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Food Supply, Feeding Habits, and Egg Production in Pacific Mole Crabs (*Hippa pacifica* Dana)[1]

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ABSTRACT: Well-studied hippid sand crabs (genus *Emerita*) on wave-washed beaches in the temperate zone obtain their food by filtering microorganisms from the water. Related mole crabs (genus *Hippa*) in the tropics and subtropics have raptorial feeding appendages, which permit these animals to grasp and feed upon fresh meat items. They apparently depend upon those organisms that move onto beaches as a result of wind-driven surface waters. In Hawaii, Portuguese men-of-war (*Physalia*) is the most obvious natural food supply, but tests with other types of bait indicated that shark or squid are equally effective in capturing animals. At Enewetak Atoll, where *Physalia* occurs only rarely, mole crabs thrive on mysids and perhaps other similar-sized zooplankton. There also existed a strong correlation between food availability and egg production, both in Hawaii and at Enewetak Atoll. In fact, an observed "seasonality" in egg production seemed to be a direct result of food availability rather than of changes in temperature or photoperiod.

SOME SPECIES of mole crabs occupy a very well-defined habitat, the wave wash zone of sandy beaches. Animals in any one area thus have a nearly linear distribution in space, which is often interrupted only by rocky headlands, river mouths, and islands. The slight discontinuities in distribution, however, do not necessarily lead to genetic differences in populations. The planktonic larvae can drift for months before settling out (Johnson 1940, Barnes and Wenner 1968). The net result in any one region is a set of discrete, perhaps genetically identical, populations that live in slightly different environmental circumstances. Four of the more well-studied species have a vast geographic range and show promise as material for a variety of ecological studies.

The common sand crab, *Emerita analoga* (Stimpson), a filter feeder, seasonally occurs in immense numbers along the west coasts of North and South America. Its counterpart, *E. talpoida*, occupies the same niche on the east coasts of those continents. The animals in these two species strain microscopic food from the water in the wave wash zone on open sandy beaches by means of their long filamentous second antennae (Weymouth and Richardson 1912). These sand crabs can also filter feed in still water by extending and waving their antennae.

At tropical and subtropical land-water interfaces in the Atlantic and Pacific, filter feeders are often replaced by year-round predator-scavengers—*Hippa cubensis* in the Caribbean and *H. pacifica* in the Hawaiian Islands and throughout the Pacific. Although these mole crabs live in the same physical niche as that occupied by *Emerita analoga* and *E. talpoida* (Bonnet 1946, Matthews 1955, Hanson 1969), a closer inspection reveals marked differences in structure in the two genera. As Matthews noted, Pacific mole crabs do not have long filamentous antennae and thus are not equipped for filter feeding. In addition, the distal margins of the first maxillipeds are lined with rows of conical teeth; the second maxillipeds have a single row of such teeth; and the third maxillipeds are raptorial,[3] with a hard and sharply pointed dactyl (Figure 1).

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[3] Although the third maxilliped has a "subchelate" appearance, the terminal segment does not fold onto the next proximal segment (Kaestner 1970: 14). Hence, the use of the term "raptorial" here.

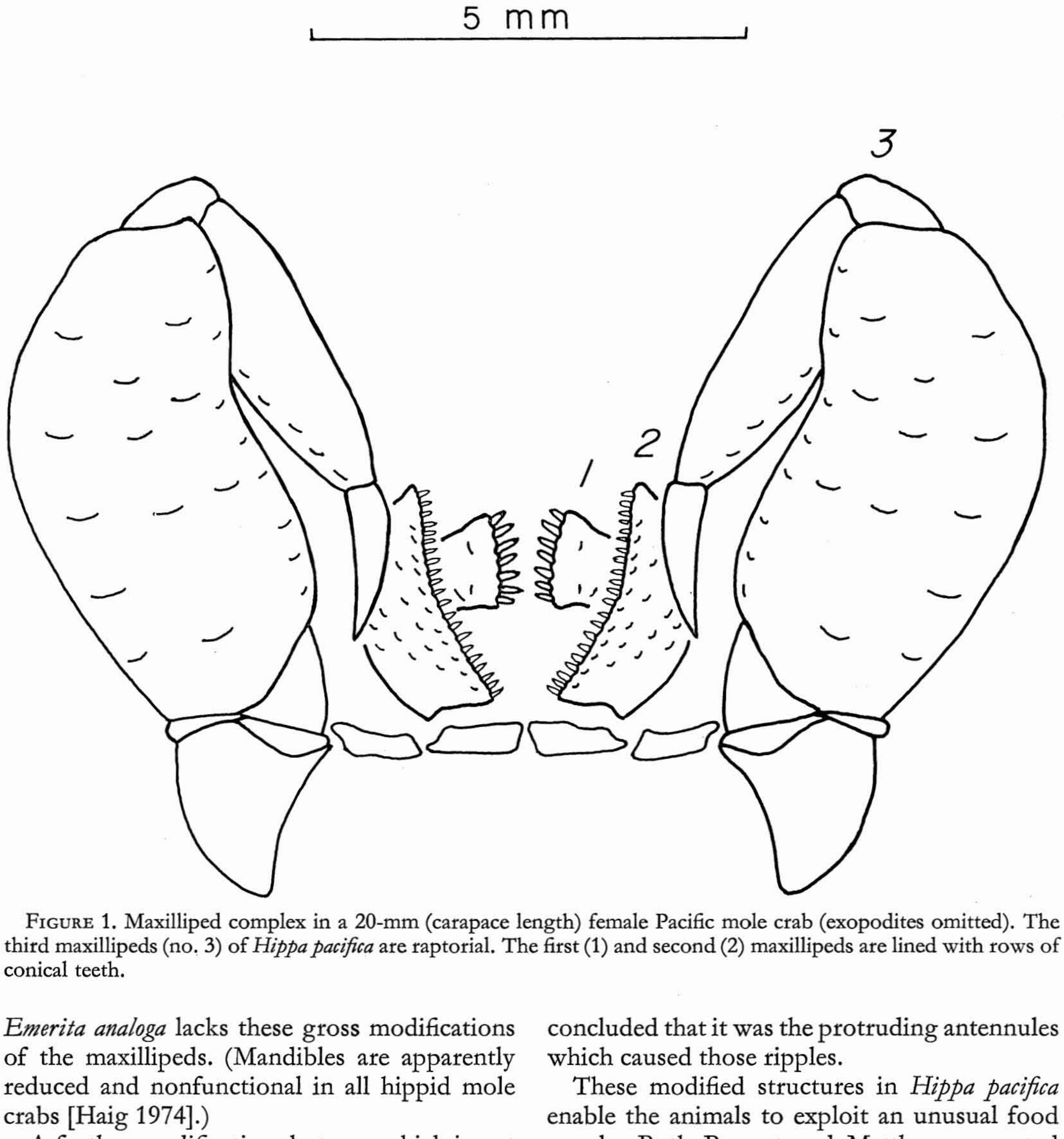

FIGURE 1. Maxilliped complex in a 20-mm (carapace length) female Pacific mole crab (exopodites omitted). The third maxillipeds (no. 3) of *Hippa pacifica* are raptorial. The first (1) and second (2) maxillipeds are lined with rows of conical teeth.

Emerita analoga lacks these gross modifications of the maxillipeds. (Mandibles are apparently reduced and nonfunctional in all hippid mole crabs [Haig 1974].)

A further modification, but one which is not obvious at first glance, is that the first pereopods in both *Hippa cubensis* and *H. pacifica* are considerably longer, relatively, than that same pair of legs in *Emerita analoga* or in *E. talpoida*. Pacific mole crabs bend the last segment of these nonchelate legs inward while grasping food, thereby also using them as raptorial appendages (see Wenner 1972: figure 1). At times the animals hold these legs (or a part of them) above the sand surface, an action which produces characteristic V-shaped ripples in the outgoing wave wash. Matthews apparently mistakenly concluded that it was the protruding antennules which caused those ripples.

These modified structures in *Hippa pacifica* enable the animals to exploit an unusual food supply. Both Bonnet and Matthews reported that *H. pacifica* feeds on Portuguese men-of-war (*Physalia utriculus* Escholtz) and found *Physalia* nematocysts in the digestive tracts. Matthews further carefully checked the digestive tract for microscopic food materials and found none. He initially concluded that the animals were "selective" feeders that might rise to some types of bait strewn on the beach.

Matthews then tested a variety of food materials on open beaches, even though Bonnet earlier had had no success when using pieces of fish and meat. Matthews found that the animals ignored most types of food proffered and would not take even *Velella* or shrimp if *Physalia* was in plentiful supply. However, the animals would rise to these other items if *Physalia* had been absent from the beach for several days. Matthews recognized that drift food appeared scarce during calm seas, but could come up with no solution as to what *Hippa* might feed upon when men-of-war were scarce.

Several implications arise from the fact that these animals live only in the wave wash zone and apparently feed only upon fresh food brought onto those beaches by wind. First of all, if the animals are almost entirely dependent on *Physalia*, as Matthews and Bonnet suggested, then animals on a windward beach should fare better than animals on a leeward beach. Secondly, animals on any given beach should fare better at one time of the year than at another, coincident with differential *Physalia* influxes. Finally, since the animals live in an essentially one-dimensional habitat (the water's edge), they can be readily caught (with bait). Sampling with bait could provide the basis for a relatively accurate and comparative measure of the relationships among three important dependent variables: population structure, food supply, and egg production (see Wenner, Fusaro, and Oaten 1974).

With all of the above points in mind, my colleagues and I have embarked on a series of studies to ascertain the impact of various environmental factors (primarily food supply) on the biology of Pacific mole crabs. The first study, reported here, concentrated on an attempt to extend Matthews' study of food and feeding habits and to test for any seasonal component in egg production in *Hippa pacifica*. Subsequently, visits to Enewetak Atoll (where "season" is less pronounced and where *Physalia* does not serve as the primary food supply for mole crabs) provided a further test of the relationship between food supply and egg production in *H. pacifica*.

POTENTIAL FOODS: SUBJECTIVE FIELD ASSESSMENT

In September 1970 I found several mole crabs consuming a young goatfish (*Mulloidichthys* sp.), despite an influx of large *Physalia* on the same beach. The feeding behavior was markedly similar to that described for *Hippa cubensis* by Hanson (1969), who found that the principal food for his animals appeared to be flying fish washed onto Carribean island beaches.

A question immediately arose. Does *Hippa pacifica* find food materials other than *Physalia* acceptable (materials other than those tested by Matthews)? As Matthews indicated, *Physalia* is not a dependable source of food in Hawaii. Any success with other materials would indicate what might serve as food during much of the year when *Physalia* is in short supply.

Prior to full-scale tests, and while men-of-war were still plentiful on the beaches, I tested a variety of food materials in the subjective manner employed by Matthews. As he indicated, one can test for the presence of *Hippa pacifica* by dropping crushed bait onto the sand during the last phase of a receding wave; the thin film of surface water then carries the meat juices downslope. Mole crabs emerge from the sand and scurry about backward in their search for that bait. (Matthews' tests indicated that the stimulus was chemical and not visual as suggested earlier by Bonnet [1946].) The relative numbers of animals that rise to the bait provide some indication of the efficacy of any food materials, though different beaches may differ in the absolute number of animals that will react. I used only those materials normally found on the beach itself, thereby assuring that they were potential food materials. (Matthews' total lack of success with algae led me to ignore that possibility.)

With repeated tossing of the various types of bait onto the beach, it soon became evident that some baits were more effective than others. Some were about as effective as men-of-war, while others evoked no response whatever. Most of the materials fell somewhere in between. *Physalia*, shark, and crushed sea urchin oftentimes resulted in from 5 to 15 animals rising to the surface and scurrying about (depending on the particular beach and on the tide level). With goatfish and squid, somewhat fewer animals reacted; and those that did react seemed less persistent. A fish gill (*Tilapia* sp.) and some fish meat (*Decapterus* sp.) were markedly less effective as bait, but they were slightly better than shrimp meat and various crushed insects (honeybees, grasshoppers, and sphinx moth). Oddly enough, saliva worked about as effectively as any of this last group of substances. Ghost crabs (*Ocypoda* sp.), octopus, and puffer fish, though effective as bait only at times, proved more attractive than fillet of sole (from a market), *Tilapia* flesh, beef, calf liver, fowl, and a whole sea urchin.

BAIT EFFICIENCY TEST

The above subjective assessment provided some information about what foods might evoke a reaction among animals on the beach, but I felt that more objective field testing could provide data for a comparison of the number of animals which not only would react but which would grasp the available foods. For these field tests I used only those materials that evoked a relatively strong reaction when tossed onto the beach.

Methods

Two different types of bait were tested against one another at any one time: one first, then the second, and then the first again, on successive stretches of beach. This procedure permitted a comparison of the first and third yields for one bait against the number caught on the in-between test with the other bait. The successive placement of bait also indicated whether animals were nonuniformly distributed along the beach. (Unfortunately, the animals do not form obvious aggregations as does *Emerita analoga*.)

In setting the bait, I pierced three 1 cm^3 pieces of bait with no. 2 knitting needles, slid the bait to a location 5 cm from the needle top, and then forced these needles into the sand until the meat was flush with the sand surface. At the mean wave wash mark (wet line), the water covered the bait approximately one-half of the time. A 10-m distance separated the three baited stakes.

After 5 minutes I scooped up the sand around each needle and sieved it, thereby obtaining the animals that had come to the bait. Each needle was replaced in the sand 1 m distant from the first position and the process repeated once or twice (an equal number of times within each experimental comparison).

At the conclusion of this double or triple set with the first bait, I moved 10 m down the beach and did an equivalent test with the second type of bait. When this second batch of animals had all been collected, measured, and tallied, I moved 10 m farther down the beach and used the same type of bait as used during the first composite set, but with fresh pieces of meat.

The entire process (three composite sets with two types of bait) required more than an hour. This meant that only one such comparison could be made during high tide on any one day. (High tide yielded more animals than did low tide.) On some days and on some beaches relatively few animals came to bait. In these cases, time permitting, the same tests were run on other days until an adequate sample size was obtained.

The tests as run did not constitute preference tests in the usual sense, because very likely no one animal ever had a choice between two types of bait (at least that was the intent). The comparisons were more one of bait efficacy; that is, one can compare the total number of animals coming to one bait with the total number of different animals coming to the other type of bait on that same day in the same general location and under the same overall conditions.

Results

Figure 2 contains the results from all comparisons, each of which must be read across. In comparison no. 6 in that figure, squid, shark, and squid were offered in that order on successive stretches of beach. The result was a combined catch of 21 animals (20 percent of the total catch) on the first test with squid on the first stretch of beach, 61 animals (59 percent) on the second test when shark was used, and 22 animals (21 percent) when squid was again offered on the third test. The reciprocal comparison (shark, squid, and shark: comparison no. 3) yielded supportive results. In either sequence, shark bait attracted more animals than did squid.

As a check of the variability to be expected, shark was tested against itself (comparison no. 2) and goatfish against itself (comparison no. 11). The differences found were not statistically significant in a within-bait comparison.

The results as a whole supported the sub-

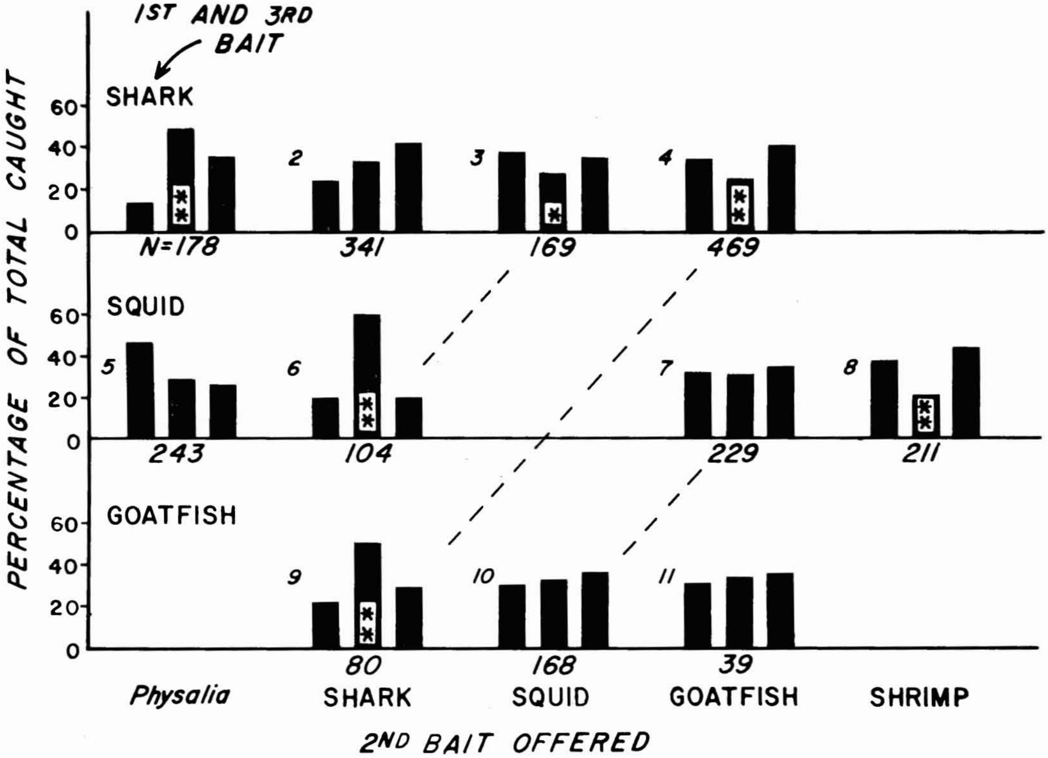

FIGURE 2. Eleven comparisons of bait effectiveness, taken two at a time. In each experimental comparison (numbered 1–11), animals were captured first as they were attracted to one bait, later as other animals were attracted to a second type of bait, and then as yet other animals were attracted to the first type of bait. The number below each set of three bars denotes the total number collected for each comparison (104 animals in no. 6). The three diagonal broken lines connect reciprocal comparisons. Asterisks within the central bars denote statistically significant differences (5 and 1 percent, χ^2 test) when the intermediate bait results were tested against the average number of animals that had come to the other bait used in the first and third sets.

jective field assessment. Mole crabs were more readily attracted to *Physalia* than to shark. Shark was more effective than either squid or goatfish, which were about equally effective. Shrimp fared badly (just as Matthews observed).

LABORATORY OBSERVATIONS

Animals kept in salt water tables at the Hawaii Institute of Marine Biology provided an opportunity for close observation of feeding habits and prefeeding behavior. If left for 2 or 3 days in clean sand and flowing seawater, the animals readily fed on bits of meat proffered with forceps (plastic colanders permitted easy handling of animals [Wenner 1972]). The use of black sand in the water table and white animals from a white sand beach permitted the observation that normally no part of the animals protruded above the sand surface. The mere holding of a piece of meat in the incurrent stream of the water table, however, produced a marked and characteristic reaction on the part of these mole crabs: several would partially emerge (prefeeding posture; figure 1 of Wenner 1972), and occasionally an animal would emerge almost one-third of the way.

The most prominent feature of the prefeeding posture (evoked by the insertion of meat juices into the water) was the protrusion of the extra long first pereopods. A mere touch of a piece of meat to the hair-covered tip of one of these legs usually led to a grasping of the meat by these same legs in a raptorial fashion. If the meat was touched to the legs and then kept just beyond reach, the animal often leaped out of the sand and grasped the meat before burrowing into the sand again.

A touch of the meat to the hair-covered antennules evoked much the same set of responses. Touching a piece of inert sponge to either antennules or first pereopods, however, only resulted in the animal retreating below the sand surface, even if meat juices had been put into the water coincident with the sponge contact. Matthews (1955) had earlier recognized the need for chemical stimulation but did not mention the presumably chemosensory nature of the hairs on these appendages.

MYSIDS AS FOOD

A visit to Enewetak Atoll resulted in the discovery of another food source normally exploited by Pacific mole crabs. In July 1971 at the Navy Pier on Enewetak Islet, mole crabs were abundant in the beach sands and virtually all females were ovigerous. A subsequent dissection of females revealed a second batch of eggs in the ovaries, indicating a steady source of food for these animals. However, *Physalia* was not visible; there was little or no mention of them in published accounts of Enewetak biology; and long-term residents could recall no men-of-war influxes onto the beaches. Finally, animals caught in the morning had fine black material in the gut, but animals taken in the afternoon had not recently fed.

Altogether the results suggested a source of food available only at night. Accordingly, I set out bait at 1-m intervals along a transect from the wave wash zone down to a 3-m depth along the bottom, both during the day and at night. When no animals came to bait placed anywhere other than in the wave wash zone (day or night), I inspected this zone at night with a flashlight and found hundreds of animals in the prefeeding position (Wenner 1972: figure 1). Occasionally an animal would move one of its first pereopods toward its mouthparts and then out again. The animals apparently were feeding diligently, as evidenced by the relative number of animals that moved their raptorial front legs; but the turbulence brought about by receding waves against extended legs prevented any sighting of food material. It was further evident that the hundreds of animals along this short stretch of beach formed a filter array, an array which would trap virtually all large zooplankton venturing into the wash zone.

Plankton tows yielded scores of mysids, but only at night—results which agree with the vertical migration data obtained by Gerber (personal communication). These mysids, when placed in colanders containing mole crabs in the laboratory, produced correlative results. When mysids were first introduced into the water, mole crabs immediately thrust their front legs out of the sand and assumed the prefeeding posture. In the still water, it was evident that mole crabs caught the mysids with the hairs on those legs and tucked them into the maxilliped complex.

The presence of such a large number of mysids at the Navy Pier was apparently fortuitous in this case. Two 750-watt lamps lighted the foot of the Navy Pier and the nearby beach and water. There was every reason to believe that these lights attracted mysids toward shore at night, where they served as food for the mole crabs—a conclusion supported by results obtained during subsequent visits to the atoll. During the summer of 1972, typhoons destroyed the two powerful lights and the beach remained in darkness after that time. By the spring and fall of 1973, virtually no females (1 and 7 percent, respectively) were producing eggs in that habitat, even though animals at other beaches exhibited a high rate of egg production.

FOOD AVAILABILITY AND OVULATION

The filter-feeding sand crabs on the California coast (*Emerita analoga*) exhibit a marked seasonality both in feeding behavior (Wenner, personal observation) and in egg bearing (Boolootian et al. 1959, Barnes and Wenner 1968, Cox and Dudley 1968). Between mid-October and mid-April in Santa Barbara, the large aggregations of feeding animals can be found only rarely. This fall disappearance occurs even if the water temperature remains unchanged. Just prior to this mass disappearance, the percentage of mature females in berry drops from nearly 100 percent to nearly zero. Those females which do carry eggs during the winter are almost always the very large individuals

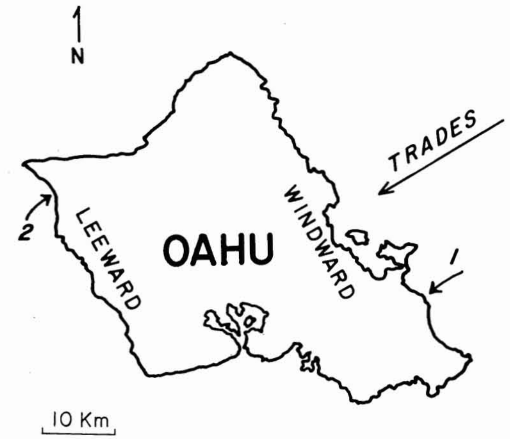

FIGURE 3. Prevailing winds in relationship to Oahu, Hawaiian Islands. During summer months trade winds drive men-of-war onto the windward beaches (e.g., site no. 1). The leeward coast receives few men-of-war during these summer months but does have onshore winds in the winter months when storms strike the islands, bringing strong southerly winds.

TABLE 1

PERCENTAGE OF OVIGEROUS FEMALE MOLE CRABS (*Hippa pacifica*) ON OAHU, HAWAIIAN ISLANDS, AS A FUNCTION OF BEACH LOCATION AND DATE

MONTH	WINDWARD		LEEWARD	
1970–1971	%	*N*	%	*N*
Mid-September	94	116		
End September	68	152		
Mid-October	41	56		
End October	29	94		
Mid-November	10	174	60	48
End November			73	88
Mid-December	88	64	84	74
End December	76	128		
Mid-February	43	90		
End June	96	54	41	97

NOTE: The decline observed on windward Oahu beaches in the first 2 months did not persist during the following winter months.

(Cox and Dudley 1968, Wenner, personal observation).

In 1970 mature female Pacific mole crabs (*Hippa pacifica*) on the windward shores of Oahu (Figure 3, site no. 1) had a fall decrease in egg production similar to that found in *Emerita analoga*, but with a slower decline in the percentage of berried females (Table 1, column 1). From a high percentage of 94 percent in September, the females in berry made up a successively smaller percentage of the females in the population. By mid-November females in berry were relatively rare (10 percent of the mature females). This reduction in the percentage of ovigerous females coincided with an approximately 5° C decline in water temperature.

The leeward shores (Figure 3, site no. 2) did not correspond to this pattern. In mid-November a majority of the females (60 percent) was in berry, even though the water temperature on the two sides of the island varied only slightly. One marked difference between these two beaches did exist, however. During the preceding 2 months the leeward shore had received strong southerly winds during winter storms. The percentage of females in berry rose further as new storms visited the islands (Table 1, column 3).

Fortunately, the problem was partially resolved by mid-December, after strong trade winds had blown for about 2 weeks. Before that time, men-of-war had been virtually absent from windward beaches. After 3 days of these winds, however, one *Physalia* could be found on each 5 m of beach, on the average, along a 1030-m stretch of beach. This represents a considerable influx, since mole crabs do not permit men-of-war to accumulate (Bonnet 1946). Within 1 week after that 2-week period, a majority (88 percent) of females was again in berry, even though the water temperature had become slightly lower than in previous weeks.

That men-of-war influx lasted only about 1 week. After that the percentage of females in berry progressively declined. The same 1030-m stretch of beach yielded an average total of only 13 animals during a 3-day period at the end of December. By mid-February, when men-of-war had not come in for 1.5 months, once again a minority of females was ovigerous (43 percent).

The foregoing set of results suggested the hypothesis that the percentage of females in berry was a function of food availability and not one either of "season" or water temperature. As a test of that possibility, I collected animals on the two respective beaches (windward and leeward) at the end of the following June, after steady tradewinds had blown large numbers of men-of-war onto only the windward beaches for more than 2 months.

The hypothesis remained intact. Almost all (96 percent) of the females on the windward coast were in berry during June (Table 1, last line). Only a minority (41 percent) of the females on the leeward coast was ovigerous, despite the arrival of summer and warmer temperatures.

DISCUSSION

Food and Feeding Habits

Hippid mole crabs generally live submerged in sand but do not feed while totally submerged. The well-known intertidal common sand crabs (*Emerita* spp.) extend their antennae above the sand surface and strain microscopic food from the water (e.g., Weymouth and Richardson 1912). These filter-feeding animals thrive in temperate zones, where microscopic food is plentiful. In the tropics, where microscopic food is relatively scarce, predacious mole crabs (*Hippa* spp.) replace filter feeders in the intertidal zone. In Hawaii this sandy intertidal habitat does not appear to harbor potential prey for these animals, but Bonnet (1946) and Matthews (1955) found a partial solution to the food supply problem of these animals. They established the fact that Portuguese men-of-war (*Physalia utriculus*) that washed onto the beach were caught and eaten by *Hippa pacifica*.

In the present study it has become apparent that consumption of *Physalia* is part of a larger problem of food dependence by *Hippa pacifica*. Pacific mole crabs apparently can live on other types of food brought onto the beaches by prevailing winds. Tests complementary to those run by Matthews indicated that a variety of food is acceptable, provided that it is fresh meat. Shark and squid, for example, proved to be about as effective as *Physalia* when used as bait. The animals also fed on other food which could be brought in by prevailing winds, such as recently killed goatfish (*Mulloidichthys* sp.) and shrimp, though the latter was not especially efficacious when used as bait.

Fusaro (unpublished) has now obtained direct evidence for the suitability of shark meat as a food source and of the real nature of food limitation in *Hippa pacifica*. In the fall of 1975, he selectively fed diced shark meat to animals on one islet at Enewetak Atoll. At the end of 18 days the percentage of females in berry rose from 32 to 56 percent ($N = 139$; $\chi^2 = 48.2$). Females at a nearby, control islet showed only a negligible increase (38 to 41 percent—$N = 91$; $\chi^2 = 0.28$) during the same time interval.

Mysids represent a potentially important food source unrecognized earlier. At night mysids migrate to the water surface and can then be attracted toward shore by lights or be carried toward shore in the surface waters by the prevailing trade winds, which blow both night and day. At Enewetak, for example, mole crabs at a lighted beach could be seen at night in a prefeeding posture. Although lights had apparently attracted the mysids to shore in that instance, surface waters could carry these and other animals into shore anywhere that prevailing winds persist throughout the night.

Egg Production and Season

The Pacific mole crab's reliance on a source of food external to its habitat permits interesting comparative studies. Depending on the season, some beaches have a more favorable location than others with respect to wind-driven foods. On those favored beaches, one would expect that animals would exhibit a faster growth rate and higher egg production rate than would those on more sheltered beaches, all other factors being equal. In fact, a greater egg production on some beaches did occur in Hawaii. Animals on the windward beaches had an egg production rate which correlated well with the duration of prevailing winds and presence of *Physalia*. In addition, a sudden influx of men-of-war in December apparently led to a dramatic increase in egg production.

The difference in egg production on different beaches, in turn, indicates that *Hippa pacifica* is a food-dependent animal in Hawaii. This is also apparently true at Enewetak Atoll (Wenner and Fusaro, unpublished). In Hawaii, men-of-war appear to be the primary food supply, though alternative foods can provide at least a maintenance level of food between periods of heavy *Physalia* influx. This conclusion agrees with an earlier observation by Bonnet (1946): "It seems unlikely that these animals feed exclusively upon

Physalia, but it is certain that this coelenterate constitutes an important item in their diet." In the absence of alternative food sources, it is also conceivable that the animals are able to survive long periods without food at all.

This food dependence can have interesting consequences. What initially appeared to be a seasonal egg production (Table 1, September to December) apparently was a consequence of food shortage, alleviated by the men-of-war influx in mid-December. A low percentage of females in berry in a given habitat thus might well indicate a food shortage for some time period prior to sampling and not be a direct consequence of "season". Conversely, a high percentage of ovigerous females could well indicate a high level of food availability and not necessarily a rise in temperature. A re-examination of this "seasonality" in egg production might indicate a food dependence as well as (or instead of) a temperature dependence in many marine crustaceans, just as Barnes and Barnes (1967) have already found true for barnacles. Such a re-evaluation could reveal why some tropic species have shown a marked seasonality (e.g. Goodbody 1962), while others breed throughout the year (e.g. Goodbody 1965, Hanson 1969).

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