day period indicated repeated clustering in 4 of the 5 sites. The fifth site was originally composed of only 19 loosely adjoined C. digueti, hence, atypical of the majority of clusters, which may range in size between 20-700 individuals.

Sequential Diving Observations at Bahia San Carlos

The above results strongly suggest a close correlation between the behavioral regimen and the tidal cycle at Playa Estación. It was, therefore, of interest to examine the behavior of C. digueti in an area where the tidal amplitude is slight. The study site chosen was Bahia San Carlos, near Guaymas, Sonora, Mexico. At this location, the tides rarely exceed an amplitude of one meter. In July 1975, a boulder with about 35 C. digueti underneath was tagged in the upper intertidal zone. During six hours of observation, at a depth of .7-.9 m (high tide), no hermit
crabs were observed on the tagged rock surface or on other rocks nearby. Unfortunately, high turbidity and increasingly stormy sea conditions prohibited further in situ observations.

On September 20, 1975, the Bahía San Carlos population was again studied. However, tagging proved unfeasible due to highly turbid conditions. Consequently, hermit crabs were surveyed by executing a one-minute dive each hour over the same horizontal area. The results are presented in Figure 2. As at Puerto Peñasco, the hermit crabs occupied upper rock surfaces when the water depth was less than .7 m. However, since the hermit crabs remained unexposed during low tides, the dispersed feeding phase was maintained throughout low tide and no aggregations were observed. In addition to the lack of clustering at low tide, the comparative paucity of individuals on upper rock surfaces should be emphasized. The rhythm exhibited by this population appeared to be far less precise, and a fairly constant low level pattern of emergence from under rocks was evident. During less pronounced tides at this location, an even less predictable pattern is probable.

**Transect Studies**

**Materials and Methods**

Monthly transects were conducted from February 1974 through February 1975 at Playa Estación, Puerto Peñasco, Sonora, Mexico, on the Gulf of California. Two standard transects were established -- one on a shell-hash beachrock (or "coquina") substrate and another through a basalt boulder field. The two transects were located approximately one
Figure 2. In Situ Pattern of Behavior of *C. digueti* in the Bahia San Carlos Intertidal Zone. Numbers observed on top of boulders during a one-minute dive each hour are graphed versus time and depth. No aggregations were seen on rock surfaces during any phase of the tides.
hundred meters apart between the Casa Garcia and the Environmental Research Laboratory premises. Each transect spanned 50 meters of the intertidal zone, running perpendicular to the shore. Within the transect, a sample .5 m² (1 m long x .5 m wide) was collected at every other meter. Thus, twenty-five .5 m² samples were collected along each transect.

The locations of the transects and the quadrat size were selected with great care. The two transect locations were chosen on the basis of substrate homogeneity. The boulder transect, thus, covered an area consistently composed of basalt boulders and the coquina transect was consistently composed of shell-hash beachrock. Areas with large sand patches or tidepools were strictly avoided. Meters 1-15 of both transects were exceptional in that these were frequently silted in by storm activity, despite the consistency of the underlying substrate. However, these meters rarely harbored more than a few hermit crabs and their influence on relative changes in the indices of clumping was negligible. The quadrat size was selected on the following criteria: the size was considerably larger (x8) than any hermit crab cluster noted, the quadrat frequently contained one or more individuals, the quadrant frequently contained one or no clusters, and only rarely were two clusters encountered within a quadrat.

Each transect was conducted during the morning low tide period of a spring tide series. During this period, four hours or more of intertidal exposure insured the fullest participation of C. digueti in clusters. Since members of clusters remain inactive throughout the
period of exposure, accurate monthly comparisons both within and between transects were possible.

Each month the transects were relocated by topographic features, tagged rocks, and sightings on tent pegs above the high tide level. All samples included both hermit crabs and snails since field sorting of snails from hermit crabs was too time-consuming. The sample area was delineated by a .5 meter wide board, which slid along a transect line. The transect line was 1/4" nylon and, therefore, subject to shrinkage. Thus, it was necessary to recalibrate the line with color-coded plastic tape prior to each monthly sampling program. Once collected, a sample was isolated in one or more prelabeled, moist glass collecting bottles. In the laboratory, snails were first separated into labeled bottles. For most months, these were not analyzed. However, from December 1974 through February 1975, the snail distributions were analyzed for both transects.

Hermit crabs from a sample were placed in fresh sea water, in which they became quite active, facilitating species identification. For each hermit crab in each quadrat sample, the identity of the hermit crab and the identity of its shell, the maximum shell length, and the maximum shell width were recorded. In the case of globose shell species, however, only width was recorded. All measurements were taken with a vernier caliper to the nearest .1 mm. These records were made at the Environmental Research Laboratory at Playa Estación immediately following collection. On the subsequent low tide, all snails and hermit crabs were returned alive to their original .5 m² locations. One rare species of
hermit crab, *Pylopagurus roseus*, proved to be rather fragile and some deaths were common when this species was collected.

In the two transects, a total of 21,955 hermit crabs were collected over the 13-month period of study. Several analyses were performed, including clustering patterns within and between transects, clustering patterns of sympatric hermit crab species, abundance patterns of snail species, and trends in size specificity of clusters. The patterns of clustering within and between transects are discussed below. Other patterns are analyzed in separate sections of this chapter.

**Clustering Patterns within Transects**

The degree of contagion, or clumping, in the boulder and coquina transects was analyzed using several measures of aggregation (Table 3).

**Table 3. Measures of Aggregation.**

<table>
<thead>
<tr>
<th>Index</th>
<th>Formula</th>
<th>Sources</th>
</tr>
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<tbody>
<tr>
<td>Variance to Mean Ratio</td>
<td>$\frac{s^2}{\bar{x}}$</td>
<td>Pielou (1969)</td>
</tr>
<tr>
<td>Morisita's Index of Dispersion</td>
<td>$\frac{q}{N(N-1)} \sum_{i=1}^{q} x_i(x_i-1)^b$</td>
<td>Hazlett (1966a)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pielou (1969)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Stiteler and Patil (1971)</td>
</tr>
</tbody>
</table>

\(s^2 = \text{variance between quadrats}; \ \bar{x} = \text{the mean number of individuals per quadrat.}\)

\(q = \text{the number of quadrats} \ (=25); x_i = \text{the number of individuals in the ith quadrat}; \text{and } N = \text{the total number of individuals for all quadrats in the transect.}\)
The variance to mean ratio provides a simple and easily visualized indication of spatial pattern. A value of one indicates a random pattern; a value significantly greater than one, a pattern of aggregation; and a value significantly less than one, a pattern of regular or uniform dispersion. Moreover, the form of this index, \((x_1 - \bar{x})^2 / \bar{x}(N-1)\), is of the same form as \((0-E)^2 / E(N-1)\). Consequently, a chi-square test of significance (\(\chi^2\) over \(N-1\), with \(N-1\) degrees of freedom) (Bliss and Fisher, 1953), is readily available for the variance to mean ratio.

The density-independent measure, Morisita's Index, \(I_{\delta}\), was chosen for several reasons. This probability-based measure is independent of population size and quadrat size, if clumping or randomness is the case, and rises monotonically with increases in clumping (Williamson, 1975). In addition to these assets, Morisita's Index was applied by Hazlett (1966a) to his hermit crab data. Therefore, its use in this work permits direct comparisons between studies.

In Tables 4 and 5, the principal statistics and the various indices of clumping are illustrated for *Clibanarius digueti* of the coquina and boulder substrates, respectively. All variance to mean ratios proved to be significantly greater than one (\(p < .01\)), indicating a clumped distribution in each transect. (No tests of significance were available for Morisita's Index.)

**Clustering Patterns between Transects**

In Figure 3, the degree of clumping for the coquina and boulder populations are compared using the variance to mean ratio. Using the criterion proposed by David and Moore (1954), significant differences
Table 4. Basic Statistics and Indices of Clumping for *Clibanarius digueti* in Each Coquina Transect. -- Two indices are presented: the variance to mean ratio ($s^2/\bar{x}$) and Morisita's Index of dispersion ($I_6$). The transect code indicates the substrate, month, and year.

<table>
<thead>
<tr>
<th>Transect</th>
<th>C0274</th>
<th>C0374</th>
<th>C0474</th>
<th>C0574</th>
<th>C0674</th>
<th>C0774</th>
<th>C0874</th>
<th>C0974</th>
<th>C1074</th>
<th>C1174</th>
<th>C1274</th>
<th>C0175</th>
<th>C0275</th>
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</thead>
<tbody>
<tr>
<td>$s^2$</td>
<td>144.1</td>
<td>165.0</td>
<td>791.4</td>
<td>395.6</td>
<td>862.0</td>
<td>4870.6</td>
<td>556.3</td>
<td>332.5</td>
<td>450.4</td>
<td>108.9</td>
<td>288.0</td>
<td>384.4</td>
<td>477.5</td>
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<td>10.4</td>
<td>14.6</td>
<td>14.3</td>
<td>19.5</td>
<td>34.8</td>
<td>13.1</td>
<td>10.7</td>
<td>14.7</td>
<td>6.7</td>
<td>8.8</td>
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<td>11.8</td>
</tr>
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<td>$n$</td>
<td>126</td>
<td>261</td>
<td>364</td>
<td>358</td>
<td>488</td>
<td>870</td>
<td>327</td>
<td>267</td>
<td>368</td>
<td>168</td>
<td>219</td>
<td>233</td>
<td>295</td>
</tr>
<tr>
<td>$s^2/\bar{x}$</td>
<td>28.6</td>
<td>15.8</td>
<td>54.3</td>
<td>27.6</td>
<td>44.2</td>
<td>140.0</td>
<td>42.5</td>
<td>31.1</td>
<td>30.6</td>
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<tr>
<td>$I_6$</td>
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<td>4.7</td>
<td>2.9</td>
<td>3.2</td>
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<td>4.2</td>
<td>3.8</td>
<td>3.0</td>
<td>3.3</td>
<td>4.7</td>
<td>5.3</td>
<td>4.4</td>
</tr>
</tbody>
</table>
Table 5. Basic Statistics and Indices of Clumping for Clibanarius digueti in Each Boulder Transect. Two indices are presented: the variance to mean ratio ($s^2/\bar{x}$) and Morisita's Index of dispersion ($I_\delta$). The transect code indicates the substrate, month, and year. The March and July samples are missing.

<table>
<thead>
<tr>
<th>Transect</th>
<th>B0274</th>
<th>B0474</th>
<th>B0574</th>
<th>B0674</th>
<th>B0874</th>
<th>B0974</th>
<th>B1074</th>
<th>B1174</th>
<th>B1274</th>
<th>B0175</th>
<th>B0275</th>
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</thead>
<tbody>
<tr>
<td>$s^2$</td>
<td>3970.6</td>
<td>2405.7</td>
<td>439.3</td>
<td>254.0</td>
<td>976.7</td>
<td>3985.0</td>
<td>4284.7</td>
<td>26056.1</td>
<td>2236.3</td>
<td>294.1</td>
<td>6701.2</td>
</tr>
<tr>
<td>$\bar{x}$</td>
<td>15.8</td>
<td>26.1</td>
<td>15.6</td>
<td>12.6</td>
<td>15.6</td>
<td>28.8</td>
<td>41.2</td>
<td>77.0</td>
<td>27.9</td>
<td>10.8</td>
<td>24.9</td>
</tr>
<tr>
<td>n</td>
<td>394</td>
<td>652</td>
<td>391</td>
<td>316</td>
<td>389</td>
<td>720</td>
<td>1031</td>
<td>1924</td>
<td>688</td>
<td>233</td>
<td>622</td>
</tr>
<tr>
<td>$s^2/\bar{x}$</td>
<td>251.9</td>
<td>92.2</td>
<td>28.1</td>
<td>20.1</td>
<td>62.8</td>
<td>136.3</td>
<td>103.9</td>
<td>338.6</td>
<td>80.1</td>
<td>23.4</td>
<td>269.3</td>
</tr>
<tr>
<td>$I_\delta$</td>
<td>6.5</td>
<td>2.4</td>
<td>4.7</td>
<td>2.9</td>
<td>3.2</td>
<td>5.0</td>
<td>4.2</td>
<td>3.8</td>
<td>3.0</td>
<td>3.6</td>
<td>11.8</td>
</tr>
</tbody>
</table>
Figure 3. Clumping of Clibanarius digueti in Boulder and Coquina Transects by Month, as Indicated by the Variance to Mean Ratio. -- This index of clumping is dependent on the number of individuals within the transect as well as their proportional distribution.
between the coquina and boulder transect populations occurred on both February dates, and also for September, October, and November. During these months, the boulder population showed a much greater degree of clumping. During July, however, the trend is reversed and the coquina reef population shows a significantly greater clumping than the boulder population for both the June and August samples. (The July boulder transect was not completed due to Portuguese man-of-war intrusions.)

The variance to mean ratio may be considered a density-dependent measure when the sample size (number of quadrats) is held constant for all transects being compared. That is, the degree of aggregation is related not only to the proportional distribution of individuals, but also to the absolute size of the population within the transect. Many of the fluctuations in the above measures are explained by changes in the mean density of the transect population. Figure 4 depicts the degree of clumping using Morisita's Index of dispersion, a density-independent measure of clumping. Here, a more consistent trend emerges. Relatively similar values of clustering occur in both coquina and boulder transect data, except in February. In both February boulder samples, the extent of clumping in the boulder habitat greatly exceeds that of all other transect samples. In other months, the degree of clumping is similar both among and between transects.

The reasons for the differences in density-dependent clumping patterns become clear when the abundance patterns of individuals in the two transect areas are examined. However, the February high values in the boulder population are clearly independent of density. A
Figure 4. Clumping of Clibanarius digueti in Boulder and Coquina Transects by Month, as Indicated by Morisita's Index of Dispersion. — This index is density-independent and increases with increases in the degree of clumping.
scrutinization of the raw data leads to the conclusion that, indeed, *Clibanarius digueti* concentrates in fewer .5 m$^2$ samples than at other times of the year. This is the only month in which there is evidence for differential migration within the *C. digueti* population. In all other samples, the application of Morisita's Index indicates comparable levels of clustering within both coquina and boulder habitats, despite seasonal progression and the great differences in substrate type.

**Rhythmical Behavior under Constant Laboratory Conditions**

Tidal rhythms of activity, skototaxis, phototaxis, and gregariousness are demonstrated under conditions of constant light, temperature, and depth. These rhythms persist in the laboratory for at least two tide cycles.

**Activity Rhythms**

**Activity Rhythm at Puerto Peñasco.** Two studies of rhythmic activity of *C. digueti* were made at Puerto Peñasco under conditions of constant light, temperature, and water depth. In the first test, five freshly collected, medium-sized individuals were placed in a 19 cm petri dish in dim light (86 lux) at 28.5 ± 2.0°C with a water depth of 1 cm. Following a one-hour period of acclimation, the number of crossings of two perpendicular lines on the container bottom was tallied each half hour for a 10-minute period. The total number of crossings per 10-minute period afforded a measure of relative locomotion or activity. The second test was similar but involved 20 medium-sized individuals in a circular
pan 36 cm in diameter at 28.8 ± 1.0°C. The two tests ran for 25.5 and 23 hours, respectively.

The results are presented in Figure 5. A tidal rhythm of activity is clearly evident. Activity is quite low during the period of low tide and high during the period of high tide. Such an activity rhythm is also indicated for C. digueti from Playa Estación in other tests (see Light and Water Depth sections). The low activity accords with the quiescent phase during which hermit crabs aggregate in nature. However, field observations have suggested that the highest activity occurs during ebb and flood tide, when hermit crabs are dispersed and feeding, rather than during high tide, when they refuge under rocks. Hence, the peak at high tide does not coincide with activity in nature.

Activity Rhythm at Bahía San Carlos. In order to compare the rhythm of activity of a high-amplitude tidal regime (Puerto Peñasco) with that of a low-amplitude tidal regime, the locomotory rhythm of C. digueti from Bahía San Carlos was investigated. In this test, a 150 watt light was used at a distance of about 8 feet, yielding a light intensity of approximately 4039 lux. The activity of twenty freshly collected, medium-sized C. digueti in a 36 cm diameter pan at 29.3 ± 1.0°C in one centimeter of sea water was measured using the aforementioned method. This test ran for 24 hours during September 20-21, 1975. No replicate test was performed.

The results are shown in Figure 6. Initially, a tidal rhythm is exhibited. However, pronounced activity is continued throughout the night, indicating a possible shift to a diurnal rhythm with nocturnal
Figure 5. Tidal Rhythm of Activity of Clibanarius digueti at Puerto Peñasco, Sonora, Mexico. -- Each datum represents the number of crossings of two perpendicular lines during a ten-minute period by 20 hermit crabs. The relative locomotion is graphed versus the tidal cycle of low tides (LT) and high tides (HT).
Figure 5. Tidal Rhythm of Activity of Clibanarius digueti at Puerto Peñasco, Sonora, Mexico. Each datum represents the number of crossings of two perpendicular lines during a ten-minute period by 20 hermit crabs. The relative locomotion is graphed versus the tidal cycle of low tides (LT) and high tides (HT).
Figure 6. Tidal Rhythm of Activity of *Clibanarius digueti* at Bahía San Carlos, Sonora, Mexico. — Each datum represents the number of crossings of two perpendicular lines during a ten-minute period by 20 hermit crabs. The relative locomotion is graphed versus the tidal cycle of low tides (LT) and high tides (HT). The horizontal arrow indicates the approximate time of darkness in nature.
activity. This test was executed during the spring tide, when the tidal amplitude is at a maximum. Possibly, *C. digueti* from this location possess a less strongly entrained tidal rhythm which is superseded by the diurnal cycle during other phases of the lunar cycle.

### Skototactic Rhythms

**Skototactic Rhythm at Puerto Peñasco.** The tidally rhythmic response of *C. digueti* to light and dark substrates (skototaxis) was first demonstrated by Snyder (1972). The following experiments were repeated in order to corroborate earlier results. As in the earlier procedure, 36 cm round plastic dishpans were spray-painted in alternate black and white quadrants. In two sets of experiments, I placed 20 hermit crabs each, five per quadrant, in two pans. The pans were arranged oppositely to control for directional responses. After one hour of acclimation, the numbers occupying different quadrants in the pans were counted every 30 minutes. In all experiments, the water level was one centimeter; the light intensity was maintained at 4039 lux. For the two sets of experiments, the temperatures were 28.5 ± 2.0°C and 26.5 ± 1.5°C, respectively. The four tests (two sets) ran for 24 and 29 hours, respectively.

In the May 18-19 test, the effect of shell color on aggregation was tested. One test group consisted of individuals with light-colored shells; the other test group consisted of individuals with dark shells. Individuals tested came from the same cluster or near vicinity and were medium-sized. In the June 3-4 test, the effect of size was assessed. Individuals with shells greater than 1 cm in length constituted one test
group; individuals with shells less than 1 cm in length comprised the second test group.

Figure 7 compares the results of these test sets with two previous sets (Snyder, 1972). A tidal rhythm of skototaxis is again evident. (This rhythm is also demonstrated in studies of water depth. See Water Depth section.) Hermit crabs select black substrates during periods of low tide and white substrates during periods of high tide. This rhythm appears to be independent of season, shell color, or hermit crab size. As in the case of the activity rhythm, the selection of black substrates at low tide is correlated with the clustering of C. digueti on primarily dark substrates at this time. Also, at ebb and flood tides, C. digueti disperses and occupies the upper illuminated surfaces of boulder and coquina substrates, in accord with their increased selection of white substrates at this time in the laboratory. The high tide selection of a white substrate in the laboratory is, however, at variance with the behavior of C. digueti in nature. During high tide, this species normally retreats under rocks and, therefore, would be expected to prefer black substrates.

Skototactic Rhythm at Bahía San Carlos. To further compare the behavioral regimen of C. digueti from an area of high tidal amplitude with that of a low tidal amplitude area, the light/dark color selection (skototaxis) of C. digueti at Bahía San Carlos was investigated. The experimental procedure followed that of the skototactic tests at Puerto Peñasco. At this location, two tests were conducted using 20 freshly collected individuals in each pan. Both tests involved a light intensity
Figure 7. Tidal Rhythm of Skototaxis of *Clibanarius digueti* at Puerto Peñasco, Sonora, Mexico. — The top two graphs are taken from Snyder (1972). The results of two concurrent tests appear in each graph. In the May 18-19 test, hermit crabs with light-colored shells (open dots) are compared with hermit crabs occupying dark shells (filled dots). In the June 3-4 test, large individuals (open dots) are compared to small individuals (filled dots).
of about 4039 lux, a temperature of 29.3 ± 1.0°C, and a depth of about one centimeter. The tests ran for 24 hours.

The results are presented in Figure 8. A strong nocturnal selection of the white substrate is evident, while only slight evidence of tidal rhythm of substrate color selection is apparent. This result, like that of the activity rhythm, supports the contention that, in the case of a low tidal amplitude environment, the tidal rhythm is supplanted by a diurnal rhythm.

Phototactic Rhythm at Puerto Peñasco

Initial studies of phototactic rhythm were negative (Snyder, 1972). According to Fraenkel and Gunn (1940), however, the rhythm of skototaxis is generally a manifestation of a rhythm of phototaxis. Hence, the phototactic response was reinvestigated using a modified experimental design in which the two quadrants with overhead shades were provided with side panels extending to within 1 cm of the water surface to enhance the shade effect. Two tests were run concurrently on each of two dates. As in previous experiments, twenty freshly collected C. digueti were placed, five per quadrant, in round, 36 cm pans under a light intensity of 4039 lux (unshaded quadrants) at a water depth of one centimeter. The temperatures in the two sets (four tests) were 28.5 ± 2.0°C and 28.8 ± 1.0°C, respectively.

The results (Figure 9) indicate that a tidal rhythm of phototaxis is present in C. digueti. This rhythm is far weaker than the rhythm of skototaxis. However, shaded areas are selected more during periods of low tide and illuminated areas are selected more during periods of high
Figure 8. Rhythm of Skototaxis of Clibanarius digueti at Bahía San Carlos, Sonora, Mexico. The percent of C. digueti occupying white (versus black) quadrants is graphed versus the tidal cycle for two concurrent tests (open and filled circles). Half-filled circles indicate the overlap of two data points. The horizontal arrow indicates the approximate period of darkness in nature.
Figure 9. Tidal Rhythm of Phototaxis of Clibanarius digueti at Puerto Peñasco, Sonora, Mexico. The percent occupying illuminated areas (versus shaded areas) is graphed against the tidal cycle. Each graph consists of two concurrent tests (open and filled circles).
tide. The low tide response correlates well with the clumping of
_C. digueti_ in shade, under rocks, and on dark substrates. Under these
conditions, stable clusters are more apt to exist, while clusters on
exposed sites are more short-lived. (Following storms, sedimentation of
the under-rock habitat is a frequent cause of clustering in highly
exposed sites.) Again, one would predict selection of illuminated areas
only during ebb and flood tides rather than during the high tide phase
also. Consequently, the high tide laboratory response is at variance
with the response in nature, when hermit crabs refuge under rocks.

Rhythm of Gregariousness at
Puerto Peñasco

Hazlett (1966a) showed in Y-tube choice experiments with
_Clibanarius tricolor_ that individuals were attracted to each other during
phases of clustering, but not during feeding phases. Similarly, Snyder
(1972) demonstrated, through analysis of time-lapse photography, that
_C. digueti_ touched shells more during low tide periods than during high
tide periods. These results do not enable the distinguishing of gregar­
iousness from the possibility of an attraction on the basis of color
attraction since the shells were mostly dark.

Preliminary tests using a Y-choice tube suggested a positive
choice of _C. digueti_ for its conspecifics during low tide. However,
their response to currents in the choice tube precluded further experi­
ments. Instead, the pattern of distribution on black quadrants is con­
trasted with the expected frequency, based on the average number of
_C. digueti_ occupying each black quadrant. The results of a Chi-square
test of randomness of quadrant selection during mean low tide of all data from Figure 7 show that the selection of one of the two black quadrants is non-random ($\chi^2 = 104.26, p < .005, df = 35$). A great propensity to cluster together in one or the other of the two quadrants is, in fact, exhibited. These data suggest that the gregariousness of *C. digueti* during low tide is not based on shell color, since skototactic responses do not account for clustering rhythms exhibited on homogeneous backgrounds. A similar conclusion may be drawn from the tests comparing the skototactic rhythms of light- and dark-shelled individuals from the same cluster (Figure 7). The amplitude of the rhythm in both tests is quite similar, suggesting that gregariousness is a separate phenomenon, based perhaps on chemical attraction.

The Role of Rhythmical Behavior in Aggregation and Dispersion

The tidal rhythms of activity, skototaxis, phototaxis, and gregariousness exhibited under constant laboratory conditions suggest the following behavioral regimen. During low tide, hermit crabs should show low activity, select dark and/or shaded substrates, and be attracted to one another, thus aggregate. During high tide, high activity, selection of illuminated and/or light-colored substrates, and the avoidance of other individuals should, conversely, result in dispersal.

A comparison between laboratory results and *in situ* observations (Figures 1 and 2) reveals that these predictions are only partially met in reality. A good correspondence between laboratory and field behavior is observable during low tide, when *C. digueti* typically aggregates in
nature. However, this prediction is only reliable during low tides in which *C. digueti* is exposed to very shallow conditions or to air. During neap tides, aggregation may not occur during the low tide period.

The "high tide" laboratory behavior is only appropriate during ebb and flood tide in nature and not during the actual period of high tide. During periods when depths are greater than .7 meters, *C. digueti* is found semi-dispersed under boulders and not on the illuminated surfaces actively feeding. Consequently, the hypothesis that aggregation and dispersal in nature stem only from tidal rhythms demonstrable under constant conditions is not supported.

Behavior in Response to the Environment

Components of the Rhythmically Changing Environment

In nature, *Clibanarius digueti* is subjected to daily changes in light, temperature, depth, current, and food supply. Conceivably, one or several of these variables may play an important role in aggregative and dispersive behavior. In the succeeding sections, the hypothesis that aggregation and dispersion in nature are the results of environmentally induced behavioral responses is tested.

**Light**. Responses to different light intensities (5385-53850 lux) were measured by raising a large, 150-watt incandescent light bulb to different heights above the experimental container. These heights were precalibrated using a GE Light Meter 213A (Color and Cosine Corrected). In the experiment, 20 freshly collected *C. digueti* from Playa Estación were first acclimated in the experimental tank provided with one
centimeter depth of sea water for one hour. Subsequently, they were subjected to each light level for 30 minutes. During the final 10 minutes at each light level, the activity of the hermit crabs was recorded by the method discussed previously (see Activity Rhythms). Two sets of data were collected: one during the low tide period and another during the high tide period.

The results are illustrated in Figure 10. During the low tide period, *C. digueti* was relatively unresponsive to changes in the light intensities. Activity increased only slightly with increasing light level during low tide. In contrast, at high tide, a strong positive linear response to changing light level is evident. Activity increased several hundred-fold from an initial zero level at the lowest light intensity. Activity during the high tide period was significantly greater than activity during the low tide period (paired t test, one tailed, \( p < .05, \text{df} = 9 \)).

**Temperature.** In the course of the light experiments, the influence of temperature, an uncontrolled variable in these studies, was also studied. Table 6 shows the temperature at each light intensity in the experiment. Note that the highest temperatures were reached at mid-intensity ranges: 43080, 37695, and 32310 lux, since the water in the experimental pan heated slowly as the light was lifted to progressively greater heights. (At higher intensities, the heat emanating from the light was more distant from the pan, which subsequently cooled.) The total range during the experiment was from 29.2-35.5°C, a total of 6.3°C.
Figure 10. Locomotor Activity of Clibanarius digueti in Response to Different Light Intensities at Periods of High and Low Tide. Each datum represents the number of crossings of two perpendicular lines during a ten-minute period by 20 hermit crabs.
Table 6. Temperatures during the Light Intensity Experiment.

<table>
<thead>
<tr>
<th>Light Intensity (lux)</th>
<th>Temperature (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>53850</td>
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</tr>
<tr>
<td>48465</td>
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<td>43080</td>
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<td>10770</td>
<td>31.8</td>
</tr>
<tr>
<td>5385</td>
<td>29.2</td>
</tr>
</tbody>
</table>
variation. Thus, circumstantial evidence supports the thesis that temperature was not a critical variable in the light experiment.

An additional experiment to test the effects of temperature was also performed. In this test, the incandescent light was placed underneath the container. Twenty *C. digueti* were placed in a uniform pattern in the container and acclimated for two hours. Activity measurements were then made during the period of high tide. As in the light experiment, activity was measured in the final ten minutes of each consecutive 30-minute period. However, the placement of the light was constant throughout the experiment. The results are presented in Table 7. Only a two-fold increase in activity is seen with increasing temperature over a 14°C range. This increase is insufficient to have appreciably influenced the effects of changing light intensity, since the effects of changing light were on the order of several hundred-fold.

Table 7. Response of *Clibanarius digueti* to Changes in Temperature. -- The activity was recorded as the number of crossings of two perpendicular lines by 20 hermit crabs for the final 10 minutes of each 30-minute observation at each temperature.

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Activity</th>
</tr>
</thead>
<tbody>
<tr>
<td>19.5</td>
<td>24</td>
</tr>
<tr>
<td>28.7</td>
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<td>31.5</td>
<td>37</td>
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<td>32.2</td>
<td>49</td>
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<tr>
<td>33.7</td>
<td>30</td>
</tr>
<tr>
<td>33.6</td>
<td>46</td>
</tr>
</tbody>
</table>
Current. Initial laboratory and field observations suggested that current may play an important role in the local distribution of C. digueti. At Black Mountain Estero, near Bahia La Cholla, this species forms very tight, large clusters on shell fragments within channels during the rapid ebbing of tide. (In adjacent channels cut off from tidal flow, such aggregations are lacking, despite the scarcity of hard substrates.) At Playa Estación, the ebb and flood tides do not channelize appreciably and are, therefore, moderate in strength. In this location, the population disperses and feeds during ebb and flood tides on all available surfaces. As the water level falls, the hermit crabs first form a "bathtub" ring on the boulders. Then individuals tend to concentrate in areas where eddies form.

A number of questions are raised: How does C. digueti respond to current? Is activity stimulated? How does this species react to changes in current direction? Can current entrain the future behavioral regimen? These subjects are investigated below.

In the first study, changes in activity of C. digueti with changes in current strength were monitored. Twenty freshly collected individuals each were placed in circular pans under conditions of no current (Control 1), constant current (Control 2), and changing current (Experimental), respectively. Currents of fresh sea water were introduced at a height of 6 cm above the bottom of the pans through polyethylene tubing. The velocity of the current was determined for water exiting from the tubing. Hence, the stated current rates should be appreciably higher (by some constant factor) than those to which the
hermit crabs were subjected. For the experimental group of *C. digueti*, the current velocity was increased at half-hour intervals. At each current velocity, activity was determined as the number of line crossings during a 10-minute period for the 20 hermit crabs. The activity of the two control groups was also monitored at half-hour intervals to enable comparisons. This experiment began at the beginning of low tide and ended at the beginning of flood tide.

The results are presented in Figure 11. Highly significant differences in activity occurred between the three test groups ($\chi^2 = 85.03$, $p < .01$, df = 12). In general, higher locomotor activity is exhibited by *C. digueti* at higher current levels. However, at strengths greater than 180 cm/sec, activity is considerably depressed. At these current strengths, *C. digueti* tended to form clumps, which seemed to prevent "rolling" in the current. The activity of the two control groups tended to be less, although the patterns of activity reflect the tidal rhythm in addition to response to current. The lowest activity was shown by hermit crabs under the no-current regime, in keeping with the low tide response expected at this time in nature. However, beginning with the fourth activity recording, activity increased, despite the maintenance of constant laboratory conditions. This increase corresponded to the end of low tide in nature, when the flood tide was imminent, and appears to be a rhythmic response. Rhythmic activity corresponding to the tides is also apparent in the low, constant-current control group, but the application of a constant current appears to delay the initiation of low activity. (The final readings for the test groups taken at a velocity of 221 cm/sec
are omitted from evaluation (although included in the $\chi^2$ test) since vibrations from a nearby Waring blender disrupted the experiment.

The results of this set of experiments suggest that dispersal and high activity likely occur during low to moderate levels of current, which accords well with field observations. In nature, C. digueti disperses onto rock surfaces at ebb and flood tides when the water level is between .1-.7 meters in depth. During these periods, tidal currents in the Gulf are weak -- less than .6 m/hr tidal change in depth occurs at Puerto Peñasco (after Thomson, 1974). When depth changes (and tidal currents) are greatest, up to 1.8 m/hr at times midway between high and low tide, C. digueti has already assumed cover under boulders and in crevices.

In the second study, the qualitative responses of C. digueti to changes in direction of current were assessed. One hundred freshly collected C. digueti were placed in a shallow, rectangular enamel tray with rounded corners. Following one hour of acclimation, a current of about 66 cm/sec was introduced in one corner. At hourly intervals, the direction was changed by 90 degrees, counterclockwise. During the four hours, the hermit crabs remained mostly along the container walls, especially in corners. The directional changes induced some change in position. However, clusters tended to form and be rather stable in position. Most interestingly, once the current was stopped, two of the clusters became even more compact one half hour later. Thus, clusters of hermit crabs tend to remain stable in the face of changing currents and may endure after cessation of current.
A similar experiment was repeated using 20 *C. digueti* in a round pan 36 cm in diameter. In this experiment, observations were made each half hour on both orientation and taction (the degree of touching of hermit crabs). The current was again changed hourly. The results, Table 8, show a strong propensity of the hermit crabs to occupy the semicircular area opposite the sea water source. In experiments using India ink, the current expanded as a plume along this area. Also, the hermit crabs showed a high degree of clustering, as indicated by both the mean group size (the average number of touching individuals per "group") and the maximum number of individuals per cluster. Both measures tended to increase following the first hour at each current direction. Maximum group size also increased throughout the duration of the experiment. These results, although not conclusive, suggest that under certain circumstances currents may be at least partially responsible for both the formation of clusters and for the position of cluster sites.

Certain long-term effects of currents on clustering were also investigated. In the first experiment, 20 freshly collected *C. digueti* were placed in each of two round pans. Following one hour of acclimation, the hermit crabs were subjected, respectively, to a 79 cm/sec current pulse for 15 min (experimental) and no current (control). One hour after the current pulse, the activity in both the experimental and control groups was measured hourly. These findings are presented in Figure 12. Approximately two hours following the current pulse, very high activity was shown, which continued for about one hour. This short, high-activity period may reflect a latent response to the current pulse;
Table 8. Response of *Clibanarius digueti* to Changes of Current Direction. -- The mean group size is defined as the average number of individuals in physical contact with one another. The maximum possible mean group size and maximum group size are 20.

<table>
<thead>
<tr>
<th>Direction</th>
<th>% in Opposite Semicircle 1/2 hr</th>
<th>% in Opposite Semicircle 1 hr</th>
<th>% Touching 1/2 hr</th>
<th>% Touching 1 hr</th>
<th>Mean Group Size 1/2 hr</th>
<th>Mean Group Size 1 hr</th>
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</table>
Figure 12. Short-Term Activity of Rhythmic Clibanarius digueti in Response to a Current Pulse. -- The pulse was given to the experimental group at 0 hours. Each datum represents the number of crossings of two perpendicular lines during a ten-minute period by 20 hermit crabs.
later bouts of activity in both the experimental and control groups are apparently spurious, since these did not occur in the following two experiments.

To test whether the peak of activity could also be induced in arrhythmic hermit crabs two similar tests were performed using *C. digueti* held in the laboratory for 24 hours prior to the experiment. In the two tests, involving 20 individuals each, a current 176 cm/sec was applied for a 15-minute period. Results are shown in Figure 13. As noted in rhythmic individuals, from one to two hours after the current treatment, a pronounced jump in activity lasting approximately one hour is revealed. These results suggest that current may entrain short-term changes in the activity of this species. Clearly, however, the current is not acting as a Zeitgeber for the entire cycle of activity. In nature, nonetheless, the high currents during each tidal rise and fall may be extremely important in synchronizing the period of feeding activity at both ebb and flood tides and the subsequent periods of inactivity during both low and high tides.

**Water Depth.** Observations during sequential dives revealed a close correlation between the behavioral regimen of *C. digueti* and the water depth. Consequently, two types of studies involving changes in water depth were initiated. In the first study, the effect of emergence versus submergence was investigated. The second study evaluated the effects of different depths of sea water *per se*.

The effects of submergence versus emergence were investigated in four concurrent, replicate tests. In each test, 20 freshly collected
Figure 13. Short-Term Activity of Arrhythmic Clibanarius digueti in Response to a Current Pulse. The pulse was given to the two test groups at 0 hours. Each datum represents the number of crossings of two perpendicular lines during a ten-minute period by 20 hermit crabs.
C. digueti were placed in dry, white plastic pans. After one half hour, the number of active individuals and the number of individuals in physical contact with each other (taction) were recorded for each group. Fresh sea water was then poured gently into each container to a depth of 2 cm. After one half hour, activity and taction were again measured for each group. The sea water was then siphoned from each container and the emergent behavior was again recorded. Lastly, each group was again immersed in 2 cm of sea water and the behavior was recorded after 30 minutes. The experimental sequence for each of the four groups was, therefore: emergence, submergence, emergence, submergence, at half-hour intervals. Although no controls were employed in this test series, these test data can be compared with activity data at various constant depths, during the low tide period (Figures 5; 15, p. 119; and 17, p. 121).

The results are illustrated in Figure 14. During emergence, C. digueti showed increased clustering and low levels of activity; during submergence, few individuals were in physical contact and most individuals were active. This is particularly true during the first series of emergence and submergence. Paired t-tests on both activity and taction of emerged versus submerged hermit crabs (both for the first and second series combined) show that these differences are significant (for activity, \( t = -4.70, p < .01, df = 15 \); for taction, \( t = 3.35, p < .025, df = 15 \)).

The second set of experiments dealt with the effects of different water depths on distribution patterns. These experiments were performed to further assess the role of water depth in the production of low
Figure 14. Activity and Taction of Clibanarius digueti in Response to Phases of Immersion and Exposure. The activity of the four test groups during emergent (E) and submergent (S) phases is shown on the left; the percentage of hermit crabs in physical contact with each other (taction) during the two phases is shown on the right. For activity, $t = -4.70$, $p < .01$, $df = 15$; for taction, $t = 3.35$, $p < .025$, $df = 15$. 
tide, ebb and flood tide, and high tide behaviors. In the first experiment, 10-minute activity and substrate color selection of 20 freshly collected _C. digueti_ were determined hourly in three different depths of water: 0, 5.5, and 11 cm, respectively. These results are presented in Figures 15 and 16. Quite unexpectedly, a clear tidal rhythm of behavior is shown only at the zero water depth (at this depth, a very thin film of water was actually provided). At the intermediate depth, a slight rhythm of activity is revealed, but no other rhythms are discernible at the intermediate or greater depth.

The above result was so surprising that the experiment was repeated. Behavior at a fourth depth, 20 cm, was also observed. This experiment yielded results similar to the first experiment (Figures 17 and 18). As previously observed, there was a pronounced rhythm of substrate selection and activity only in the group of _C. digueti_ at the zero depth. The mere absence of water is not likely to be critical, since rhythms of activity, skototaxis, phototaxis, and gregariousness were previously demonstrated under shallow water depths (1 cm).

There are several possible interpretations of these data. One possibility is that emergence (or subjection to a very shallow depth as in the rhythm experiments) may entrain or release tidally rhythmic behavior. Alternatively, perhaps light is acting as a Zeitgeber or as a releasing mechanism, since more light is available in shallow depths. Field observations would tend to support the former interpretation. During the sequential diving series, both nighttime and daytime behaviors were of similar amplitude, suggesting that in nature light is not the
Figure 15. The Rhythm of Activity of Clibanarius digueti in Three Different Water Depths. — Arrows pointing downward indicate the period of low tide and the arrow pointing upward indicates the period of high tide.
Figure 16. The Rhythm of Skototaxis of Clibanarius digueti in Three Different Water Depths. — The percent of hermit crabs occupying the white (versus black) quadrants is shown versus time. The arrows pointing down indicate the periods of low tide; the arrow pointing up indicates the period of high tide.
Figure 17. The Rhythm of Activity of Clibanarius digueti in Four Different Water Depths. — The arrow pointing downward indicates the period of low tide; the arrow pointing upward indicates the period of high tide.
Figure 18. The Rhythm of Skototaxis of *Clibanarius digueti* in Four Different Water Depths. The percent of hermit crabs occupying the white (versus black) quadrants is shown versus time. The arrow pointing down indicates the period of low tide; the arrow pointing up indicates the period of high tide.
controlling mechanism. However, under constant laboratory conditions, light intensity plays a critical role in determining both the amplitude and breadth of the high tide response. This can be seen by comparing results of activity rhythms with the present results. In the activity rhythm experiments, the light intensity was about 86 lux, as compared to about 1885 lux in the depth experiments. The increased breadth and amplitude of the high tide response in the depth studies as compared to the activity rhythm studies is perhaps attributable to the increased light intensity. The results of the light intensity experiments (Figure 10) also support this conclusion.

In nature, the role of light is likely to be limited to the period of low tide. At other tidal stages, C. digueti is likely to be exposed to only very low light intensities. At low tide, C. digueti is not very sensitive to even high light intensities. In nature, then, the initial immersion, the subjection to tidal currents, and the depth are likely to be the most effective stimuli controlling the high tide behavior of C. digueti in the northern Gulf of California. In more southerly areas of the Gulf, with low tidal amplitudes, light may, indeed, be of great importance.

To further define the role of water depth as opposed to the roles of changes in light and changes in pressure, 20 freshly collected Clibanarius digueti each were subjected to the following contrasting experimental conditions: 1) constant water depth of 5 cm, 2) constant water depth of 70 cm, 3) increasing water depth, and 4) constant water depth of 70 cm with change from light to dark after two hours. For all
of these experimental conditions, a basalt rock occupying about half the container provided cover. The number of hermit crabs visible on each substrate surface was recorded hourly for the 7-9.5 hour periods.

The results are presented in Figure 19. The highest percentage of *C. digueti* dispersed onto upper surfaces when immersed, subjected to a rising depth, and then stabilized at a particular depth. The number of exposed hermit crabs under this condition was significantly higher than under a constant depth of 70 cm (paired t-test, p < .01, one tailed test). The lowest activity occurred when hermit crabs were maintained in shallow water. Under shallow conditions, significantly lower exposure occurred than at 70 cm depth (paired t-test, p < .01, one tailed test). Immersion at a constant depth of 70 cm originally produced high occupancy of surfaces, but this level was not later maintained. In the conditions under which illumination preceded dim light, no consistent alteration of behavior was seen. Even under dim light, individuals dispersed onto upper surfaces, suggesting that dispersion in nature is depth- or current-induced rather than light-induced.

**Food Supply.** Within the intertidal zone, both planktonic and particulate food supplies should fluctuate with tidal stage due to tidal migrations (Chapter 3) and to changes in physical concentration. During the lowest depths of ebb and flood tide, the greatest food densities would be expected. When phytoplankton and zooplankton abundances at Puerto Peñasco (Kellogg and Kellogg, 1966) are compared to tidal stage, this thesis is supported. The highest concentrations occurred during ebb and flood stages and lowest concentrations during high tide. Increased
Figure 19. Distribution of Clibanarius digueti in Response to Different Conditions of Depth and Light. The percent of hermit crabs occupying upper surfaces (as opposed to under the rock) is graphed versus time from beginning of the experiment. The response of 20 C. digueti at constant depths of 5 cm and 70 cm may be compared with response to rising depth, and to constant depth and changing light. Under the changing light regime, 20 hermit crabs were subjected to bright light for the first 2 hours of the experiment, after which the hermit crabs were subjected to dim light.
Figure 19. Distribution of Clibanarius digueti in Response to Different Conditions of Depth and Light.
activity in the presence of food is characteristic of many hermit crab species (Hazlett, 1968b). Although no quantitative observations were made in this study, periods of intensified activity correspond to predicted periods of high food availability of C. digueti. It is assumed that food may, therefore, act as a stimulus to activity during ebb and flood stages, although its role may be supplemental to other behavioral responses at this time rather than of primary significance.

Components of the Static Physical Environment

Substrate Heterogeneity. Comparisons between the boulder and coquina transects using Morisita's Index show that the degrees of clumping in both habitats are similar. This result is surprising in view of the differences between substrates in these habitats. The beachrock ("coquina") habitat is quite rugose, consisting of a highly pitted surface, while the boulder habitat is comprised of many large, relatively smooth basalt boulders, affording a large amount of cover.

In the first study, the influence of holes in the substrate was examined. Two 19 cm Petri dishes were filled to within two centimeters of the brim with paraffin (M.P. 52.5°C, Certified Tissue Mat). Cylindrical holes one centimeter deep were then carved in the wax as follows: Dish I, 16 1-cm holes; Dish II, 6 2.5-cm holes. In each dish, the area of the holes was about equal to the area of flat surface. Twenty freshly collected C. digueti were then spaced uniformly in each Petri dish and allowed to acclimate for one hour. In the first test series, the sea water covered both the holes and the surface, the latter to one
centimeter in depth. In the second test series, sea water was placed only in the holes and the surface was dry. During each test series, hourly readings were taken of the number of hermit crabs inside and outside of holes.

The results appear in Figure 20. In the first test series, in which both the surface and holes were submerged, a tidal rhythm of hole occupancy is seen. Holes were selected with an appreciably greater frequency at low tide than at high tide. Thus, selection of crevices and potholes for clustering at low tide would be predicted. This result suggests that, while spatial heterogeneity may not cause clumping, it may be an important factor in determining the degree and site of clustering when available sites are limited. The size of the available holes may also be critical in determining the degree of clumping in a certain habitat. In the first test, a significantly greater degree of clustering occurred when few, large holes rather than many, small holes were provided (paired t-test, p < .05).

In the second test series, a tidal rhythm is not evident. The general lack of change through time seems to have resulted from initial preference for the dry surface rather than the wet holes. This behavior induced continued inactivity of the dry individuals. Such behavior has also been noted in choice experiments involving the basalt boulder. Individuals which initially selected the dry boulder surface remained inactive throughout the experiment. In this series, no size preference is evident.
Figure 20. Hole Occupancy of Clibanarius digueti throughout a Tide Cycle. — The percent of hermit crabs occupying small and large holes is shown versus time when the total surface is submerged (a) and when only the holes contain sea water (b). The arrows pointing down indicate the times of low tide; the arrows pointing up indicate the times of high tide.
A great propensity to select shaded areas or cover under boulders is also shown by *C. digueti* at low tide. In depth experiments employing a basalt boulder, hermit crabs in shallow water exhibited this preference to a much greater degree than those at depth. Thus, at low tide in the boulder habitat, the under-rock habitat is utilized for aggregation sites when suitable. It would be interesting to examine this problem further since sedimentation, especially from storms, and stagnation may limit the number of suitable sites. It is likely that the similar degrees of clustering noted in the transect studies of the boulder and coquina habitats resulted because of the abundance of cover in either holes (coquina habitat) or under boulders (boulder habitat). In areas scarce in these microhabitats, such as esteros, *C. digueti* remains closely affiliated with shell debris, stingray potholes, and other surface deformities. In this habitat, the degree of clustering may reflect the abundance and distribution of cluster sites.

Components of the Biotic Environment

In addition to physical factors, the abundance patterns of species which act as competitors, predators, or cooperators may also affect the spatial patterns of *C. digueti*. The distribution of snails, which ultimately afford the necessary shell resource, may thus influence the pattern of spacing of hermit crabs, as may the distribution of sympatric hermit crab species. The relationships between these factors and the degree of clustering of *C. digueti* is investigated below.

**Sympatric Hermit Crab Species.** Figure 21 illustrates the species abundance patterns for the two transects as a function of month. Note
Figure 21. Hermit Crab Abundance from February 1974 through February 1975 in the Boulder and Coquina Transects. For the boulder transect, the number of individuals of three species of hermit crabs within the transect is graphed versus month of the year. For the coquina transect, only C. digueti was present in sufficient abundance to graph; other species were quite rare.
that *Clibanarius digueti* greatly predominates in the coquina habitat. Numbers of the other species were too low to depict graphically and constituted only 7% of the total population. In contrast, within the boulder habitat, *Paguristes anahuacus* rivals *C. digueti* in abundance, and *Pagurus lepidus* also occurs here in appreciable numbers. In fact, *C. digueti* comprised only 45% of the total boulder population of hermit crabs.

Since mixed species clusters are common to the boulder region, it is worthwhile to investigate their effect on the pattern of spacing within the boulder transect. To what extent do the different species segregate and, therefore, dilute the measure of clumping? To what extent do they enhance the degree of clumping by distributing themselves in a similar manner to *C. digueti*? Table 9 shows the effects on various clumping measures when all species of hermit crabs are considered together. Except for the February samples, the values for Morisita's Index are fairly comparable to those when *C. digueti* was considered alone (Table 5). No significant difference in the degree of clustering $I_S$ of *C. digueti* alone versus all species combined is indicated (Wilcoxon's matched pairs signed ranks test, $\chi^2 = 0, p > .05, df = 10$). Therefore, some interspecies clumping is indicated by these data. Field observations abundantly support this contention. On numerous occasions, particularly in the lower intertidal zone, *Paguristes anahuacus* and *C. digueti* both occurred in sizable numbers within a given cluster. *Pagurus lepidus* was also found to cluster with these species, although scattered individuals were also found on attached algae, a microhabitat
Table 9. Basic Statistics and Indices of Clumping for All Hermit Crab Species Combined in Each Boulder Transect. — Two indices are presented: the variance to mean ratio ($s^2/\bar{x}$) and Morisita's Index of dispersion ($I_\delta$). The transect code indicates the substrate, month, and year. The March and July samples are missing.

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in which it predominated. Likewise, the rare species *Pylopagurus roseus* also participated in mixed clusters.

In connection with the above discussion, it is of interest to examine the extent of spatial overlap of *C. digueti* and *P. anahuacus*. Figure 22 shows the spatial overlap between *C. digueti* and *P. anahuacus*, as calculated by Horn's index of niche overlap (Horn, 1966):

\[
C = \frac{2}{q} \sum_{i=1}^{q} x_i y_i \cdot \frac{1}{q} \sum_{i=1}^{q} x_i + \frac{1}{q} \sum_{i=1}^{q} y_i
\]

where \(x_i\) and \(y_i\) are relative proportions of species \(x\) and \(y\) in the \(i\)th sample and \(q\) is the total number of samples. Overlap is greatest in both fall and spring when environmental conditions are most moderate. During the summer and winter months (especially February), *P. anahuacus* seems to retreat back into the lower intertidal and sublittoral zone. Figure 22 also shows the center of distribution of *C. digueti* throughout the year. *Clibanarius digueti* seems to maintain about the same position in the intertidal zone throughout the year and does not respond to the shifts of distribution of *P. anahuacus* by shifting to a lower position in the intertidal zone. These data, however, suggest a positive relationship between spatial overlap and the center of distribution of *C. digueti* in the intertidal zone (Spearman's rank correlation, \(C = .64, p < .05, df = 10\)). Therefore, *C. digueti* may move lower in the intertidal zone as *P. anahuacus* moves higher, thus increasing the degree of overlap. If
Figure 22. Spatial Overlap of Clibanarius digueti and Paguristes anahuacus by Month and Center of Distribution of C. digueti by Month in the Boulder Habitat. — Spatial overlap was calculated using Horn's Index of Niche Overlap, $\hat{C}_\lambda$; the monthly center of distribution of C. digueti is the meter in which an abundance of 50% is achieved. The transect meter begins with 0 in the upper intertidal zone and ends at 49 in the lower intertidal zone.
these two species did compete for space, or associated benefits, such as shells or shelter, one would predict that migration of *P. anahuacus* would be followed by physical displacement of *C. digueti*.

No direct observations were made on the possibility of competition for shell resources, particularly possible between *C. digueti* and *P. anahuacus*. However, *C. digueti* and *P. anahuacus* are similar in size for a given shell size. This conclusion follows from detailed studies of shell fit of the two hermit crabs. In comparisons of fit of five common shells for which highly significant regressions of hermit crab size on shell size were found, *P. anahuacus* exceeded *C. digueti* in mean size when inhabiting *Tegula corteziana*, *Liocerithium judithae*, and *Morula ferruginosa*. However, *Clibanarius digueti* was the larger of the two hermit crabs for *Acanthina angelica* and *Turbo fluctuosus*. Hence, there is no evidence that either hermit crab species is in a position to preempt shells from the other species as would be expected if one species was consistently smaller when occupying a shell of a certain size.

**Sympatric Snail Species.** The shell often represents the limiting resource of hermit crabs (Provenzano, 1960; Reese, 1962, 1969; Orians and King, 1964; Hazlett, 1966a, 1970a; Markham, 1968; Childress, 1972; Vance, 1972a, b; Grant and Ulmer, 1974; Kuris and Brody, 1976). Thus, the pattern of shell distribution may be important to that of hermit crab distribution. This hypothesis was investigated by comparing the abundance patterns of *C. digueti* with the abundance patterns of live snails and empty shells.
The distribution of all snail species was followed from December 1974 through February 1975 in both boulder and coquina transects. Figure 23 depicts the abundance of hermit crabs for these months as a function of the abundance of live snails. No correlation was found between the abundance of hermit crabs and snails in the .5 m² samples along the transects (for 5 of 6 transects, $r^2 < .25$, $p > .05$). In comparison to live snails ($N = 3797$), few empty shells ($N = 88$) were present in the data collected. Therefore, clustering of hermit crabs near empty shells is also improbable on the scale in which these observations were recorded.

The interpretation of use patterns of inhabited shells is more difficult. However, the field observation that some clusters consisted of a dominant shell type invites explanation. Table 10 shows the patterns of shell use of hermit crabs during the 13-month sampling program. The raw data for the three most abundant species of hermit crabs were subjected to a Chi-square analysis using an $r \times c$ contingency table. This analysis revealed highly significant differences in shell use among *C. digueti*, *P. anahuacus*, and *P. lepidus* ($\chi^2 = 2033.44$, $p < .01$, df = 34). Significant differences also occurred between *C. digueti* and *P. anahuacus* ($\chi^2 = 1633.4$, $p < .01$), between *C. digueti* and *P. lepidus* ($\chi^2 = 338.6$, $p < .01$), and between *P. anahuacus* and *P. lepidus* ($\chi^2 = 566.97$, $p < .01$). Although it was not possible to include *P. roseus* in this analysis due to the small sample size, *P. roseus* clearly discriminates against many shell species. Its tendency to select globose shell types may stem from the
Figure 23. Corresponding Abundance Patterns of *C. digueti* versus Live Snails in Coquina and Boulder Transect Samples. -- Each small datum represents a single sample. Larger points include more than one sample.
Table 10. Frequencies of Shell Occupancy by Four Species of Hermit Crabs in Coquina and Boulder Transects. — Initials of shell species are given; the full names are provided for these species in the Appendix.

CD = *Clibanarius* *dugueti*  
PA = *Paguristes* *anahuacus*  
PL = *Pagurus* *lepidus*  
PR = *Pylopagurus* *roseus*

<table>
<thead>
<tr>
<th>Shell Species</th>
<th>Coquina Transect</th>
<th>Boulder Transect</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>CD</td>
<td>PA</td>
</tr>
<tr>
<td>Aa</td>
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<td>-</td>
</tr>
<tr>
<td>Pn</td>
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<td>Ac</td>
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<tr>
<td>Na</td>
<td>.002</td>
<td>-</td>
</tr>
<tr>
<td>Tg</td>
<td>-</td>
<td>-</td>
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<td>-</td>
</tr>
<tr>
<td>Total</td>
<td>4165</td>
<td>77</td>
</tr>
</tbody>
</table>
possession of a large operculate left cheliped, which is used to plug the shell entrance.

A strong argument for low mobility among the various snail and hermit crab species can be made. In some cases, the different habitat preferences of the snail species is reflected in their frequency of use by the different hermit crab species. For example, in the coquina habitat, the most common snail shell occupied by *C. digueti* is *Morula ferruginosa* (Mf). *Liocerithium judithae* (Lj) is occupied to a much lesser extent. In contrast, in the boulder habitat, *C. digueti* most frequently occupies *L. judithae*. Within-habitat zonation of shell species may also affect patterns of shell use. *Turbo fluctuosus* (Tf), *Tegula corteziana* (Tc), and *Morula ferruginosa* (Mf) dwell in the lower mid-intertidal zone of the boulder habitat. Their greater use by *P. anahuacus* living in this zone thus parallels this zonal pattern.

However, size differences may also be critical in determining the relative proportions of each shell type inhabited. For all transects, the mean sizes of *C. digueti*, *P. anahuacus*, *P. lepidus*, and *P. roseus*, calculated from regression formulas (see Appendix), were 66.5 ± 163.9, 80.0 ± 227.4, 18.6 ± 24.4, and 72.5 ± 62.1 mg each, respectively. The size differences for the first three species are highly significant (*p* < .01, *t*-tests for unpaired observations and unequal variances). In the case of *Pagurus lepidus*, individuals were concentrated in smaller shell types: *Liocerithium judithae*, *Tegula corteziana*, *Mitrella guttata*, and *Anachis* sp. Size differences may also explain the greater use of
Acanthina angelica by P. anahuacus than C. digueti, despite this shell's wide range within the intertidal.

Discussion and Conclusions

The early behaviorists (Loeb, 1918; Allee, 1926, 1931, 1938; Fraenkel and Gunn, 1940; Carthy, 1958) advanced the hypothesis that aggregation and dispersal of individuals within a population is explicable in terms of taxes and kineses. Accordingly, the formation or abandonment of clusters results from simple orientational and kinetic responses to single environmental stimuli.

This concept has been supported by numerous studies. Allee (1926) showed that aggregation of several species of land isopods results mainly from their habits of seeking moist, dark areas. In the laboratory, Allee (1931) showed that aggregation of an ophiuroid is due to positive thigmotaxis. Bovbjerg (1952) demonstrated that clusters of the freshwater snail Campeloma result from rheotactic responses which cause accumulations at physical barrier. Moulton (1962) related the aggregation and dispersal of the marine snail Cerithium to changes in thigmotaxis induced by changes in hydrobarometric pressure. Cubit (1969) has related the aggregation of the mole crab Emerita to thixotrophic responses in conjunction with their physical accumulation by lateral wave flow. Dix (1969) found that clustering of the echinoid Evechinus stems from a positive chemotaxis between individuals. Similar findings could be cited ad infinitum.

However, although aggregations may be explicable in terms of only one or a few taxes or kineses, frequently a number of other mechanisms
come into play. Thus, in the case of *Cerithium* above, Rohde and Sandland (1975) found aggregation and dispersal to be regulated by behavioral rhythms and influenced by both light and depth. In the case of *Emerita*, Efford (1965) offers evidence for gregariousness between individuals.

None of the various forms of contagion among crustaceans, including swarms, clusters, schools, migratory assemblages, and vertical stratifications, conform easily to the single-mechanism concept. Upon close examination, an array of mechanisms, including vectoral, stochastic-vectoral, reproductive, social, and coactive components (Stavn, 1971), may jointly regulate the contagion exhibited in crustaceans. Some of these components may be redundant, as in the case of the reversible tropisms, optimal light intensity, and endogenous rhythms which together bring about vertical migrations or the multiplicity of independent mechanisms which control the settlement of cyprid larvae in permanent clusters.

Even more perplexing, and possibly more complex, instances of aggregation occur among crustacean species which periodically aggregate and disperse. Many of these phenomena clearly involve not only responses to exogenous stimuli but also responses controlled by endogenous or entrained rhythms. These allow the periodic alternation or reversal of responses to environmental stimuli or conspecifics, and thus permit versatility of tactic and kinetic responses under changing environmental cycles (e.g., tide cycle, the diurnal cycle, seasonal or annual cycles). A multiple-control system also enables different patterns of behavior in different habitats; for instance, in tideless versus tidal habitats.
In the present chapter, the mechanisms of aggregation and dispersion of the hermit crab, *Clibanarius digueti*, were analyzed. Like many crustacean species, *C. digueti* exhibits a regular pattern of aggregation and dispersal concording with the tidal cycle. This species was found to manifest tidal rhythms of activity, skototaxis, phototaxis, and taction in the laboratory under constant conditions. In combination, these rhythms appear to regulate the behavior of *C. digueti*, both in nature and in the laboratory, insuring not only synchrony of behavior, but also the contact between individuals at low tide. The rhythms provide an opportunity for sociality, an opportunity that may preadapt this species to its congeners for other forms of association such as migratory assemblages or schools.

However, the rhythms exhibited by *C. digueti* were only expressed when certain environmental prerequisites of light and depth were met. Under other conditions, such as continuous bright light or constant moderate depth, the behavior of *C. digueti* was uncoupled from the underlying rhythms. Other environmental factors, such as current, also played an important role in the behavior of this hermit crab.

A synthesis of the interacting components in the behavior of *C. digueti* is presented in Figure 24. This model attempts to incorporate and link both rhythmic and exogenous responses. Thus, clustering at low tide is inferred to initiate from tidal rhythms of low activity, positive skototaxis (selection of dark substrates), negative phototaxis (selection of shade), and positive taction (gregariousness), when coupled to environmental conditions of exposure or near exposure (very shallow
Figure 24. Flow Diagram of Component Mechanisms of Aggregation and Dispersal in Clibanarius digueti. -- This diagram summarizes both laboratory and field data. The only speculative component is food, which should be most concentrated and available to benthic filter-feeders during ebb and flood tides. The cross-out of skototaxis and phototaxis (top of diagram) indicates that negative skototactic and positive phototactic responses are not activated under conditions of diminished light. The reader can begin at any tidal stage. If the stated conditions are met, arrows indicating "yes" should be followed to the resulting pattern of spacing until a change in tidal stage occurs.
depths) at low tide. The degree of clustering at this time is enhanced when rugose substrates or cover is afforded but are not over-abundant. At ebb and flood tides, high activity and consequent dispersal stem from rhythmically increased activity, negative skototaxis, positive phototaxis, and negative taction. These responses apparently cause the hermit crabs to abandon their dark and/or shaded clustering sites and to seek lighted upper surfaces. In conjunction with rhythmical inducement of activity and dispersal exogenous stimuli operate, and may actually be of over-riding importance. Stimulation and possible short-term entrainment of the brief periods of activity at ebb and flood tides is initiated by weak currents and increasing depth. The presence of increased amounts of plankton and detritus at the substrate interface during ebb and flood stages may also amplify activity and dispersal. During high tide in nature, high activity is apparently suppressed in the absence of light and due to short-term current entrainment occurring during the flood stage. Increasing currents during mid-tidal stages may also deter activity, as may increased predator presence. Another possible influence may be inhibition by increased pressure at depth, but it was not possible to investigate this phenomenon.

In the laboratory, the recorded behavior deviated from that in the field at high tide. Under calm conditions, in shallow depths, and in light, the ebb and flood responses are seemingly protracted so that they were manifested during the high tide period in the laboratory. This interpretation leads to the conclusion that rhythmic laboratory behavior alone cannot be used as a reliable predictor of field behavior. However,
the proposed model by incorporating both rhythmic and exogenous responses may be adequate to explain both the laboratory and field regimen of *C. digueti*.

The interacting mechanisms proposed to regulate the aggregation and dispersal of *C. digueti* may prove to be even more complex than the present study indicates. However, as modelled, the possibilities for the maintenance of different spatial patterns under different environmental conditions are numerous. The flexibility inherent in *C. digueti* would appear to account for this species' numerical abundance throughout the Gulf of California. If the spacing behavior of *C. digueti* were rigidly controlled either by rhythms or by the environment, this hermit crab would undoubtedly occur only in a limited number of habitats.
CHAPTER 5

THE ADAPTIVE VALUE OF AGGREGATION

IN CLIBANARIUS DIGUETI

In Chapter 4, the component mechanisms of aggregation and dispersal in *Clibanarius digueti* were investigated. A model of their behavior was then constructed. This model showed the relationship between the various mechanisms regulating the behavioral regimen, both in nature and in the laboratory. The ultimate cause of aggregation, i.e., the adaptive value, remains to be discussed.

A variety of adaptive values may be postulated to account for the clustering habit of hermit crabs, including both behavioral and physiological adaptations. Among the former possible benefits are facilitation of shell exchange and mating, increased opportunity for shell cleaning, and predator avoidance. Physiological advantages may include increased resistance to current, cold, or desiccation. These hypotheses and evidence, pro and con, are discussed below.

**Hypotheses**

*Shell Exchange*

In the land hermit crab *Coenobita clypeatus*, individuals may cluster for the purpose of a mass shell exchange (Radinovsky and Henderson, 1974). The possibility, therefore, exists that clusters of marine species may serve a similar function. However, Reese (1963) found
that *Calcinus laevimanus* cluster more and are less active when situated in preferred *Tegula* and *Trochus* shells. In the less desirable shell *Olivella*, individuals aggregate to a lesser extent, and shell-less individuals, which exhibit the greatest shell-searching behavior and are most active, do not cluster. Thus, a shell exchange function of this marine species is unlikely. It is also unlikely in those species in which the young are more prone to cluster, since shell availability is usually limiting to large rather than small individuals. Lastly, a shell exchange function is unlikely in the case of quiescent aggregations, which seem to be the most common type of regular clusters.

Despite these arguments against the shell exchange hypothesis, it is curious that aggregations of *C. digueti* often appear to be size-specific in character. The results of a one-way analysis of variance on the calculated size of individuals for each transect support this observation (Table 11). F tests applied to the data indicate significant size differences between samples for all transects except boulder transects during June and August, when the numbers of small individuals were quite low. Therefore, a size specificity of samples is clearly supported. Since samples usually included either one or no clusters, a size specificity within clusters may also be inferred. This specificity could be advantageous in shell exchanges if relatively small changes in shell size are undertaken. On the other hand, it could be argued that a cluster composed of a wide size range of individuals would be more advantageous for shell-exchange purposes.
Table 11. Results of One-Way Analyses of Variance in Size of *Clibanarius digueti* between and within Meters for Each Transect. -- The null hypothesis tested is that size differences of hermit crabs between quadrats are equal to size differences of hermit crabs within quadrats for each transect.

<table>
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To clarify the role of clusters in shell exchange, empty tagged shells were introduced into clusters and into shallow areas where hermit crabs were numerous but dispersed and active. In each of 11 tests, 3-5 empty shells of a variety of commonly utilized species were placed among a group of hermit crabs. The introduced shells were all tagged with brightly colored fingernail polish. Tests were performed when hermit crabs were: 1) dispersed and in shallow water; 2) clustered in exposed locations and inactive; and 3) under rocks, either damp or immersed in shallow water.

The results are shown in Table 12. A clear trend of shell exchange is evident only when the hermit crabs were active and dispersed or wet and under rocks. Since most aggregations of C. digueti occur when the hermit crabs are exposed to the air during the low tide, the shell exchange hypothesis is, therefore, shown unlikely to be important for this population of C. digueti. Perhaps in a low density environment or in habitats not totally emergent at low tide, appetitive behavior is increased during cluster formation.

It was notable that, when the hermit crabs were active and dispersed in shallow water, shell exchanges occurred within minutes of the deposition of the empty shells. In one case, a fight ensued between two individuals for an empty shell. Within minutes, some 14 hermit crabs were wrestling and a mass shell exchange occurred. This is, I believe, the first record of a mass shell exchange among marine hermit crabs.

Although results presented in this section indicate that shell exchanges are rare within clusters, the localization of similarly sized
Table 12. Frequency of Shell Exchanges in Clustered versus Dispersed *Clibanarius digueti*. The ratio of empty shells occupied to empty shells introduced (final column) is given for hermit crabs under different conditions of dispersion and in different habitats.

Exposed Sites

<table>
<thead>
<tr>
<th>n&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Active &amp; Dispersed</th>
<th>Inactive &amp; Clustered</th>
<th>Under Rock Sites</th>
<th>Shells Occupied</th>
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<tbody>
<tr>
<td>30</td>
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<tr>
<td>25</td>
<td>x</td>
<td></td>
<td></td>
<td>5/5</td>
</tr>
<tr>
<td>50&lt;sup&gt;b&lt;/sup&gt;</td>
<td>x</td>
<td></td>
<td></td>
<td>4/5</td>
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<tr>
<td>10</td>
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<td></td>
<td>x</td>
<td>0/5</td>
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<sup>a</sup>Estimated number of hermit crabs.

<sup>b</sup>In this instance, hermit crabs were removed from rock surfaces and placed on the bottom of the tidepool.
individuals may be of considerable benefit at times other than low tide. Since hermit crabs are most vulnerable to predation during the time of shell exchanges, the frequency of appropriate exchanges may be enhanced by the maintenance of size specificity in the neighborhood of each cluster. Perhaps, then, some epideictic function regarding size relations may be served by clustering, the advantage of which is secured at ebb and flood tides, rather than within the cluster. (On the other hand, size specificity may be regulated by encounters during active periods.)

Mating

Females of many species of crustaceans (Carlisle, 1957), including many hermit crabs (Hazlett, 1966a, 1968b), must molt just prior to or following copulation. The rapid location of molting females may be facilitated within a cluster, since hormones of many crustaceans are received only at very short distances (Hazlett, 1966a; Dahl, Emanuelsson, and von Mecklenburg, 1970; Katona, 1973; Griffiths and Frost, 1976) and may be released only intermittently (Ryan, 1966; Eales, 1974). In some hermit crabs, however, females need not molt in order for successful fertilization to occur (Hazlett, 1968b). In these cases, participation in aggregations may be highly protective, since exposure of the abdomens places the mating pair in a most perilous position with respect to predators. Despite these rationales, there is no evidence to suggest a mating function for clusters. To the contrary, the year-round presence of clusters indicates that mating cannot be a primary function for most species, since mating is usually highly seasonal (Pike and Williamson, 1959; Lewis, 1960; Reese, 1968).
The hypothesis that aggregations serve to enhance the location of a mate is not supported by observations on the *C. digueti* population at Playa Estación. Here, individuals are exceedingly numerous. In fact, the densities of the population of *C. digueti* as high as 100 individuals per m² in the boulder habitat are not uncommon. Such densities exceed those of any other species of macroinvertebrate or vertebrate. Thus, securing a mate would not appear to pose a problem.

Also, *C. digueti* was observed copulating in nature only over a limited time period from May through September. Mating activity was particularly intense only in May and June. This seasonal specificity further indicates that clustering, which is a year-round phenomenon of relatively unchanging intensity, does not subserve a mating function.

Field and laboratory observations of mating corroborate this view. Numerous instances of couple formation were observed both within and outside clusters. Courtship, in which the larger male clasps the smaller female, endures for twelve hours or more. This period exceeds the duration of clustering and suggests that protection of mating individuals within clusters is not the case.

Yet another indication that mating is not a function of clusters is the interspecific character of many clusters. The occurrence of as many as four species within one cluster would tend to suggest that a more general purpose may be served by aggregations.

Shell Cleaning

In addition to shell volume, an important criterion in the adoption of a gastropod shell is its weight, for the shell must be
easily transportable (Reese, 1962; Markham, 1968; Hazlett, 1970b). Excess epiphytic and epizoic baggage, unless assuming a protective function (Ross, 1959; Grant and Pontier, 1973; Grant and Ulmer, 1974), presumably reduce shell desirability. It is, therefore, not surprising that, in some species of hermit crabs, individuals will mount each other piggy-back style and graze upon each other's shells (Hazlett, 1966a; Snyder, 1972). Within an aggregation, such behavior may afford the mutual benefit of a shell cleaning for the recipient and a meal for the cleaner.

Although not uncommon in the laboratory, instances of the grooming of epiphytes from one individual's shell by another individual were only infrequently observed in nature. Field observations suggest that, in the case of *C. digueti*, this activity is normally confined to the ebb and flood tidal stages. During these periods, hermit crabs generally remain dispersed and are actively feeding. Shell-cleaning episodes ensue only following seemingly chance encounters and are short-lived. Hence, shell cleaning at low tide when hermit crabs cluster is likely to be quite rare and coincidental in nature.

Predator Avoidance

There are numerous conditions under which clusters may enhance predator avoidance (see Chapter 1). As yet, however, there are no arguments or evidence to suggest that the clustering of hermit crabs may lower predation rates. Mutual defense is unlikely, since hermit crabs retreat into their shells when attacked. Similarly, because clusters involve quiescent individuals, mutual warning is unlikely. The fact that
clusters frequently occur during vulnerable times, low tide and during the day, does suggest a possible predator-escape function. By clustering, hermit crabs may enlarge the search area of the predator and, hence, minimize the probability of encounter. This strategy may be particularly effective in the case of easily satiated predators, whose take, once a cluster is located, would be small. However, most records suggest that hermit crabs are only rarely preyed upon in nature (Reese, 1969). Moreover, clustering also occurs at night, when many visual predators are not effective.

Field observations have also suggested that predation is not a significant factor in the clustering of C. digueti at low tide. At this time, no shore birds were ever observed feeding in the vicinity of clusters. Instead, the main activity of shore birds which frequented the coquina and boulder habitats was perching and preening. Feeding activity was concentrated in tidepools and in the sandy upper intertidal zone.

On only one occasion was an apparent case of predation of C. digueti noted at low tide. On this occasion, an Octopus digueti in a small tidepool on the coquina platform was found clutching a large Turritella shell. Following a tug of war, the shell was pulled from the octopus and examined in the laboratory. After .5 hour in fresh sea water, a C. digueti emerged and became active.

Toward the end of ebb tide and at the beginning of flood tide, marine predators such as fish begin to invade the intertidal zone. It is at these times, when C. digueti is dispersed on tops of boulders and other substrates, that predation is most likely. However, Heliaster
kubinijii apparently rejects C. digueti when it is retracted into the shell (Fitzgerald, 1976). Similarly, the blenny Malacoctenus gigas seems to prey upon C. digueti only when it is emerging from its shell in order to execute a shell exchange (pers. obs.). Larger fish predators, which subsequently invade the intertidal zone during high tide may prey upon C. digueti more easily. However, at depths greater than .7 meters, C. digueti refuges under rocks and is, therefore, inaccessible to such potential predators.

Resistance to Current

Earlier, it was mentioned that, in the estero habitat, clusters of C. digueti frequently occur on shell fragments within channels of rather high currents. These clusters consisted of tightly packed individuals which formed layers several individuals deep. The dislodging of individuals from such clusters repeatedly resulted in the hermit crab rolling away in the current. In similar adjacent channels, where there was no current, C. digueti did not cluster appreciably. Therefore, in habitats lacking sources of cover with strong channelization of currents, resistance to current would appear to be a major function of aggregation. This phenomenon was also noted locally in Playa Estación where smaller channels occurred.

Resistance to Cold

The unexpected result that the degree of clustering in the boulder habitat was increased both in February 1974 and 1975 (Chapter 4) suggested the possibility that clustering may sometimes be related to
cold. Two questions are: Can cold temperature elicit aggregation? and Can clustering in cold enhance survival? In an attempt to answer the former question, the spatial patterns of 16 *C. digueti* upon cooling to -1°C were examined at 15-minute intervals. The hermit crabs were uniformly spaced in shallow (1 cm) sea water at the beginning of the experiment. During the experiment, the taction (number of hermit crabs touching each other) and mean group size were recorded. The final observation was made 15 minutes after removal of the hermit crabs from the freezer.

The results are presented in Table 13. The results do not suggest that clustering increases under conditions of cooling. However, the spatial patterns do indicate inactivity in cold. Over a prolonged period of cold, recruitment to clusters may, therefore, increase. Does survivorship increase in clusters, versus isolated individuals, during cold?

Table 13. Taction and Mean Group Size of 16 *Clibanarius digueti* under Cold Conditions.

<table>
<thead>
<tr>
<th>Time</th>
<th>Temperature (°C)</th>
<th>Taction</th>
<th>Mean Group Size</th>
</tr>
</thead>
<tbody>
<tr>
<td>0910</td>
<td>20</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>0925</td>
<td>1</td>
<td>6</td>
<td>1.23</td>
</tr>
<tr>
<td>0940</td>
<td>-1</td>
<td>7</td>
<td>1.14</td>
</tr>
<tr>
<td>0955</td>
<td>-1</td>
<td>7</td>
<td>1.14</td>
</tr>
<tr>
<td>1010</td>
<td>8</td>
<td>7</td>
<td>1.14</td>
</tr>
</tbody>
</table>
An experiment to test resistance by *Clibanarius digueti* in different group sizes to cold was performed using three insulated coolers filled with crushed ice. Three group sizes were compared: isolated individuals, groups of 50, and groups of 100. In all, 70 isolated individuals, 400 individuals in groups of 50 each, and 700 individuals in groups of 100 each were tested. These individuals were of all sizes and were freshly collected at low tide one hour prior to beginning the experiment. Damp individuals were placed in styrofoam cups, which were imbedded half-way in the crushed ice. At seven different time intervals, ranging from 3 to 16.5 hours, individuals were withdrawn and tested. For each test, survivorship, judged by the exhibition of locomotor movement within two hours of placement in fresh sea water, was recorded for 10 isolated individuals, 1 group of 50 individuals, and 1 group of 100 individuals. However, for the final test, two groups of 50 individuals were utilized.

The results of the cooling experiment appear in Table 14. A Chi-square evaluation of the raw data was used to compare test groups taken from a given cooler at the same time. Highly significant differences between different group sizes are apparent (\(\chi^2 = 140.61, p < .01, \text{df} = 14\)). Inspection of the data reveals a pronounced tendency for groups of larger size to show increased survival. However, this result is difficult to interpret in view of temperature gradients existing within each cooler. For the three coolers, the range of temperatures between the inside cup bottom and the inside cup tops were 2.5-8.0°C, 4.2-10.9°C, and 3.2-7.6°C, respectively. Thus, the hermit crabs in the larger groups
Table 14. Resistance to Cold by Clibanarius digueti in Large Clusters. -- Different temperatures were found in each cooler. \( \chi^2 = 140.61, p < .01, \) and \( df = 7. \)

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Exposure Time (hr)</th>
<th>Group Size</th>
<th>Survivorship (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.5</td>
<td>3.0</td>
<td>100</td>
<td>100 100 100</td>
</tr>
<tr>
<td>2.5</td>
<td>10.0</td>
<td>20</td>
<td>20 48</td>
</tr>
<tr>
<td>4.2</td>
<td>12.5</td>
<td>10</td>
<td>12 86</td>
</tr>
<tr>
<td>4.2</td>
<td>13.5</td>
<td>10</td>
<td>62 80</td>
</tr>
<tr>
<td>4.2</td>
<td>14.5</td>
<td>20</td>
<td>37 87</td>
</tr>
<tr>
<td>3.2</td>
<td>15.5</td>
<td>0</td>
<td>0 2</td>
</tr>
<tr>
<td>3.2</td>
<td>16.5</td>
<td>0</td>
<td>1 8</td>
</tr>
</tbody>
</table>
were subjected to warmer temperatures. Their enhanced survival may be directly attributable to this factor, rather than to group size per se, but the cluster, nevertheless, is critical to the result.

Resistance to Desiccation

Reese (1969) advances the hypothesis that aggregation in intertidal hermit crabs is a means of reducing desiccation during exposure at low tide. Such effects have been demonstrated in isopods by Warburg (1968). By reducing the surface-to-volume ratio, groups of five or more Oniscus showed a 50% savings in water loss over isolated individuals. It is interesting, in this context, that Allee (1926) found that drying actually induced aggregation by land isopods (including Oniscus asellus). Whether such a mechanism could apply to hermit crabs, which are protected by gastropod shells, is, however, questionable.

Schmitt (1926) claims that Clibanarius africanus and C. cooki cluster at low tides only in warm, sunny weather and otherwise remain where stranded by the tides. It is puzzling that some clustering species appear to mount rocks and sun with their apertures up for the duration of low tide (Reese, 1969; Snyder, 1972; Ball and Haig, 1974). This behavior is difficult to explain by the desiccation hypothesis unless evaporative cooling is somehow achieved. At any rate, desiccation resistance cannot act as the primary adaptive value of clustering in many hermit crabs, which aggregate in cool intertidal habitats or under water.

To test the desiccation hypothesis, two field experiments were performed. In the first experiment, survivorship of 410 C. digueti in three different-sized groups -- isolated individuals, groups of 10
individuals, and groups of 20 individuals — were tested under desiccating conditions. This experiment was conducted on June 23, 1975, under a ramada in close proximity (about 60 m) to the natural habitat, using medium-sized (about 1 cm in shell length) hermit crabs freshly collected at the beginning of low tide. Each individual or group occupied a single styrofoam cup. There were 110 cups with isolated individuals and 10 cups each with groups of 10 and 20 individuals each. The cups were imbedded half-way into a rectangular sand plot approximately 13 cm deep. Cups were spaced at 8-cm intervals. The sand was used in order to insure uniform temperature conditions. Cups were arranged and removed according to random draw with the restriction that only 10 individuals and one group of 10 and 20 were selected each time. The experiment began one hour after collection of the hermit crabs. The temperature during the experiment was 26.8 ± 3.6°C. The humidity was 63%. Survivorship was judged by the demonstration of locomotor activity within one hour of submergence in fresh sea water.

The results appear in Table 15. No clear trend is evident between groups of different sizes. All sampled *C. digueti* survived through 1400 hours, nine hours after their initial exposure at the ebb tide, and 4.5 hours after their natural period of immersion. A Chi-square test of independence using an r x c contingency table indicated no significant differences between groups of different sizes ($\chi^2 = 6.51$, $p > .05$, df = 18).

A second desiccation experiment was conducted on May 30, 1977. The survivorship in larger groups was compared to the survivorship of
Table 15. Resistance of *Clibanarius digueti* in Small Clusters to Desiccation. — For each exposure time and each cluster size, the percentage survivorship is presented. Ten isolated individuals, one group of 10 individuals, and one group of 20 individuals were tested during each time period. This test was performed on June 23, 1975. Prior to this experiment, the hermit crabs were exposed for 6 hours during low tide. $\chi^2 = 6.5$ (survival values for raw data), $p > .05$ (ns), and $df = 18$.

<table>
<thead>
<tr>
<th>Exposure Time (hr)</th>
<th>Cluster Size</th>
<th>Survivorship (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>10</td>
</tr>
<tr>
<td>0</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>1</td>
<td>100</td>
<td>-</td>
</tr>
<tr>
<td>3</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>5</td>
<td>90</td>
<td>100</td>
</tr>
<tr>
<td>6</td>
<td>80</td>
<td>90</td>
</tr>
<tr>
<td>7</td>
<td>80</td>
<td>90</td>
</tr>
<tr>
<td>8</td>
<td>70</td>
<td>80</td>
</tr>
<tr>
<td>9</td>
<td>70</td>
<td>50</td>
</tr>
<tr>
<td>11</td>
<td>30</td>
<td>30</td>
</tr>
<tr>
<td>12 $^a$</td>
<td>23$^a$</td>
<td>30</td>
</tr>
<tr>
<td>20</td>
<td>20</td>
<td>18$^b$</td>
</tr>
</tbody>
</table>

$^a$Nine instead of ten individuals were accidentally included in this sample.

$^b$Eleven instead of ten individuals comprised this test group.
isolated individuals. In this experiment, individuals and groups were randomly placed in open petri dishes on a rectangular sand plot similar to that in the previous experiment. Twelve groups of 100 individuals, 12 groups of 50 individuals, and 150 isolated individuals were utilized in this experiment. Individuals were of all sizes. As in the previous experiment, individuals and groups were removed for testing according to random draw. The experiment began at the time of mean low tide, one hour after the initial collection of the hermit crabs. The temperature during the experiment was 26.0 ± 4.0°C. Twenty-five isolated individuals, three groups of 50 individuals, and three groups of 100 individuals were each tested for survivorship at 5, 10, and 15 hours after the beginning of the experiment. The remaining 56 isolated individuals, three groups of 50 individuals, and three groups of 100 individuals were tested at 21 hours.

The results appear in Table 16. A chi-square evaluation of the raw data indicates highly significant differences in the survival of isolated individuals and clustered individuals for each time period ($\chi^2 = 49.28, p < .01, df = 8$). The trend of enhanced survival of clustered individuals versus isolated individuals is quite consistent to 15 hours. At 21 hours, survival of isolated individuals exceeded survival in groups of 50, but not in groups of 100. However, at this time, survivorship in all groups was minimal.

These data thus support the hypothesis of Reese (1969) that clustering may enhance individual survival under conditions of desiccation. Even if extreme or prolonged desiccation is quite rare, the ameliorating effect of clustering in large groups may increase the
Table 16. Resistance of *Clibanarius digueti* in Large Clusters to Desiccation.—For each exposure time and each cluster size, the percentage survivorship is presented. Three replicates each are averaged to give the mean survivorship of clusters of 50 and 100 individuals. Twenty-five isolated individuals were also sampled at each time interval, until 21 hours when 56 isolated individuals were tested. Prior to this experiment, the hermit crabs were exposed for 10 hours during low tide. $\chi^2 = 49.28$ (mean survival values for raw data), $p < .01$, and df = 8.

<table>
<thead>
<tr>
<th>Exposure Time (hr)</th>
<th>Group Size</th>
<th>Survivorship (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>50</td>
</tr>
<tr>
<td>5</td>
<td>60</td>
<td>64</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>82</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>79</td>
</tr>
<tr>
<td></td>
<td>$\bar{x}$ = 60</td>
<td>75</td>
</tr>
<tr>
<td>10</td>
<td>28</td>
<td>43</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>53</td>
</tr>
<tr>
<td></td>
<td>$\bar{x}$ = 28</td>
<td>44</td>
</tr>
<tr>
<td>15</td>
<td>16</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>$\bar{x}$ = 16</td>
<td>20</td>
</tr>
<tr>
<td>21</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>$\bar{x}$ = 5</td>
<td>2</td>
</tr>
</tbody>
</table>
overall fitness of *C. digueti*. Certainly the desiccation hypothesis is attractive in the light of the mixed-species composition of clusters, since clustering is likely to benefit all species in proportion to the absolute cluster size. However, it is difficult to account for the development of regular, year-round clustering based solely on the desiccation hypothesis. If resistance to desiccation is the primary function of clustering, why is clustering not restricted to warm, clear days, as in the cases of *C. africanus* and *C. cooki* (Schmitt, 1926)? Why do some aggregations occur under boulders and in damp situations while others appear exposed on boulder surfaces? One possible explanation to the latter question is that exposure at low tide is often necessitated following storms, when the under-boulder habitat is silted-in. Since storms are unpredictable in nature, regular clustering may enable the ready assembly of hermit crabs in exposed sites adjacent to former sites of clustering. Exposed clusters often appear to be numerous following storms, supporting this explanation.

**Discussion and Conclusions**

The clustering of *Clibanarius digueti* is manifested both during the day and at night on a regular tidal basis. Cluster sites appear to be constant in location and individuals within a cluster tend to exhibit size specificity. These characteristics of clusters pose a number of questions when the adaptive significance of clustering is considered. One might ask, is aggregation attributable to regularly recurring factor(s) or is the regularity an adaptation to the unpredictability of certain features of the environment? Does clustering occur in response
to a single selective pressure or are there multiple advantages to the behavior?

Perhaps the most fruitful approach to these topics is to examine the geographical trend of clustering exhibited by *C. digueti*. In comparison to more southern Gulf of California locations, the degree of clustering at Puerto Peñasco seems to be maximum. During each low tide, hermit crabs form larger, denser clusters than in other Gulf locations. The tidal amplitude at Puerto Peñasco is also greater than to the south -- over 7.5 m during spring tides (Thomson, 1974).

As a result of the tides, the hermit crabs at Puerto Peñasco are periodically exposed to the arid climate of the surrounding Gran Desierto, characterized by thermal extremes. In the summer, the mean monthly sea temperatures are comparable to those of Panama (27-29°C) (Thomson and Lehner, 1976), and daily air temperature extremes have been recorded as high as 41.7°C (Thomson and Lehner, 1976). Very cold conditions may be encountered in the winter at Puerto Peñasco; mean monthly sea temperatures approach those of San Francisco, California (14°C). Thomson and Lehner (1976) report one cold spell in December and January lasting 14 days when the minimum air temperatures that ranged from 6 to -8.3°C cooled the nearshore waters and caused massive fish mortalities.

Throughout the year, *C. digueti* is exposed to desiccation as well. Due to the irregular, semidiurnal nature of the tides, the exposure time is highly variable. For example, the exposure time at +1.7 m (+5.6 ft), the approximate upper limit of *C. digueti* in the intertidal zone, may range from 4 hrs to 10 hrs at Playa Estación (Eger,
Thus, one might predict that the combined effects of high heat and desiccation during lengthy exposures may present formidable adaptive problems to this species during the summer months.

The results of experimental studies presented in this chapter indicate that the clustering of *C. digueti* may improve the resistance of individuals both to desiccation and to cold. Are the experimental conditions ever met in the intertidal zone at Puerto Peñasco? In the desiccation experiments, conducted at temperatures of 26-27°C, some deaths occurred 11 hours after exposure at the beginning of low tide. Since these temperatures were far below those recorded for the exposed intertidal zone, it is reasonable to assume that, on hotter days, some mortalities could occur and that clustering could minimize the loss of individuals. In the cold experiments, temperatures ranged from 2.5-4.2°C, and deaths were recorded 10 hours following exposure to cold. Both the exposure times and experimental temperatures are within the range encountered in the intertidal zone. Therefore, it is concluded that enhanced resistance to cold and to desiccation may both be important functions of clustering of *C. digueti* at Puerto Peñasco. The fact that clustering occurs both during the day and at night is consistent with the combined desiccation and cold hypotheses.

However, lethal conditions are only infrequently encountered in the intertidal zone. Why, then, is clustering manifested on a regular basis? At Black Mountain Estero, where currents in tide channels are quite strong, *C. digueti* must form clusters on available shell fragments prior to each ebb tide. At this location, regular clustering is clearly
adaptive to prevent loss of intertidal position, since isolated individuals may be swept away. In other locations, where hermit crabs remain slightly submerged at low tide, shell exchange opportunities within the confines of the cluster may also provide the basis of regular clustering. Sufficient selective pressure may, therefore, be exerted on the total gene pool of C. digueti to promote the regularity of clustering throughout the year.

On the other hand, it may be argued that the regularity of clustering at Puerto Peñasco is based on the needs of C. digueti to anticipate adverse, unpredictable conditions. Following storms in the Gulf, sites under boulders may become clogged with sand. At such times, C. digueti may be forced to occupy substrate surfaces which afford little protection from either desiccation or freezing conditions at low tide. The regular pattern of clustering may, therefore, prepare C. digueti to meet these unexpected conditions en masse.

Consistent with the idea that clustering serves multiple functions is the fact that clustering is manifested by C. digueti in a variety of habitats: in rocky intertidal areas, sandy esteros, and in mangrove swamps. Clustering occurs in a variety of geographical locations also, ranging from the northern Mexico mainland to southern Baja California. The original advantage of clustering may well have been resistance to desiccation, since C. digueti is evidently derived from the very similar Panamic species, Clibanarius albidigitus. High temperatures, together with large tidal amplitudes, are characteristic of many regions of the Panamic Province, where the clustering of C. albidigitus is
pronounced (Ball and Haig, 1974). Within the Gulf of California, the auxiliary functions for which *C. digueti* was "preadapted" may have maintained or increased the selective pressure for clustering. At Puerto Peñasco, the behavior of clustering is almost universal. The strong tendency to cluster may, therefore, be related to the multiplicity of advantages. Certainly, numerous mechanisms act to engage clustering at low tide, indicating, perhaps, strong selective pressures in action.

The complexity both of the mechanisms and of the adaptive advantages of clustering of *C. digueti* lead to the perspective that the behavior of crustaceans may be anything but simple. Certainly only a small portion of crustacean behavior is revealed in the present study. When the paradoxical behavior of other species of crustaceans is more fully unraveled, it may well be demonstrated that this arthropod class rivals the insects in behavioral complexity.
APPENDIX

HERMIT CRAB VERSUS SHELL SIZE

The best regression formulas for hermit crab weight from shell size at Puerto Peñasco are given for each shell species. For formulas involving exponents, the original best regression formula was of the form \( \log wt = a + bx \) or \( a + bx + cy \). Therefore, \( wt = 10^{a+bx} \) or \( 10^{a+bx+cy} \).

L is the shell length and W is the shell width. Volume (Vol) is for a geometric cone.
<table>
<thead>
<tr>
<th>Species</th>
<th>Range of Weight (mg)</th>
<th>Formula</th>
<th>N</th>
<th>$r^2$</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthina angelica</td>
<td>4-696</td>
<td>$10^{(.53+.08L)}$</td>
<td>41</td>
<td>.91</td>
<td>.01</td>
</tr>
<tr>
<td>Anachis sp.</td>
<td>9-55</td>
<td>$10^{(.28+.03L+.12W)}$</td>
<td>21</td>
<td>.62</td>
<td>.01</td>
</tr>
<tr>
<td>Cerithidea mazatlanica</td>
<td>52-146</td>
<td>$10^{(1.33-.03L+.13W)}$</td>
<td>10</td>
<td>.77</td>
<td>.01</td>
</tr>
<tr>
<td>Cerithium maculosum</td>
<td>19-687</td>
<td>$10^{(1.01+.02L+.07W)}$</td>
<td>18</td>
<td>.90</td>
<td>.01</td>
</tr>
<tr>
<td>C. stercusmuscarum</td>
<td>3-190</td>
<td>$10^{(-.21+.03L+.19W)}$</td>
<td>18</td>
<td>.96</td>
<td>.01</td>
</tr>
<tr>
<td>Columbella fuscata adults</td>
<td>45-152</td>
<td>$10^{(-.96+.56+17.06W)}$</td>
<td>29</td>
<td>.10</td>
<td>.09</td>
</tr>
<tr>
<td>juvemales</td>
<td>13-174</td>
<td>$10^{(.15+.09L+.04W)}$</td>
<td>16</td>
<td>.83</td>
<td>.01</td>
</tr>
<tr>
<td>Crassispira pluto</td>
<td>29-72</td>
<td>$10^{(.48+.08L)}$</td>
<td>5</td>
<td>.92</td>
<td>.01</td>
</tr>
<tr>
<td>Liocerithium judithae</td>
<td>2-120</td>
<td>$10^{(-52.11+6.88L)}$</td>
<td>69</td>
<td>.83</td>
<td>.01</td>
</tr>
<tr>
<td>Mitrella guttata</td>
<td>3-18</td>
<td>$2.77+.05 Vol$</td>
<td>10</td>
<td>.61</td>
<td>.01</td>
</tr>
<tr>
<td>Morula ferruginosa</td>
<td>3-94</td>
<td>$-37.43+7.05L-2.72W$</td>
<td>34</td>
<td>.80</td>
<td>.01</td>
</tr>
<tr>
<td>Nassarius angulicosus</td>
<td>16-79</td>
<td>$10^{(.01+.02L+.19W)}$</td>
<td>16</td>
<td>.55</td>
<td>.01</td>
</tr>
<tr>
<td>Nerita finiculata</td>
<td>15-174</td>
<td>$10^{(.58+.10W)}$</td>
<td>10</td>
<td>.90</td>
<td>.01</td>
</tr>
<tr>
<td>Olivella dama</td>
<td>25-191</td>
<td>$17.35+.04 Vol$</td>
<td>13</td>
<td>.91</td>
<td>.01</td>
</tr>
<tr>
<td>Pilsbyspira nympha</td>
<td>55-84</td>
<td>$-12.32+4.32L$</td>
<td>10</td>
<td>.41</td>
<td>.05</td>
</tr>
<tr>
<td>Polinices sp.</td>
<td>59-669</td>
<td>$26.36+.03 Vol$</td>
<td>4</td>
<td>.98</td>
<td>.05</td>
</tr>
<tr>
<td>Tegula corteziana</td>
<td>4-391</td>
<td>$-8.77+.06 Vol$</td>
<td>42</td>
<td>.90</td>
<td>.01</td>
</tr>
<tr>
<td>T. mariana</td>
<td>23-147</td>
<td>$.33+.14W$</td>
<td>7</td>
<td>.85</td>
<td>.01</td>
</tr>
<tr>
<td>Turritella leucostoma(?)</td>
<td>42-938</td>
<td>$10^{(.75+.15W)}$</td>
<td>28</td>
<td>.89</td>
<td>.01</td>
</tr>
<tr>
<td>Turbo fluctuosus</td>
<td>4-1560</td>
<td>$10^{(1.00+.08W)}$</td>
<td>61</td>
<td>.81</td>
<td>.01</td>
</tr>
<tr>
<td>Unidentified spp.a</td>
<td>-</td>
<td>$10^{(.66+.06L+.03W)}$</td>
<td>402</td>
<td>.73</td>
<td>.01</td>
</tr>
</tbody>
</table>

*a* This sample consisted of all known shell species data except adult *Columbella fuscata* and *Turritella leucostoma*.
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