Feeding Habits of the Sand Crab *Hippa pacifica* (Dana)[1]

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BURROWING SAND CRABS, *Hippa pacifica* (Dana), [*Remipes pacifica* Dana of Edmondson, 1925; *Emerita pacifica* (Dana) of Edmondson, 1946, and Bonnet, 1946], were observed feeding on Portuguese man-of-war (*Physalia utriculus* Eschscholtz) at Waimanalo Beach, Oahu, during the high surf of June, 1954. However, these sand crabs completely ignored another colonial hydrozoan, *Velella pacifica* Eschscholtz, present in the surf at the time. Viewing these two colonial hydrozoans from above, astute man could easily differentiate between the gas filled float of *Physalia* and the flattened, elliptical float and oblique sail of *Velella*, but less sagacious sand crabs, viewing these colonial hydrozoans from below, could not be expected to discern subtle differences of color or length of suspended zooids. This would be especially true during a high surf because of increased turbidity, yet, in no instance did I observe even a tentative approach to *Velella*. Even though *H. pacifica* has well developed eyes, the likelihood that selection of *Physalia* and rejection of *Velella* could result solely from visual discrimination is unlikely.

Whereas unselective feeding by antennal straining has been investigated in *Emerita*, insofar as could be ascertained, no published work on selective feeding in *H. pacifica* has been reported. Therefore the experiments reported on here were performed to investigate the method by which selective feeding is accomplished.

My appreciation is extended to Dr. Maxwell Doty, University of Hawaii, for the phycological determinations and to Dr. Fenner Chace, Jr., United States National Museum, for the identification of the Hawaiian sand crabs.

METHODS AND TECHNIQUES

A. Sand crabs collected during the high surf were usually attached (singly or in groups of five or six) to their captured *Physalia*. These crabs were removed and taken immediately to the laboratory where antennae, antennules and the contents of the dissected digestive systems were examined microscopically for the presence of minute plants and animals (exclusive of bacteria), an abundance of which would indicate unselective, filter feeding.

B. *Physalia* and *Velella* disappeared from the surf as the wind subsided but, washed high on the beach, stranded colonies formed an almost unbroken line as evidence of their previous abundance in the sea. These served as a ready source of food for subsequent experiments. Sand crabs likewise disappeared from the surf as the sea calmed, leaving the wave-washed region of the beach bare. Upon this region of the beach I tossed (1) pieces of algae (*Ulva fasciata* Delile, *Turbinaria ornata* J. Agardh, *Sargassum obtusifolium* J. Agardh, *Polyopes clarionensis* Sethchell & Gardner) broken to approximately the size of *Physalia;* (2) *Velella;* (3) pieces of commercial shrimp discarded by fishermen; and (4) *Physalia*.

Sand crabs which responded to any of these materials were collected and taken to the

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laboratory where antennae, antennules and the contents of the dissected digestive systems were examined microscopically for evidence of filter feeding.

C. The methods employed in B were repeated, one week later. Sand crabs collected were taken to the laboratory and the antennae, antennules and contents of the dissected digestive systems examined microscopically for evidence of filter feeding.

D. Approximately equal portions of *Ulva*, *Velella*, shrimp and *Physalia* were separately ground with sand and sea water, filtered through number 40 mesh grit gauze and each filtrate (approximately 25 cc.) diluted to 1,000 cc. of sea water. Each solution was thrown on the thin film of a receding wave and the effects, if any, noted. For each solution, a new location on the beach was chosen. Again, sand crabs which responded to any of the solutions were taken to the laboratory where antennae, antennules, and the contents of the dissected digestive systems were examined microscopically for evidence of filter feeding.

E. Twenty-five male and 25 female sand crabs were collected and their compound eyes were removed leaving the major portion of the eye stalks intact. These blinded sand crabs were placed in a small tank and allowed one day to recover from operative shock, during which time they received additional sea water. *Physalia* was again ground in sand and sea water, filtered through number 40 mesh grit gauze and the filtrate (25 cc.) diluted with approximately 1,000 cc. of sea water. The diluted filtrate, colored with 0.5 grams of neutral red was placed in a clean, 1 liter bottle fitted with four discharge pipettes. Adjustment of a single Hoffman clamp permitted the simultaneous, drop by drop, delivery of the filtrate into four paper cups (300 cc. capacity) each of which contained beach sand, sufficient to cover the bottom 2 cm., and 75 cc. of sea water, sufficient to produce a water depth of 2 cm. Four sand crabs were simultaneously tested: (1) a control male, (2) a control female, (3) a test male, and (4) a test female; each in a separate paper cup. In no case was the filtrate introduced until all four sand crabs had buried themselves in the sand. Ten drops (approximately 0.5 cc.) of filtrate were simultaneously introduced into each of the four paper cups and the reaction time recorded. This was regarded as the interval from the instant the tenth drop struck the surface of the water, to any visible response by the crab. The observed times, both for control and test animals, was averaged for five separate trials. After each experiment, paper cups and contents were discarded. These blinded sand crabs and the controls were also examined microscopically for evidence of filter feeding.

F. The methods employed in E were repeated (with fresh paper cups, sand, and sea water) except that both the compound eyes and the antennae were removed.

G. The methods employed in E were repeated, except that the compound eyes and the antennules were removed.

H. An attempt was made to test crabs with compound eyes, antennae and antennules removed. However, only 24 (of 50) sand crabs survived the severe operative shock. Of these, over half remained on their backs on the surface of the sand, displayed little or no action and were dead the following morning. The colored *Physalia* solution was introduced to the remaining 12 survivors in the small tank and the results noted. These crabs were dead on arrival at the laboratory and I regret that the contents of their digestive systems were not examined microscopically. Male and female controls were run as before (E,F,G).

RESULTS

A. Microscopic examination of sand crab antennae and antennules collected during the high surf revealed sand grains but no organisms enmeshed in the setae. The dissected digestive systems, especially the pyloric caeca, were blue, gorged with nematocysts and the shredded remains of *Physalia* zooids. There were no microorganisms nor was there any evidence, either from nematocysts or zooids, that *Velella* had been eaten.

B. As the wind subsided and *Physalia* and *Velella* no longer appeared in the surf, pieces of algae (*Ulva fasciata*; *Turbinaria ornata*, *Sargassum obtusifolium*, *Polyopes clarionensis*), *Velella* and shrimp tossed into the thin film of receding waves all failed to evoke any visible response from sand crabs but when *Physalia* was used, sand crabs emerged. Often 4 or 5 would seize a single colony simultaneously and, submerging, all take part in pulling it below. Others, often arriving at the scene too late and finding no prey, would quickly submerge as the wave receded. It was not difficult to collect 25 or more sand crabs by using a single *Physalia* colony over and over again in this manner. Microscopic examination of the antennae and antennules revealed sand grains but no organisms enmeshed in the setae. The dissected digestive systems were, as before, gorged with nematocysts and the blue remains of shredded *Physalia*, but no microorganisms were present.

C. As in B, when the waves of the calm sea broke on the beach, no crabs responded to *Ulva*. However, when *Velella*, commercial shrimp, and *Physalia* were tossed separately onto this region of the beach, crabs emerged. Microscopic examination of antennae and antennules again revealed sand grains but no organisms enmeshed in the setae. The dissected digestive systems were empty save for sand grains and what appeared to be mucus.

D. Filtered and diluted portions of ground *Ulva*, *Velella* and shrimp thrown on receding waves failed to evoke any visible response from the submerged crabs. However, when the *Physalia* filtrate was used sand crabs emerged, excitedly ran up and down the beach but, failing to locate the *Physalia*, quickly submerged. Microscopic examination of the antennae and antennules of these collected sand crabs revealed a few sand grains but no microorganisms enmeshed in the setae. Again the dissected digestive systems revealed nematocysts and the bluish remains of *Physalia* but no microorganisms.

E. Of the 50 sand crabs collected for this part of the experiment, only 18 males and 15 females survived the operative shock of eye removal. Many, even when molested, remained motionless on their backs; others righted themselves and, colliding one with another scurried around the tank. Finally, without any definite pattern of orientation, most submerged. Although the *Physalia* solution was clearly discernible as it left the four pipettes and entered the salt water of the paper cups its course became less apparent as it approached the sand so that determination of the exact moment of contact of filtrate and crabs was impossible. This condition was often further complicated by the spontaneous emerging of crabs before the first drop of filtrate could possibly have reached them. The addition of 0.5 grams of neutral red to the solution made it easy to follow the course of the filtrate. Sand crabs in all four cups emerged in great confusion during the introduction of the first six drops of filtrate. It was impossible for me to determine whether the control males and females or the blinded males and females responded more quickly. Microscopic examination of test and control crabs revealed only a few sand grains enmeshed in the setae of antennae and antennules. The digestive systems contained the remains of *Physalia* but there was no evidence of microorganisms.

F. Of the 50 sand crabs collected for this experiment, only 30 survived the operative shock of the removal of both the eyes and antennae. These exhibited about the same activities as those described in E. Again there was much confusion. Some turned over on their backs, whereas others, colliding one with another, hurried around and around the tank and finally, without special orientation, submerged. Compared to crabs having only the compound eyes removed the reaction of these crabs to the introduced filtrate was dilatory and weak. Often 3 to 5 minutes elapsed after the tenth drop of *Physalia* solution was introduced before the crabs stirred. As in E the controls emerged before the tenth drop of *Physalia* solution was introduced. Microscopic examination of the antennules of operative and control crabs revealed only sand grains enmeshed in the setae and the contents of the dissected digestive systems again revealed unaltered nematocysts but no microorganisms.

G. Of the 50 sand crabs collected for this experiment about the same number (30) survived the operative shock of removal of eyes and antennules as survived the removal of eyes and antennae. These exhibited about the same activities as those described in F. There was the same confusion, the same colliding one with another, the same running around the tank and the same submerging without any special orientation. Again 3 to 5 minutes elapsed after the tenth drop of *Physalia* solution was introduced before the crabs emerged. No difference, either in time or in magnitude of response, was discernible between blinded sand crabs with antennae removed and blinded sand crabs with antennules removed. As in E the controls emerged before the tenth drop of *Physalia* solution was introduced. Microscopic examination of the antennae of test and control crabs revealed only sand grains, and the contents of the dissected digestive systems revealed only unaltered nematocysts.

H. After the tenth drop of the colored *Physalia* solution reached the 12 sand crabs that had survived the removal of eyes, antennae and antennules 15 to 21 minutes was required before any visible response occurred. As in previous experiments the controls emerged before the tenth drop of *Physalia* solution was introduced. For the most part the test crabs merely broke the surface of the sand, appeared to "tread water" momentarily, and then settled below the surface. As previously mentioned, these crabs were dead on arrival at the laboratory and their digestive systems were not examined. No microorganisms were present on the controls.

DISCUSSION

Gregarious sand crabs lie submerged in large "beds" with only eyes and antennules projecting above the shifting, wave-washed sand. In *Emerita*, for example, exceedingly long antennae, folded behind the maxillipeds (*vide* Weymouth and Richardson, 1912, pl. 1, fig. 7), are thrust out anterolaterally as waves recede; thus characteristic **V**-shaped ripples, which mark the "bed's" location, are formed (*vide* MacGinitie and MacGinitie, 1949, figs. 145–146, p. 302). However, Hawaii's only hippid (Edmondson, 1946, p. 265), has exceedingly short antennae (*vide* Dana, 1855, Atlas: Crustacea, pl. 25, fig. 7a), thus the characteristic **V**-shaped ripples result from water striking the antennules, rather than the antennae.

Weymouth and Richardson (*op. cit.* p. 11) conclude that microorganisms found in the stomach of *Emerita analoga* were strained from waves and that antennae and mouth parts "are remarkably adapted to this form of feeding, and unfitted for any other." In *Emerita analoga* the function of sensory antennal pits in feeding appears negligible as highly diversified materials generally reported from their stomachs (diatoms, radiolarians, foraminifera, spicules, one-celled algae and sand) are "about what would be obtained by unselective straining of the water along shore" (Weymouth and Richardson, *op. cit.*, p. 9).

In contrast to the unselective antennal straining of *Emerita*, feeding by *H. pacifica*, at least during high surf, is selective as evidenced by their acceptance of *Physalia* and their rejection of algae, shrimp, and *Velella*. Moreover, this selectivity is attributed, in part at least, to some sense other than sight for, although all experimental solutions probably appeared similar to the crabs, the *Physalia* solution alone evoked visible responses. Yet, so long as the eyes remained intact, selection based on some chemical sense (*vide* Moncrieff, 1946, p. 152; Ramsay, 1952, p. 85; and Prosser *et al.*, 1950, p. 453) although a strong probability, could not be held entirely responsible for this phenomenon.

However as blinded *H. pacifica* reacted to *Physalia* solutions almost immediately, the presence of some selective chemical sense is demonstrated and, in light of similar research among other arthropods, attention was at once centered on antennae, antennules and mouth parts.

The removal of the antennae of blinded *H. pacifica* and the subsequent increase in reaction time (3–5 minutes) indicates that the chemical sense is in part located on these structures. Likewise, the removal of the antennules of blinded *H. pacifica* and the subsequent increase in reaction time (3–5 minutes) also indicates that the chemical sense is in part located on these structures. Inasmuch as the increased reaction time following the removal of the antennae so nearly approximates the increased reaction time following the removal of the antennules, one can conclude that these two structures are equally important in the degree of selectivity of the chemical sense.

To determine whether the chemoreceptors were limited to the antennae and antennules in blinded *H. pacifica*, both structures were removed. The increased reaction time (15–21 minutes) following the removal of both antennae and antennules indicates that probably there are chemoreceptors present on the still intact mouth parts, although they are much less effective than those of the antennae and antennules.

The chemoreceptors located on antennae and antennules of *H. pacifica* are therefore, responsible for the detection of *Physalia* during the high surf; the sense of sight being responsible primarily for actual location and subsequent seizure. This same chemical sense must also be responsible for detection, during calm seas, of shrimp and *Velella* which *H. pacifica* quite readily seizes once its digestive tract is empty and its preferred food scarce.

Neither the presence of shredded *Physalia* in the digestive tracts, nor the absence of minute organisms enmeshed in the setae of the antennae and antennules precludes the possibility of unselective feeding by *H. pacifica*, especially during the weeks of calm which often follow periods of heavy surf. Inasmuch as during periods of calm sand grains and mucus but no microorganisms have been found in the digestive tract of *H. pacifica* the question of unselective feeding remains unanswered.

REFERENCES

BONNET, DAVID D. 1946. The Portuguese man-of-war as a food source for the sand crab (*Emerita pacifica*). *Science* 103 (2666): 148–149.

DANA, J. D. 1855. Crustacea, Atlas. *United States Exploring Expedition* . . . under the command of Charles Wilkes, U.S.N. C. Sherman, Printer, Philadelphia.

EDMONDSON, C. H. 1925. Marine zoology of tropical central Pacific, Crustacea. *Bernice P. Bishop Mus., Bul.* 27: 1–26.

——— 1946. Reef and shore fauna of Hawaii. *Bernice P. Bishop Mus., Spec. Pub.* 22: 1–388.

MACGINITIE, G. E., and N. MACGINITIE. 1949. *Natural history of marine animals.* xii + 473 p. McGraw-Hill Book Company, New York.

MONCRIEFF, R. W. 1946. *The chemical senses.* vii + 424 p. John Wiley & Sons, New York.

PROSSER, C. LADD, *et al.* 1950. *Comparative animal physiology.* ix + 888 p. W. B. Saunders Co., Philadelphia.

RAMSAY, J. A. 1952. *A physiological approach to the lower animals.* ix + 148 p. Cambridge University Press, London.

WEYMOUTH, F. W., and C. H. RICHARDSON. 1912. Observations on the habits of the crustacean, *Emerita analoga*. *Smithsn. Inst., Misc. Collect.* 59 (7): 1–13.