

Biogeography of *Hemisquilla ensigera californiensis* (Crustacea: Stomatopoda) with Emphasis on Southern California Bight Populations

Lawrence V. Basch¹ and John M. Engle²

¹Biology Board of Study & Institute of Marine Sciences,
University of California, Santa Cruz, CA 95064

²Department of Biological Sciences, University of California, Santa Barbara, CA 93106

Abstract. – The mantis shrimp *Hemisquilla ensigera californiensis* (Crustacea: Stomatopoda) ranges from south of Point Conception in southern California to the Golfo de Chiriqui, Panama. *Hemisquilla* populations occur off four of the eight California Islands: Santa Cruz, Anacapa, Santa Catalina and San Clemente, as well as numerous islands off Baja California and mainland Mexico. Insular and continental populations occur in habitats usually characterized by: 1) generally stable, low physical disturbance regimes; 2) silty sand sediments with a high organic content; 3) abundant food resources; 4) variable predation pressure and 5) fluctuating light regimes. Mechanisms that may influence the observed patterns of distribution and abundance include: 1) ocean currents favorable for dispersal of planktonic larval stages; 2) habitat suitable for successful recruitment; 3) sufficient food resources and 4) low levels of predation pressure and physical disturbance.

Introduction

The crustacean order Stomatopoda represents a primitive group (Holthuis & Manning 1969; Schram 1977, 1979), whose center of radiation occurs in tropical latitudes. The phylogenetically separate position of stomatopods is reflected by Calman's (1904) establishment of the superorder Hoplocarida, which is postulated to have a distinct origin separate from the eumalacostracan Crustacea (Schram 1969a,b, 1986). More than 350 species in four superfamilies are known, most dwelling in warm tropical seas throughout the world. Many genera appear to be relicts, broadly

distributed but containing few species, each with relatively restricted ranges (Manning 1980). Four species occur in the warm temperate waters off southern California. They are *Pseudosquilla marmorata* (Lockington 1877), *Nannosquilla anomala* Manning 1967, *Schmittius politus* (Bigelow 1891) and *Hemisquilla ensigera californiensis* Stephenson 1967. This study focuses on *H. e. californiensis*, the largest and most common of the California mantis shrimps, which is distinctive among the Stomatopoda in its distribution, size, visual characteristics, and aspects of ecology and behavior (Basch & Engle 1989, in prep.).

Hemisquilla ensigera californiensis is a large (to 30 cm TL), compact, dorso-ventrally compressed mantis shrimp with a heavily armored telson, bright coloration and well developed vision (pers. obs.; Schiff *et al.* 1986 and included references). These stomatopods possess a very powerful strike mechanism in the second maxilliped or raptorial claw, the most rapid animal movement known (Burrows 1969; Burrows & Hoyle 1972).

In this paper we discuss the relictual (*sensu* Ekman 1953) distribution of this species, focus particular attention on populations occurring in the Southern California Bight, and address aspects of population biology relevant to observed local distribution and utilization of stable sand habitats.

Methods

Biogeographic data on *Hemisquilla ensigera californiensis* were compiled from direct observations and collections from populations off the California Islands and southern California mainland, and from personal communications (including solicited surveys),

museum collection records, and review of the literature. Whenever possible, data were collected on: locality; latitude and longitude; depth; habitat; animal abundance and size; date; time and method of sighting or collection and the source of information.

Population studies were conducted at several sites off Santa Catalina Island (33° 28' N, 118° 20' W; Fig. 2). The Willow Cove population on the northern leeward shore of Santa Catalina Island was studied most intensively. Population spatial and temporal distribution and abundance patterns were elucidated by repeated diving surveys performed at various times throughout several 24 hr periods. A 50 m x 60 m sampling grid (longest axis parallel to shore) was established from 6-18 m depth. Five transects were surveyed on numerous dates and times in order to obtain data on all visible burrows. All burrows sighted within and near the grid were marked and mapped. Data collected included: time of observation; burrow depth; diameter; whether the burrow was open or closed by a sand plug constructed by the resident; whether or not the animal was observed; maturity and sex (juvenile, subadult, female or male).

Results

Biogeography: Zoogeographic distribution in the Stomatopoda is just now becoming clear as taxonomic revisions approach stability. The vast majority of genera and species are shallow, tropical warm water forms (Schram 1986). Of the many extant genera of stomatopods only two, including *Hemisquilla*, may be considered strictly warm-temperate in distribution (Manning 1977). *Hemisquilla* (Hansen) includes two species (Manning 1969; Stephenson 1967), *H. braziliensis* (Moreira) from the western Atlantic and *H. ensigera* (Owen), with Californian, Chilean, and Australian subspecies (Stephenson 1967). The species *H. ensigera* appears to support the principle of taxonomic bipolarity (Ekman 1953) by formation of relictual populations and subsequent

morphological divergence. Details of global distribution and morphological variation in the genus *Hemisquilla* may be found in Manning (1977) and Stephenson (1967), respectively.

The geographic distribution of *Hemisquilla ensigera californiensis* (Figs. 1-2) ranges from Santa Barbara County, south of Point Conception (35° N latitude) in the Southern California Bight, south to the Golfo de Chiriqui, Panama (5° N latitude) (present study; Hendrickx & Salgado-Barragan 1987; Manning 1977). The southern range limit is based on two specimens, a single juvenile from Jicarita Island (Stephenson 1967) and an adult male from the Golfo de Chiriqui (Manning 1971). The next northern-most records are from Islas Clarion, Socorro, and Tres Marias off the Mexican mainland, south of Cabo Falso, Baja California Sur (18° N latitude, Fig. 1). Data obtained to date indicate that the Californian *Hemisquilla* occur in mainland and insular populations in the Gulf of California at least as far north as Isla San Nicolas, north of Guaymas, Sonora, Mexico (28° N latitude, Fig. 1) (present study; Hendrickx & Salgado-Barragan 1989).

Hemisquilla is known from numerous peninsular and insular sites along the Pacific coast of Baja California (Fig. 1). Populations appear to be common in or near embayments, lagoons and off many south-facing points, coasts, and island shores as well as other areas north to, and including, the Islas del Coronados near the U.S.-Mexico border.

Observations from many points along the southern California coast range from San Diego Bay and Point Loma in the south to the area just south of Point Conception (Fig. 2). California mainland populations occur in the same geographic and habitat types as indicated by Mexican records (see above). Areas of high abundance include San Diego and Mission Bays, the Orange County coast and numerous harbor, bay and sandflat habitats from southern Los Angeles County (Seal Beach) north, at least to Goleta, Santa Barbara County (Fig. 2).

Hemisquilla recently was recorded from sand

flats off the southeastern side of East Anacapa Island in depths of 17-30 m, at two sites off Santa Cruz Island between 15-17 m and three locations off San Clemente Island (Fig. 2) in depths of 13-17 m. Santa Catalina Island (Fig. 2) was surveyed most extensively. Populations were observed in depths between 5-33 m at 19 stations (Fig. 2), where mantis shrimp were common to moderately abundant.

Habitat Characteristics: Based on personal sightings and distributional records, it is inferred that *Hemisquilla* populations may occur whenever suitable oceanographic conditions and habitats coincide. These environments include bays, lagoons and off protected low energy coastlines. Most of these areas have the following habitat characteristics in common. The substrate consists of flat or gently sloping (0° to 30°) stable sand plains ranging from a minimum of 3 m depth inshore to ≥ 33 m depth seaward. A shallow zone with few or no resident stomatopods usually is present from 5-8 m depth. The adjacent inshore area consists of either physically disturbed sediments (delineated by wave ripple marks), small boulders, surf grass or rock reef. Sediments are silty sands with a poor to moderately sorted particle size distribution and a high organic content (Basch 1985). In some areas they are stabilized by matrices of infaunal invertebrate tubes, and/or surface diatom or algal mats.

These areas usually have a low to moderate physical disturbance regime, exhibiting protection from most heavy swells. Predominant water movements result from mixed-diurnal tides and fairly predictable tidal and other long-shore currents. Exceptions to this pattern include strong surge induced by powerful winter storm activity that causes shifting sediments, scouring and/or destructive water movement. In more protected areas the bathymetric peak in abundance occurs in relatively shallow water, 10-16 m depth. In areas that regularly or intermittently experience high energy conditions, highest population densities may occur at greater depths (approximately 16-30 m).

The typical bathymetric range extends from 3 m in protected embayments (e.g. San Diego Bay sand flats) to >30 m in many areas. Observed peak burrow densities at California Islands sites occur between 10-16 m depth. Mainland sightings and collections are from 10-70 m; animals appear to be locally common between 50 and 70 m, and peak abundances appear in the 15-25 m range. Extreme depth records range from an individual observed foraging nocturnally in the rocky intertidal (<1 m) at high tide (M. Michael pers. comm.), to 1,800 m for a trawl caught specimen in the Guaymas basin east of Isla Tortuga, in the Gulf of California.

The silty sand substrate most commonly inhabited by *Hemisquilla* is found along extended stretches of coast, throughout coves and bays, or in patches (10's-100's m in diameter) within other, generally coarser sediment types. For example, *Hemisquilla* is widely distributed in Santa Monica Bay from north of Malibu to the Palos Verdes Peninsula (Fig. 2). The local distribution pattern here appears to be primarily influenced by the presence of patches of suitable silty sands within areas of predominantly coarser sands. The overall distribution of the patches may change in some shallow areas as a result of seasonal onshore-offshore sand movements, sediment resuspension by storm waves and other transport mechanisms (J. Cross pers. comm.).

Population Biology: Recruitment to the stable sand community has been documented since 1983. Postlarvae are capable of rapid burrowing and apparently build and occupy burrows almost immediately upon settlement, since very small postlarvae have been collected from burrows with entrance diameters of only 3-4 mm (pers. obs.). At present we have limited data on *Hemisquilla* population parameters. Based on regression analysis of burrow diameter vs. carapace width, population size distribution ranges from about 3-65 mm (carapace width) (Basch & Engle in prep.). As in other stomatopods (Reaka 1979) the observed size distribution of *Hemisquilla* is

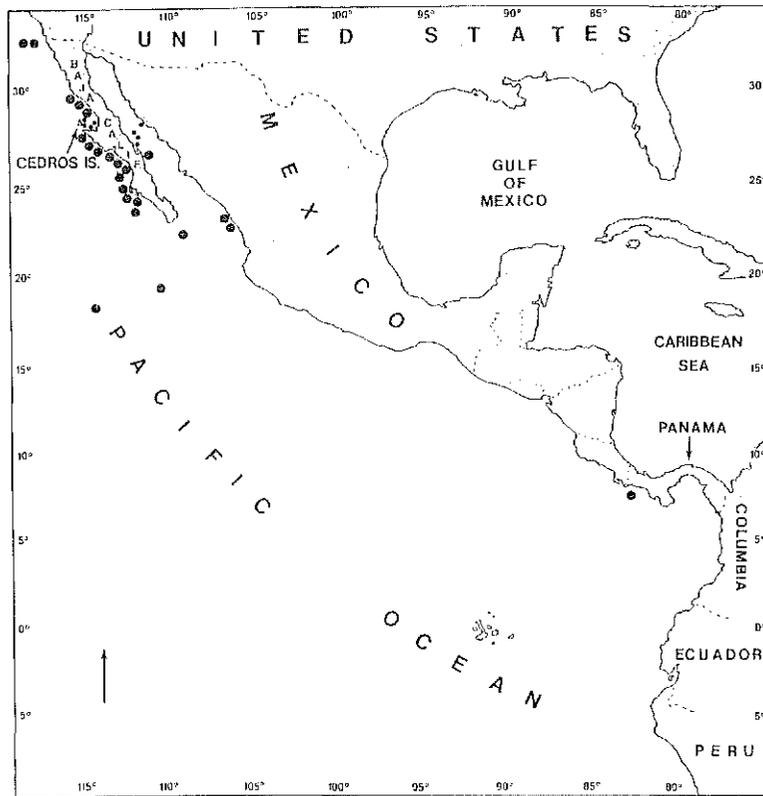


Figure 1. Distribution of *Hemisquilla ensigera californiensis* from Mexico to Panama.

strongly skewed with a predominance of adults over juveniles. The largest animals sampled are almost exclusively males. A realistic estimate of population sex ratio is not possible at present due to seasonal changes in observed abundance (Basch & Engle in prep.) and the inability to determine the sex of some individuals in the field. Of a total of 63 adults collected at Willow Cove, Santa Catalina Island in 1985 and 1986, the sex ratio (female:male) was: 12:15 (November 1985); 0:17 (May 1986); 15:4 (November 1986). The absence of females in May 1986 along with relatively low apparent population density strongly suggests that females remain in plugged burrows for extended periods in the spring, presumably while copulating or brooding eggs.

In addition to use of the burrow for mating and reproductive purposes, the burrow also undoubtedly functions as shelter from extremes of the external physical environment and predators. Protection from extreme physical disturbance provided by the burrow is suggested by the absence of open burrows in shallow (≤ 12 m) depths during storm-induced strong surge (pers. obs.). Several potential predators inhabit stable sand communities. The predator guild changes throughout the latitudinal range of *Hemisquilla*, with some large piscine predators occurring more frequently in waters south of California. Several large black sea bass and grouper off Baja California are known to have ingested up to 5-6 adult *Hemisquilla* (each ≥ 20 cm TL) per predator (E. Sigler pers. comm.). Despite

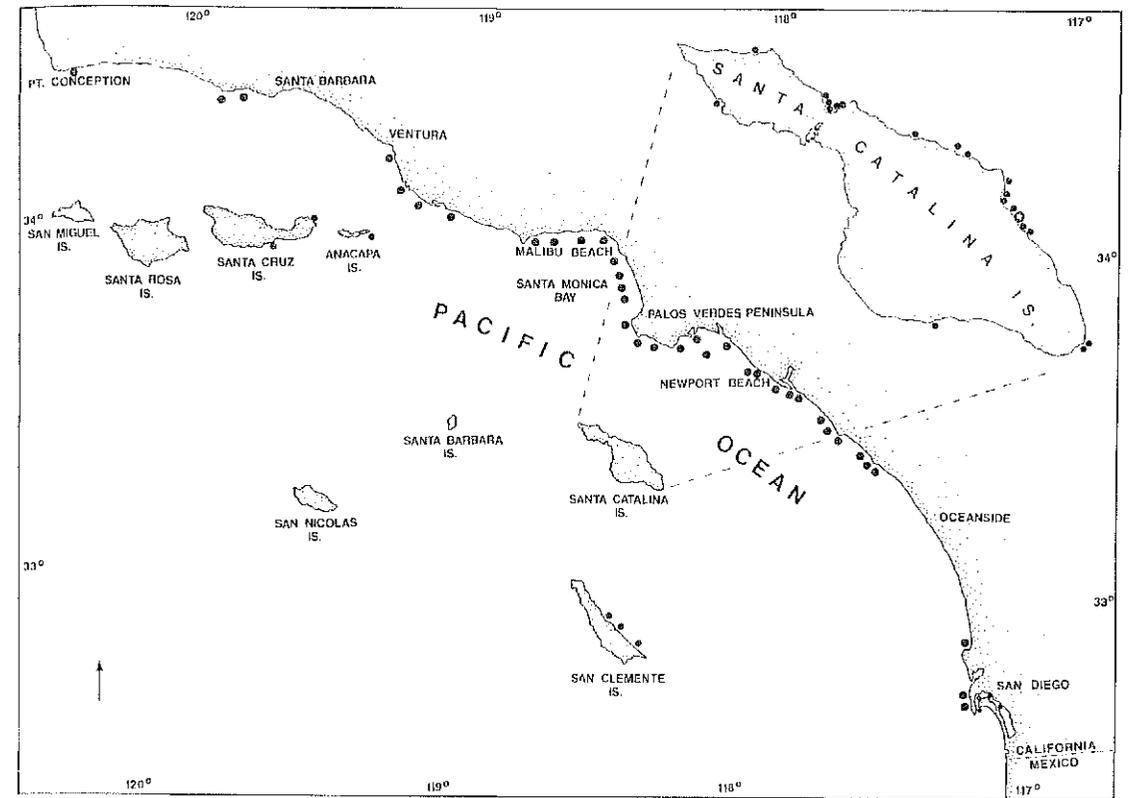


Figure 2. Distribution of mainland and island populations of *Hemisquilla ensigera californiensis* in the Southern California Bight. Blowup shows locations of survey sites on Santa Catalina Island.

extensive work on feeding ecology, widespread predation on stomatopods by fishes and other potential predators has not been documented in California (Hobson & Chess 1976, 1986; pers. obs.). At present only one instance of predation on an adult *Hemisquilla* has been noted in California (P. Haaker pers. comm.)

Hemisquilla forage from burrows to a variety of habitats including subtidal sand flats and sand channels, and infrequently onto rocky substrata including kelp forests and the intertidal zone. They may range a great distance (to 60 m) from burrows and prey on a wide variety of invertebrates (Basch & Engle 1989). Animals frequently have been observed and captured in soft bottom communities with high infaunal biomass and in locations where food abundance is artificially enhanced (e.g., in

the vicinity of ocean sewage outfalls, below bait barges, off public fishing piers and other frequently fished areas).

Discussion

With a perspective on historical and present distribution and aspects of the biology of *Hemisquilla* and other stomatopods, we may infer mechanisms contributing to biogeographic distribution and evolutionary and ecological patterns relating to the dispersal, colonization and persistence of tropically derived animals such as *Hemisquilla* in cold, high latitude environments.

Historical Events: The absence of *Hemisquilla ensigera* in equatorial latitudes in the eastern Pacific (Manning 1977) suggests a

case of taxonomic bipolarity (Ekman 1953) where, in this instance, the same species may have initially been represented in high latitudes by two relict populations, and later by two subspecies, *H. e. californiensis* in the northern hemisphere and *H. e. ensigera* in the southern, with a gap in distribution between the two.

Present Biogeographic Distribution: As indicated by Fig. 1-2, *Hemisquilla ensigera californiensis* exhibits a broad distribution, spanning 30° latitude. Possible limitations on knowledge of the detailed distribution patterns south of the Southern California Bight may be a reflection of a relatively coarse-grained picture (*i.e.*, comparatively few sightings in a large area made over many years). In contrast, the image in southern California is fine-grained (*i.e.*, frequent, accurate sightings with good spatial coverage of the region over the past fifty years). As a result, the biogeographical pattern off southern California may be more indicative of the actual distribution of *Hemisquilla*.

To understand the modern biogeographic distribution of *Hemisquilla*, recruitment and the biological and physical factors influencing it must be considered on several scales. Large scale factors (*i.e.*, interacting biotic and abiotic mechanisms) affect the dispersal of larvae and the overall pattern of larval availability over the distributional range. Small scale factors affect larval settlement. Lastly, factors such as competition, predation and physical conditions associated with early benthic life mediate post settlement survival of postlarvae and juveniles. These processes may all interact on a variety of levels to produce a complex pattern of recruitment and resultant adult distribution (Cowen 1985).

***Hemisquilla* Biology:** At present there is little information on life history in *Hemisquilla*, however, based on the work of Reaka and others (see Reaka 1986) on the relationships between larval dispersal capability, postlarval and adult size, habitat and latitudinal distribution, we can infer several aspects of *Hemisquilla* life history from patterns in other stomatopod species. Stomatopods typically

have several larval instars including few to many (*e.g.*, 4-9) pelagic stages (Williams *et al.* 1985). Hence, their dispersal is closely tied to currents. Since *Hemisquilla* postlarvae and adults both fall in the large size categories established by Reaka (1986), we infer that this species possesses several pelagic life history stages which spend long periods (up to several months) in the plankton. It follows that *Hemisquilla* probably has a high dispersal potential, and this may explain its broad latitudinal range. A long planktonic residence time likely is associated with more larval mortality via predation and starvation (Vance 1973) and less predictable recruitment to any given site (Thorson 1946). High juvenile mortality suggests great longevity and iteroparity in adult stomatopods (Reaka 1979, 1986).

Large Scale Mechanisms: The principal large scale mechanisms underlying observed recruitment patterns and population distributions are currents. Seasonal and aperiodic atmospheric and oceanographic conditions, including near shore eddies, permit northerly current flow from Panama to central Baja California (Wyllie 1966; Norton *et al.* 1985). Below 31° N nearshore current flow is predominantly southward throughout much of the year. However, by late summer to early fall, flow in this region is complicated by eddy formation which may produce northward nearshore currents (Wyllie 1966). In the Southern California Bight, the southward flow of the California Current diminishes somewhat within 150 km of shore in August through October. In late November through January it reverses to become a weak northerly flow (Hickey 1979). The Southern California Eddy, similar to the California Current shows considerable, within-year variation (Reid 1965). Its axis corresponds roughly with the Santa Rosa-Cortez ridge (Sverdrup & Fleming 1941). Highest northward flow occurs shoreward of this axis in the southern part of the eddy. Warmer water is moved progressively northward from July through October by the inshore flow of the eddy. By July this water

mass typically extends to San Clemente and Santa Catalina Islands and by September or October it reaches north to Anacapa and Santa Cruz Islands. This summary of water movement patterns illustrates the mechanism for potential dispersal of larvae and the adult distributions of *Hemisquilla* as far north as the Southern California Bight. It also may account for the absence of *Hemisquilla* at San Nicolas and the other northern Channel Islands, despite the availability of suitable habitat in deeper water, because these islands are seaward of the Santa Rosa-Cortez Ridge and, hence, are not influenced by the north flowing shoreward portion of the Southern California Eddy. This flow would be expected to carry larvae from mainland populations to those California Islands with known *Hemisquilla* populations, and few, if any, larvae would be expected to reach other islands. In addition, these flow patterns indicate that the Pacific coast of Baja California may receive larvae both from southern California populations and from populations south of 23° N.

The area just south of Point Conception is the northern limit of *Hemisquilla* and many other southern species of marine invertebrates. Except for the two small Santa Cruz Island populations, all known populations of *Hemisquilla* occur south of the 13° C surface isotherm during most of the year. That populations occur near this environmental/latitudinal extreme may be explained by year to year variation in oceanographic conditions (Jones 1971). In exceptional years warm southern waters extend north of the latitude of Santa Cruz Island. These anomalous events, characterized by northward transport of warm water throughout the Southern California Bight, are frequently associated with El Niño events. These dramatic warm water incursions last occurred in 1972, 1977-1978, and 1982-1983 (Chelton 1981; Norton *et al.* 1985) and dominated current patterns in the Southern California Bight. According to Norton & co-authors (1985) evidence points to weakening of the south flowing California Current, onshore

transport of offshore water, increased downwelling and countercurrent intensification as the primary mechanisms which bring warming to southern California waters. Atmospheric and oceanic forcing of warming processes occurred together during the 1982-1983 California El Niño (Norton *et al.* 1985).

Several lines of evidence indicate a recent large recruitment event for this warm water radiated species. *Hemisquilla* was never observed to be common or in high abundance off the California Islands from 1973-1983 (pers. obs.; R. Given pers. comm.). Since the early 1970's increased mainland trawl catches of adult *Hemisquilla* have been recorded approximately two years after warm water events (R. Fay & S. Anderson pers. comms.). Observations of intense recruitment to several locations from 1983 to the present, as well as numerous observations and records of large increases in abundance of adult *Hemisquilla* throughout the region during the same period (unpublished data) indicate a strong influence of warm water events, particularly the 1982-1983 El Niño, and a continuing warm water influence on the distribution and abundance of *Hemisquilla*. During this period the persistence of *Hemisquilla* populations has been stable in place and time. Similar observations of anomalously high recruitment and numbers of adult crustaceans and fishes also have been noted by Cowen (1985).

Small Scale Mechanisms: Acting in combination, near shore physical transport mechanisms, larval behaviors and the local availability of suitable habitat types are the principal small scale factors influencing larval settlement. We have seen that most stomatopods, and probably *Hemisquilla* as well, have current dispersed larval phases. Nearshore current patterns implicated in larval transport can be influenced by within-year changes in wind direction, bottom topography and anomalous oceanographic events (Jones 1971; Norton *et al.* 1985). Shanks (1983) has demonstrated on a smaller scale, the association of surface slicks with shoreward

moving internal waves which are believed to transport larval invertebrates and ichthyoplankton to nearshore environments. Larval invertebrates, particularly crustaceans, exhibit several behavioral mechanisms that would permit transport in these slicks (Ennis 1975; Rice 1966; Thorson 1964). More specifically, Reaka (1986) and Dingle (1969) have shown both diel and ontogenetic changes in the behavior of stomatopod larvae which may allow them to utilize such small scale transport mechanisms. In addition to nearshore larval advection mechanisms, the ability of stomatopod larvae to undergo diel vertical migrations (Reaka 1986) suggests a fine tuning of larval settlement response. For example, if larvae are transported inshore to an unsuitable habitat, vertical migration may allow their exit on an outgoing tide or rip current followed by longshore transport and subsequent inshore advection to habitat suitable for settlement. Assuming that little or no post-settlement emigration occurs, the relative consistency of recruitment to different populations may have important consequences, over several generations, on population distributions and densities.

Post-Settlement Mechanisms: Once settlement has occurred the interplay of various ecological factors determines juvenile survivorship and ultimately the persistence of *Hemisquilla* populations. The local scale spacing between adjacent *Hemisquilla* burrows, while not yet subjected to rigorous scrutiny, may be a mechanism for minimizing intra-specific competition and possible cannibalism by resident adults on new recruits. The burrows are excavated by postlarvae almost immediately upon settlement and they confer a critical refuge, for this and all size classes, from potential predation by fishes (pers. obs.; Reaka 1985) as well as from physical environmental extremes (Dingle & Caldwell 1972; Basch & Engle in prep.).

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