

AN ABSTRACT OF THE THESIS OF

WALTER HOWARD PEARSON for the degree of DOCTOR OF PHILOSOPHY

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Title: THE EFFECTS OF PCB EXPOSURE ON THE BEHAVIOR OF THE SHORE CRAB

HEMIGRAPSPUS OREGONENSIS

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Abstract approved: _____

Robert L. Holton

The behavior of the shore crab Hemigrapsus oregonensis was assessed with and without exposure to polychlorinated biphenyls (Aroclor[®] 1260). After describing the crab's behavioral repertoire, activity budgets were developed from observations of the time crabs spent in 20 categories of shelter use, posture, and activity while held in habitat replicas with sinusoidal tides of 12.4 hours.

Without PCBs exposure female crabs spent more time sheltered and feeding but less time displaying than males. The sexes also differed in the kinds of displays given. For both sexes certain activities prevailed at certain tidal stages.

Crabs readily accumulated PCBs from contaminated sand. Whole body burdens reached as high as 190 ppm PCBs and were related to sex and time spent in feeding.

In two experiments the primary effect of PCBs exposure upon the activity budgets of both sexes was to decrease the time spent in pre-feeding and feeding behaviors. When given a variety of food types in a third experiment, crabs under exposure shifted from feeding upon PCBs-contaminated sand to uncontaminated food. By changing its feeding behavior Hemigrapsus oregonensis actively reduced the received dose of

PCBs and its presumed adverse effects from what they would otherwise have been.

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The Effects of PCB Exposure on the Behavior
of the Shore Crab Hemigrapsus oregonensis

by

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THE EFFECTS OF PCB EXPOSURE ON THE BEHAVIOR
OF THE SHORE CRAB HEMIGRAPSUS OREGONENSIS

INTRODUCTION

As a test of the competence of their theories, scientists wish to predict events. Moreover, society views the ability to predict events as one of the chief virtues of scientists. Predictions as to the fate of marine organisms exposed to pollutants are increasingly sought out and given. Society is continuously choosing among several courses of action that will affect the marine environment, and the scientists' contribution is the prediction of the consequences of the different courses. Unfortunately what can be predicted is not always what needs to be predicted. Present theory is not even adequate to begin to indicate the fate of organisms exposed to pollutants (Todd et al, 1972; Slobodkin, 1968; Slobodkin and Rapoport, 1974).

This study arose out of a dissatisfaction with conventional toxicity testing as a meaningful exercise in predicting the consequences of pollution. Conventional toxicity testing commonly uses death of 50% of the test organisms within 96 hours as an endpoint much the same way as chemistry uses a color change as an endpoint in titration. Death may not be an appropriate endpoint. For example, reproduction may fail (Grosch, 1973) or behavior may be disrupted (McLarney et al, 1974) at levels below those at which death occurs. Aside from the inappropriateness of the endpoints chosen, the toxicity test gives a one-sided view, i.e., the failure of the organism to adapt is discovered, but innovation by the organism that allows adaption is not even examined.

To move beyond conventional toxicity testing is not simply to seek a different endpoint, such as behavioral disruption, but to seek a broader understanding of an organism's responses. This study aims not so much to make quantitative predictions, such as the particular concentration of a pollutant at which a specified number of organisms are damaged in some way, as to seek qualitative explanation about patterns of events, such as the manner in which the organism attempts to adapt to a pollutant.

In order to understand the adaptive processes of a marine organism under stress, the behavior of the yellow shore crab Hemigrapsus oregonensis was assessed with and without exposure to polychlorinated biphenyls (PCBs). The time spent by crabs in various activities was measured, and the data used to construct activity budgets. An endeavor was made to be alert to any innovative behavior leading to adaption while examining possible disruption of the ordinary behavior.

Systems philosophers (Emery, 1969) suggest that one cannot describe the behavior of open systems like living organisms without characterizing their environment. To see ordinary behavior in the laboratory, then, one must provide the crabs with an environment approximating their natural environment. Consequently, physical replicas complete with sand, shelter, food, tides, and light regimes were constructed. In these habitat replicas behavior of the crab under ordinary and stressing conditions was investigated.

A. THEORETICAL BACKGROUND

Following the suggestion of Steen and Jager (1971) that philosophical analysis should precede scientific sophistication, the theoretical background to this study is an exposition of the concepts guiding the direction taken in the experiments.

First, ideas about behavior and how it is to be investigated flow from ideas about the nature of a living organism. The theoretical model of a living organism under which this study moved is drawn from three areas of thought: (1) Ethology, e.g. Russell (1934), Tinbergen (1951), Lorenz (1974); (2) Philosophy of Science, e.g. Beckner (1959, 1969), Hull (1974), Steen and Jager (1971); and (3) Systems Thinking, e.g. Bertalanffy (1950, 1968), Emery (1969), Koestler (1967). The ethologists (Russell, 1934) begin with the recognition that an animal is goal-directed, primarily active rather than reactive, exhibits memory or retentiveness, and has in its actions temporal unity, continuity and directedness. The animal is not passively waiting for a stimulus to cause it to act but is actively seeking to satisfy its needs in the

world. Bertalanffy (1950) indicates that goal-directedness is more than just homeostasis and that one of its characteristics is equifinality, i.e. under a variety of circumstances an organism achieves the same goal, e.g. food, by different but appropriate actions.

What one will observe as behavior follows from one's model of the living organism. Beckner (1959) gives two alternative methods for the description of behavior: one can describe behavior either as motion in relation to some geometrical background or in terms of objects manipulated and things done and left undone. Generally ethologists follow the second approach because Tinbergen (1951) and Russell (1934) both warn that the first approach is too low a level of analysis. Close attention to action patterns, e.g. minute description of how the crab moves his chelae, will not yield results of very wide application. Functional categories coupled with the second approach yield results of wide applicability and have other useful properties (Beckner, 1959, 1969). The same movement of the crab's chelae may be an aggressive display or feeding. Without coupling the movement to its function its adaptive significance is lost and one remains unable to make comparison with other taxa.

Ideas about the nature of living organisms and their behavior enter directly into the practical problems of designing reasonable behavioral experiments. Because an animal is primarily active and goal-directed, considering the stimulus-response relation to be causal can lead to inappropriate experiments. In behavioral experiments failure to obtain responses upon giving stimuli is often taken to mean motivation or drive of the subject varied. The next step is usually to manipulate the animals to achieve some desired motivational state, e.g. the animals are starved so that a strong response to food can be obtained. The difficulty, as Steen and Jager (1971) point out, is that the manipulation has changed the boundary conditions and the experimental results are no longer applicable to the original situation that was to be investigated. It may very well be that as long as one accepts the model of causality hidden in the idea of stimulus-response chains (Steen and Jager, 1971), one will be unable to avoid making robots out of animals by manipulation toward some

desired response upon stimulus presentation.

Now it is appropriate to ask whether an investigation of an organism's behavior will help to predict possible consequences of exposure to pollutants. From the major tenet of biological science that behavior is adaptive and subject to evolution (Lorenz, 1974), one might expect to discern a change in an organism's behavior with a change in its environment. More specific but sometimes conflicting answers to the question of the fruitfulness of studying behavior as a predictor of pollutant effects are coming from two groups, ethologists (Todd et al, 1972; Atema et al, 1973) and evolutionary biologists (Slobodkin, 1968; Slobodkin and Rapoport, 1974).

After equating behavioral complexity with the number of different behavior patterns exhibited by an organism, Todd et al (1972) give their main hypothesis that the more behaviorally complex an organism is the more vulnerable is its behavior to disruption by a pollutant. Indeed some evidence to support their hypothesis is seen in their finding that the more complex social behavior of yellow bullheads is disrupted at sublethal levels of oil while at comparable levels the less complex behavior of sunfish and golden shiners is not disrupted (Todd et al, 1972). Other evidence indicates that it may be the more complex behaviors that are disrupted. McLarney et al (1974) found that yellow bullheads subject to increasing temperature showed an increasing frequency of aggressive behaviors that brought damage. A loss of the ability to recognize individuals and thus to maintain dominance hierarchies was suggested as the cause of the increased aggression.

Aside from the preliminary nature of the evidence, the findings of Todd et al (1972) may be incomplete because while the investigators watched for failure of behavior, they may have overlooked the innovative behavior described by Koestler (1967) that often arises in response to an environmental challenge. The possibilities open to the challenged animal are not just two (maintain the status quo or suffer damage), but three or four (no change, damage, adjustment, or even improvement). Unless one specifically watches for adjustment, an important activity bringing adjustment may be seen by the observer as no apparent overall change.

Another related conceptual problem with Todd's approach derives from equating diversity of behavior types with behavioral complexity. Feibleman (1969) recognizes the flexibility of an organism as its capacity to give a variety of responses to the same stimulus. This recognition brings one to the question whether having a great number of behaviors is more adaptive than being versatile with the ones the organism has. In addition, diversity of behaviors can be an artifact of the holding condition. If there are no stones in the aquaria, the crab which normally pushes stones about finds it difficult to exhibit stone pushing behavior. Thus an argument can be made that the number of behavioral units exhibited may not by itself be the only or the best measure of behavioral complexity.

While Todd et al (1972) choose behavioral complexity, a property primarily of the organism, to be investigated for its predictive value, another ethological approach (Atema et al, 1973) is to examine as a possible predictor of a pollutant's consequences the chemicals naturally sensed by the organism, a property of the organism and its environment together. Because chemoreception is such a large part of the Umwelt of an aquatic organism, Atema et al (1973) expect the chemical senses to be disrupted by extremely low levels of pollutants and hope to predict the identity or character of disrupting pollutants from the identity of natural chemicals important in the behavior of fish.

Still a third indication that behavior can be investigated fruitfully derives from the idea that behavior permits adaption to environmental perturbation, a part of a predictive theory of evolution now being developed (Slobodkin, 1968; Slobodkin and Rapoport, 1974). The hope is to achieve the ability to predict categories of responses to stress rather than what particular species will succumb to what particular insult. Slobodkin believes that the organism follows an optimal strategy and gives us two different, not necessarily mutually exclusive, views of what constitutes optimal strategy. The organism can seek to maximize its homeostatic abilities (Slobodkin, 1968) or minimize the stakes (Slobodkin and Rapoport, 1974). Under the first view a change in behavior is seen to be the initial response to stress and if a behavior change proves

adequate other slower and more fundamental responses, e.g. change in metabolism, do not occur. The second view tells us that the organism minimizes the stakes involved in responding to an environmental perturbation by using its least expensive ploy first. Both views can be derived from the concept that the organism's capacity to respond is hierarchically organized. The lowest level of response, changing behavior, being both inexpensive and short term, is utilized first. The higher levels, physiological and genetic adjustments, come into play when the lower level adjustment has proved inadequate. Prevention of the behavioral response by experimental design, intentional or accidental, can give a biased view of the organism's capacity to adapt. For example, Sparks et al (1972) find that adding shelter to aquaria in which groups of bluegills, Lepomis macrochirus, are exposed to zinc allows the submissive fish to survive as long as the dominant one.

Both Slobodkin and Todd distinguish historical stressors, those previously experienced in an organism's evolutionary history, from artificial stressors, those not so experienced. Todd makes the distinction because he expects organisms to be more susceptible to the artificial stressors. Slobodkin makes the distinction because he wishes to point out that the novelty of an artificial stressor may prevent its perception by the organism. Without the sensory input that the environment has changed, an adapting response will probably not occur. If so, Slobodkin's point is a plausible reason behind Todd's expectation. It may very well be that organisms succumb to pollutants because pollutants are novel events that are not perceived.

Two warnings by Slobodkin and Rapoport (1974) concern us here. First, knowing the properties of the organism is not enough to permit prediction. This position is reminiscent of the systems philosopher's call to understand the behavior of an open system through characterizing its environment, and differs from Todd's which seeks a property or properties of organisms which allows prediction of their fate under stress. Second, one response alters the relationship of the animal to the environment and thus determines the subsequent course of events. As indicated above, the initial response is expected to be a behavioral change.

The above discussion now permits assessment of the possible fruitfulness of behavioral studies in predicting pollution consequences and hopefully gives some insight into how to proceed. (1) Because behavior is adaptive, one knows that a change in behavior has consequences for the organism's population biology. (2) From Slobodkin's theory one expects behavior changes to be the initial responses to stress by a pollutant and from Todd's work one expects complex behavior to be particularly vulnerable to disruption by pollutants. (3) Behavior is intimately tied to perception. Indeed, at the extreme, Powers (1973) suggests that behavior is control of perception. A failure to perceive novel environmental perturbances (Slobodkin and Rapoport, 1974) or a distorted perception of them (Atema et al, 1973) can be expected to influence the fate of the organism. (4) Ethology no less than nuclear physics suffers with Heisenberg's Uncertainty Principle. How and what the observer observes influences the outcome of the observation. Close attention to the conditions under which the experimental animals are held and observed is necessary for understanding the import of the observations.

Hopefully one begins to get a glitter that one's predictions should not be couched in terms of ppm of pollutant and disruption of 50% of the population but rather in terms of the patterns of behavior flowing from the organism's attempts to adapt given a particular strategy and set of boundary conditions.

B. NATURAL HISTORY

The yellow shore crab, Hemigrapsus oregonensis, with its congener, Hemigrapsus nudus, ranges the Pacific coast of North America from Alaska to the Gulf of California (Rathbun, 1918), and the two species often occur in the same intertidal areas (Hiatt, 1948; Low, 1970; Batie, 1974). H. oregonensis is smaller and more hirsute than H. nudus (Rathbun, 1918) and as an adult may reach 3.5 cm wide in the carapace but averages 1.5 cm wide (Batie, 1974).

Hemigrapsus oregonensis occurs in muddy substrates with rocks (Hiatt, 1948; Low, 1970), the banks of sloughs in tidal marshes (Hiatt, 1948),

and subtidally on oyster bars (Dimick et al, 1941) and in tidal channels (Kuris, 1971). In the marsh and rock-mud habitats H. nudus may also occur but usually at a higher tidal height (Hiatt, 1948; Batie, 1974). The abundance of the two Hemigrapsus species increases with increasing cover and their relative distribution is a function of the reducing potential of the substrate and predation (Low, 1970). H. oregonensis can live in mud with greater reducing potential than can H. nudus, which appears to displace H. oregonensis from cover in sandy substrates.

The reproductive season of Hemigrapsus oregonensis varies with latitude. In Puget Sound, Washington, egg deposition begins in mid-February and is completed by the end of April (Knudsen, 1964). Hatching follows from May to July. A second brood occurs in late summer with egg deposition in August and hatching finished by the end of September. For Yaquina Bay, Oregon, egg deposition occurs mainly from February to May with a peak in March and appears to follow more closely the single brood pattern of its congener, H. nudus, found in California by Boolootian et al (1959) than the Washington double-brood pattern (Batie, 1974). The Yaquina Bay crab population differs from both California and Washington populations by not being totally synchronized in reproduction as evidenced by the occurrence of brooding females in Yaquina Bay throughout the year (Batie, 1974).

The timing of egg deposition and some limited behavioral observations suggested to Knudsen (1964) that in Washington the period of copulation extended from the beginning of February to mid-April for the first brood and a second copulation period from May to mid-July was probably required for the second brood. In Yaquina Bay, Oregon, the presence of egg brooding females throughout the year indicated to Batie (1974) that copulation occurred throughout the year. During this present study copulation was observed among captive animals from Yaquina Bay from January into September and probably occurred throughout the rest of the year as well.

The occurrence of hybridization between Hemigrapsus oregonensis and H. nudus is still an open question. Dehnel (1960) stated that evidence existed for interbreeding between the two species and in British Columbia

a continuum of crabs with characters ranging from those of H. oregonensis to those of H. nudus could be found. Despite his stated intention, Dehnel evidently has not yet published the evidence (Kuris, 1971). In California, Kuris (1971) found no evidence of hybridization. Both Low (1970) and Batie (1974) made no mention of hybridization while Wright (1966) cited a personal communication from Phillip Symons that the two Hemigrapsus species interbreed in northern portions of their range. During specimen collection for this present study crabs with characters apparently intermediate between H. oregonensis and H. nudus were noted in the field. For example, crabs with the more rounded carapace of H. nudus had the hairiness or coloration of H. oregonensis. The evidence for hybridization between the two species remains circumstantial awaiting more rigorous studies.

While Hemigrapsus oregonensis has been generally considered a scavenger because it will consume dead animal tissue and other readily available organic matter (Hiatt, 1948), stomach analysis led Knudsen (1964) to believe that the crab was primarily an herbivore scraping off the micro-turf, the diatoms, desmids, and small growths of green algae found on rocks. Low's (1970) behavioral observations indicated that H. oregonensis may be more than an herbivore-scavenger. Broken mussels and barnacles were readily consumed by the crab which also took intact mussels and barnacles if small. Although the crab did not appear to stalk other animals, if an amphipod or isopod swam past, H. oregonensis did catch it and tear it up to consume it. Dimick et al (1941) believed H. oregonensis to be a major predator of oyster spat and young oysters. Stomach analysis done during this present study showed H. oregonensis from Yaquina Bay to consume sand, silt, and plant debris along with barnacles, mussels, isopods and macro-algae. In the marsh habitat, plant roots and sand predominated in the gut of H. oregonensis while in the rock-mud habitat plant debris and sand-silt predominated (Table 1).

For several species of birds and fish Hemigrapsus oregonensis is occasional prey. The crab has been found in the stomachs of the Staghorn Sculpin, Leptocottus armatus armatus (Jones, 1962), Pile Perch, Rhacochilus vacca (Wares, 1968), and Kelp Greenling, Hexagrammos

TABLE 1. Frequency of occurrence of various food items in stomachs of Hemigrapsus oregonensis collected from two different habitats.

| | Marsh Habitat N=13 | Rock-Mud Habitat N=17 |
|---------------|-----------------------|--------------------------|
| Macroalgae | 8% | 29% |
| Mussel | 0 | 7 |
| Barnacles | 0 | 7 |
| Isopod | 8 | 7 |
| Herring Eggs | 15 | 0 |
| Leaves | 0 | 88 |
| Plant Roots | 85 | 12 |
| Sand and Silt | 100 | 88 |

decagrammos (Low, 1970), as well as in the stomachs of several diving ducks (Low, 1970). In Yaquina Bay gulls, crows, and whimbrels were seen to capture and consume H. oregonensis at low tide while diving ducks preyed on crabs at high tide (R. D. Bayer, 1975, personal communication). Low (1970) found H. oregonensis to be more subject to predation than H. nudus, presumably because H. nudus was the more thigmotactic crab.

After placing individual Hemigrapsus oregonensis in tilt boxes under constant laboratory conditions, Batie (1974) found weak tidal and diurnal rhythms of locomotor activity in only half of the crabs tested. In those showing rhythmicity, the great activity occurred at high tide and was heightened by darkness. Williams (1969) found a seasonal variation in the rhythmicity of the New Zealand rock crab, Hemigrapsus edwardsi. The tidal rhythm with peak activity one or two hours before high tide was exhibited by H. edwardsi during the warmer months and faded in the winter when the animals in the field moved down the shore to the low water mark.

Various aspects of the behavior of Hemigrapsus oregonensis described by Hiatt (1948), Knudsen (1964), Wright (1966), Low (1970), and Symons (1964, 1970) are discussed in a following chapter on the ordinary behavior of the crab.

THE ORDINARY BEHAVIOR

One productive way to gain insight into the ecological meaning of behavior is to ask where and how individual crabs spend their time (Wiens, 1969; Wiens et al, 1970). The initial working hypothesis of this study was that an ecologically meaningful behavioral change induced by a pollutant is most likely to become evident as a shift in the activity budget of the crab. One may expect the crab to adapt to stress by doing only the most important things or by more frequently performing maintenance behaviors ordinarily found at low frequency, or perhaps by failing to perform some important activity.

Having decided that examining activity budgets for changes is the appropriate approach, the first step is to develop a behavioral repertoire, a listing and description of the various behaviors performed by the shore crab.

A. THE BEHAVIORAL REPERTOIRE

Materials and Methods

Hemigrapsus oregonensis was watched in the field and laboratory for some months in order to develop as complete a repertoire as possible. The repertoire was judged complete enough for practical use when behavior patterns that were novel to the observer became rare.

Manipulation of laboratory holding conditions influenced the frequency of certain behaviors and led to the realization that a replica of the intertidal zone was necessary for any reasonable activity budget to be forthcoming. Crabs held in round chambers were more active, irritable, and defecated more than those in rectangular chambers. Even under crude, unreliable tidal regimes social behaviors such as displays were more evident and in tune with the tidal regime.

The final development of the repertoire and observations for the activity budget under various conditions were made in two banks of four chambers, each of which was designed to simulate the crab's mud-rock

habitat (Figure 1). In each bank of habitat replicas a tidal period of 12.4 hours was maintained with a tide generator modified after DeBlok (1964), Evans (1964), and Underwood (1972). Underwood (1972) described in detail the construction and use of tide models which give a sinusoidal change in water level through rotation of some component of the device. Each 40-liter replica in this study was constructed of glass, silicone rubber, and fibreglassed plywood and received a constant flow of seawater drawn from the running seawater system of the OSU Marine Science Center on Yaquina Bay, Oregon. A hose from a PVC-drain at the replica bottom ran to a rotating arm driven by a one-RPH synchronous motor with a 12.4:1 gear train. The tide generator and replicas were oriented to one another to give a four hour period of exposure to air in the replicas and a water height of 20 cm at high tide. The tides were set to match those at Coquille Point, Newport, Oregon, the site where the crabs used in this study were collected. The tide generator only required a weekly resetting of about 5 min to approximate the crab's natural tidal regime. Appendix I gives the water heights, temperature and salinity at the various stages of the tidal cycle.

The habitat replicas were lighted by daylight-type fluorescent light with a spectrum approximating noon sky plus sunlight and by incandescent bulbs behind Kodak No. 2 (dark red) safelight filters. The daylight lights were placed on a timer in order to give a natural photoperiod which was maintained throughout the study while the dark red lights burnt continuously and gave enough light for night observation. Most crustaceans including grapsoid crabs appear to have a peak in spectral sensitivity near 500 nm and have negligible ability to see beyond 600 nm (red) (Briggs, 1961; Fernandez, 1973; Goldsmith and Fernandez, 1968; Waterman, 1961). As a No. 2 safelight passes no light below 638 nm, illumination by red safelight alone should be the same as night to the crabs.

Within the habitat replica 2 kg of dried fine sand along with crushed oyster shell were placed on the bottom to an approximate depth of 2 cm. Two rocks with barnacles and four whole oyster shells provided

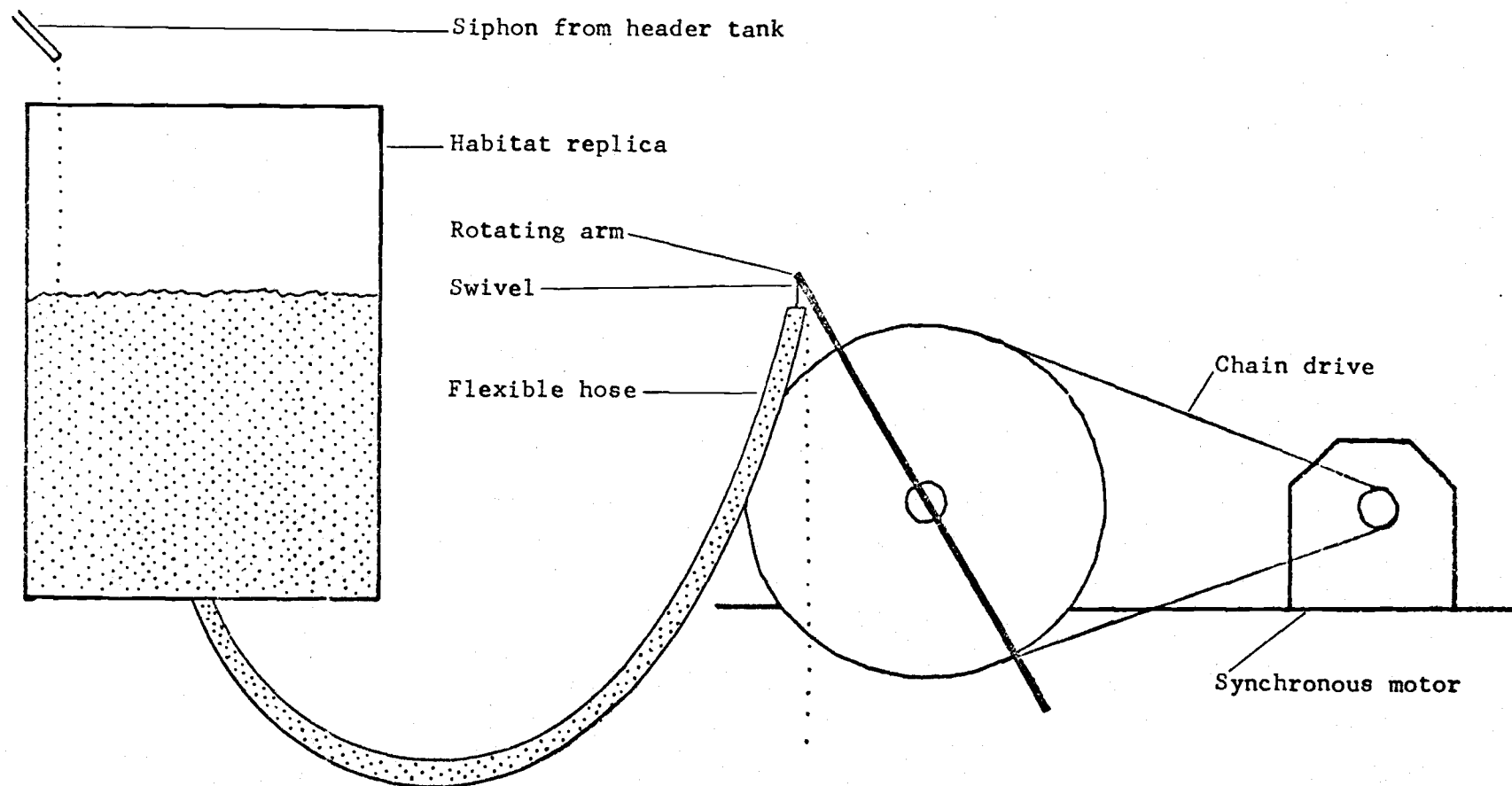


Figure 1. A schematic diagram of the tide-generator.

shelter. A growth of microalgae was allowed on the rocks, shells and portions of the tank walls.

Three crabs of each sex were held in each replica and were fed commercial shrimp pellets, small mussels, and isopods. The amounts and times of addition varied and are described later for each experiment.

Results and Discussion

Table 2 gives 62 behavioral units identified as the behavioral repertoire of the shore crab Hemigrapsus oregonensis in regard to shelter use, posture and activity. The repertoire is only a catalog of signposts, an abstraction of landmarks from the continuous stream of the crab's behavior. To understand the countryside one must take the journey. A few hours simply watching the crabs will give one the content of most of the behavioral units. Even the relatively detailed descriptions of behavior like those of Wright (1966) are only the beginning.

By and large this study confirmed the descriptions given by Wright (1966, 1968) and Symons (1964, 1970) and gave a more complete insight into the kinds of behavior of which Hemigrapsus oregonensis was capable. Where observations of this study confirmed Wright's and Symons's description, their nomenclature is retained or only slightly modified. In the following discussion of the behavioral units only differences in observations from or additional details to Wright and Symons are mentioned.

Within the habitat replicas, crabs used the rocks and whole oyster shells in several ways. They sheltered themselves under or perched upon the rocks or shells. While unsheltered, a crab usually was backed up to a rock or the replica wall. After digging, a crab was buried in the sand with only its eyestalks protruding.

The four postures, huddled, low, high and display, described by Wright (1966) constituted a continuum from huddled where the crab was close to the substrate, and had its limbs drawn close to its body, to display where the limbs were fully extended and the crab was high above the substrate. Observation of the angle between the carapace and the

TABLE 2. The behavioral repertoire of Hemigrapsus oregonensis including behavioral units observed by others.

Shelter Use

1. Unsheltered
2. Sheltered
3. Perched
4. Buried

Posture

- | | |
|------------|--------------|
| 5. Mating | |
| 6. Display | Wright, 1966 |
| 7. High | Wright, 1966 |
| 8. Low | Wright, 1966 |
| 9. Huddled | Wright, 1966 |

Activities

Locomotion

- | | |
|--------------|----------------------------|
| 10. Standing | |
| 11. Walking | Symons, 1964; Wright, 1966 |
| 12. Running | |
| 13. Climbing | |
| 14. Swimming | Hartnoll, 1971 |
| 15. Chasing | |
| 16. Fleeing | |

Social Behavior

- | | |
|---|--------------|
| 17. High Intensity Lateral Merus Displaying | Wright, 1966 |
| 18. Mid Intensity Lateral Merus Displaying | Wright, 1966 |
| 19. Low Intensity Lateral Merus Displaying | Wright, 1966 |
| 20. Claw Shuddering | Symons, 1970 |
| 21. <u>Hemigrapsus</u> Displaying | Wright, 1966 |
| 22. Walking Leg Contacting | Wright, 1966 |
| 23. Piling Up | Low, 1970 |
| 24. Lunging | |
| 25. Striking | Wright, 1966 |
| 26. Pinching | Wright, 1966 |
| 27. Pushing | Wright, 1966 |

Pre-Feeding

- | | |
|-----------------------------|----------------------------|
| 28. Claw Probing | Symons, 1964; Wright, 1966 |
| 29. Dactyl Searching | Wright, 1966 |
| 30. Maxilliped Sweeping Out | |

TABLE 2. Continued.

Activities Continued

Feeding

- | | |
|-----------------------------------|----------------------------|
| 31. Maxilliped Sweeping Substrate | |
| 32. Claw Feeding | Symons, 1964; Wright, 1966 |
| 33. Scraping Feeding | Wright, 1966 |
| 34. Claw Tearing | Symons, 1964; Wright, 1966 |
| 35. Spitting | |

Environmental Manipulation

- | | |
|--------------------|---------------------------------------|
| 36. Digging | Symons, 1964 |
| 37. Claw Shoveling | Symons, 1964 |
| 38. Bulldozing | |
| 39. Sandscraping | |
| 40. Lifting | |
| 41. Ice Tonging | Low, 1970; Symons, 1964; Wright, 1966 |

Mating

- | | |
|----------------|---------------|
| 42. Grabbing | Wright, 1966 |
| 43. Embracing | Knudsen, 1964 |
| 44. Struggling | Knudsen, 1964 |
| 45. Copulating | Knudsen, 1964 |

Body Maintenance

- | | |
|----------------------------|-------------------------|
| 46. Eye Bobbing | Naughton, 1969 |
| 47. Claw Picking | Wright, 1966 |
| 48. Dactyl Picking | Wright, 1966 |
| 49. Claw Rubbing | Naughton, 1969 |
| 50. Leg Rubbing | Wright, 1966 |
| 51. Claw Sweeping | |
| 52. Eye Sweeping | Wright, 1966 |
| 53. Antennule Sweeping | |
| 54. Mouthpart Mashing | |
| 55. Abdomen Flapping | |
| 56. Egg Ventilating | |
| 57. Egg Grooming | Wright, 1966 |
| 58. Foam Bathing | Wright, 1966 |
| 59. Antennule Flicking | |
| 60. Scaphognathite Beating | Burrows & Willows, 1969 |
| 61. Molting | |
| 62. Defecating | |

substrate was helpful in distinguishing the postures. In huddled posture the carapace was parallel to and its ventral side completely rested on the substrate. The carapace made a 45° angle with the substrate during low posture and only the posterior portion of the ventrum contacted the sand. A crab in high posture had its carapace parallel or slightly angled to but not in contact with the substrate. In display posture the carapace was usually more angled and considerably higher from the sand than in high posture. Male crabs exhibited the mating posture when the limbs were fully extended and the carapace was high off the substrate. The abdomen was held down and sometimes waved. Only in the mating posture was the anterior portion of the carapace lower than the posterior. The chelae were held down usually touching the substrate. The mating stance of the male Pachygrapsus crassipes upon presentation of pheromone-laden water described by Takahashi (1974) was almost identical to the mating posture seen in Hemigrapsus oregonensis.

While Wright (1966) believed that grapsoid crabs only gave displays while in display posture, Hemigrapsus oregonensis in this study gave displays from all postures except perhaps huddled. Crabs did present the chelae in displays without extending legs or lifting the ventrum from the substrate. Displays made while the crab was just inside or outside shelter were often given from a low posture.

The contents of the locomotor patterns listed in Table 2 are straightforward. If the crab was not moving, he was standing in one of the five postures described above. Although Wright (1966) found that walking occurs mainly while in high position, this study found walking in all postures. In low and huddled postures walking was rare and part or all of the crab's ventrum was dragged along the substrate. Walking in the lowest postures usually occurred in shallow water just before the tide receded.

Although the crabs can walk in any direction, they usually walked sideways, occasionally forwards, rarely backwards. Running occurred when a crab moved rapidly sideways and the walking legs on one or both sides left the substrate. Fleeing occurred usually following a lunge or strike from another crab. After directing a lunge or strike at

another, the lunging crab may have chased the other. Both fleeing and chasing had quick onsets and were of short duration, less than 5 sec. Hemigrapsus oregonensis proved an agile climber and climbed the corners of the habitat replicas gaining purchase with its dactyls on the silicone rubber sealant.

Hartnoll (1971) found the Grapsidae capable of swimming but with few species having specific morphological modification for swimming. Pachygrapsus spp. can be observed feebly swimming, but there are no recorded observations in Hemigrapsus. The only swimming motions seen in this study occurred when a crab lost its purchase on a rock or tank wall and rapidly flailed its walking legs to slow its rate of descent.

The lateral merus displays described in detail by Wright (1966, 1968) are common to the grapsoid crabs and constitute a continuum rather than three distinct displays. Often only the chelae nearest the other crab was used in a lateral merus display. The Hemigrapsus display, waving one or both chelae in a circle, Wright found to be unique to the genus. Another display described only for H. oregonensis is claw shuddering which Symons (1970) observed only males performing. Both claw shuddering and Hemigrapsus displaying were dramatic and distinct from one another and varied in frequency between the sexes. In accord with Symons (1970) female shore crabs never did claw shuddering during this study. Although the Hemigrapsus display was done by males, during this study this display was characteristically given by females both to other females and males. The walking leg contact mentioned by Low (1970) and described in good detail by Wright (1966) occurred between two individuals concurrently with and/or just prior to displaying or other social behaviors.

The piling up or aggregation of several individuals can be observed in the field and laboratory for both Hemigrapsus species. Low (1970) found the aggregation of several crabs into a pile occurred when conditions were crowded and/or cover was in short supply. Under such stressing conditions agonistic behavior was not observed. Pachygrapsus crassipes aggregated in large numbers in rocky crevices when exposed during daylight but in tide pools no aggregation occurred and aggressive

interactions limited one crab to a crevice (Bovbjerg, 1960). In Yaquina Bay during both day and night low tides aggregations of up to 20 individuals of Hemigrapsus nudus occurred under rocks where there was considerable vertical distance between the substrate and the rock. In the laboratory Hemigrapsus oregonensis formed piles in tank corners when no shelter or sand was available. If in addition the crabs were exposed to air, the piles of H. oregonensis were stable with little activity. Conditions in the habitat replicas were apparently equitable enough that piling up did not occur.

Wright (1966) viewed fighting as a combination of striking and pinching with the chelae and occasionally pushing against one another with the faces of the chelae. Lunging was not mentioned by Wright and differed from a strike in that lunging involved the whole body being thrown toward another crab. Usually in lunging both chelae were held out and open, and a strike may have ended a lunge. Fights began and ended in seconds, and events in fights moved rapidly but were not highly structured.

The prefeeding and feeding behaviors were discussed in Low (1970), Symons (1964) and Wright (1966) and as indicated by Wright were similar to those described by Hiatt (1948) for Pachygrapsus crassipes. One mode of feeding, sweeping the substrate with the maxillipeds, Wright found only performed by crabs that had lost the chelae. However almost all the crabs observed in this study routinely used maxilliped-sweeping to bring sand particles from the substrate to the mouth. The other three feeding patterns concern how the chelae were used to manipulate the food. In claw feeding sand or other fine material was brought to the mouth by one of the chelae or both chelae alternately. The crab in scraping feeding used the chelae tips to scrape the algal growth off rocks, shells, and other surfaces. Claw tearing occurred when a crab had large food, such as a captured isopod, and consisted of the chelae singly or alternately tearing off portions of tissue and passing them to the mouth.

A bout of feeding usually had a fairly consistent sequence. Initially the crab moved about with dactyls and/or chelae probing the substrate and the maxillipeds sweeping out from the mouth but not touching the

substrate. After a time the crab either stopped such prefeeding activity or began to feed by passing sand with the chelae to the mouth and/or sweeping the substrate with maxillipeds. During active feeding claw feeding and claw probing alternated with one another in such rapid succession as to have appeared concurrent. While claw feeding and probing alternated, maxilliped sweeping of the substrate continued. Spitting occurred either amidst or following feeding movements. The scaphognathite was beaten to establish a water current flowing from the mouth and carrying with it a stream of debris, pieces of shell and other presumably inedible material. Spitting was difficult to discern unless the debris was highly visible, and its occurrence appeared to be a function of the size and taste of the debris.

Hemigrapsus oregonensis was quite capable of manipulating its environment with the consequence of better shelter for itself. Digging was done in the sand or mud using the walking legs and was often accompanied by claw shoveling (Symons, 1964; Wright, 1966). In claw shoveling the whole body stood still and the chelae pushed the sand forward and to the side. Bulldozing was done with the faces of the chelae held before the crab which then moved its whole body forward. Both sand and rocks were bulldozed. The pushing behavior used in fighting was similar in its movements to bulldozing. Sand scraping was done to remove sand from a burrow built under a rock or shell. The crab moved sideways with the trailing claw and walking legs forming a basket with which the sand was caught and dragged from the burrow. The hairiness of the walking legs of H. oregonensis probably increased the sand-retaining efficiency of the legs. Sand scraping was similar to mud-burrow excavation behavior described for the crab Goneplax rhomboides by Atkinson (1974) and Rice and Chapman (1971). H. oregonensis readily lifted surprisingly large rocks and other objects. After moving or burrowing under the rock, the crab extended its walking legs and the chelipeds. As its carapace moved off the substrate due to the extension of its limbs, the crab lifted the rock and often shifted its position. "Ice tonging" was used by Wright (1966) to refer to a habit

of both Hemigrapsus species also recognized by Low (1970) and Symons (1964). The crabs habitually held the fourth walking legs off the substrate and in contact with a vertical or overhanging surface. The fourth walking legs also were used to maintain a hold within a refuge.

The mating behavior of Hemigrapsus oregonensis as described by Knudsen (1964) differed only slightly from that of Hemigrapsus nudus (Knudsen, 1964), Hemigrapsus crenulatus (Yaldwyn, 1966) and Pachygrapsus crassipes (Bovbjerg, 1960). Copulation occurred in the hard shell condition for these four species. With no obvious courtship ritual, the male grabbed the female with a rapid movement of the walking legs and chelae which Wright (1966) believed derived from a feeding movement (dactyl search). After grabbing the female, the male positioned her in a ventrum to ventrum embrace then rolled over on the dorsal side of its carapace. Thus during copulation the female was superior to the male. Although Yaldwyn and Knudsen stated that they saw no copulation with ovigerous females, several instances of copulation with ovigerous females were observed during this study.

The body maintenance behaviors included mainly cleaning movements along with other behaviors associated with basic functions such as respiration. Cleaning behaviors did occur amidst feeding bouts but usually followed cessation of a long series of feeding bouts, and several of the cleaning behaviors were often performed simultaneously. Eye-bobbing consisted of moving one or both eyestalks into and back out of the orbital socket and most often occurred at low tide while buried. Claw picking and dactyl picking consisted of scraping, plucking and picking motions which served to clean the crab's carapace and limbs.

Claw rubbing was the passing of the inside of the wrist and arm of the cheliped over the suborbital and pterygostomian regions of the carapace. Sometimes the movement was extended enough to pass the sponge-like mass of the setae on the inside of the palm of the claw over the eyestalk. The movement was reminiscent of a small child rubbing his cheek with the back of his wrist. Claw rubbing and the Hemigrapsus display superficially resembled each other but were distinct. In Hemigrapsus displaying the crab pointed the chelae, which were open,

outward forming a 90° angle between the claw's hand and the anterior of the carapace. During claw rubbing the chelae were closed and pointed down and across the carapace front. Claw rubbing was prevalent during air exposure and may have served to pass water to the eyestalks from the Milne-Edwards openings at the base of the chelipeds (Naughton, 1969).

Cleaning was also accomplished by the mouthparts. Sweeping movements by the palps of the third maxillipeds were used to clean the chelae, eyes, and antennules and antennae resulting in the behavioral units claw sweeping, eye sweeping, antennule sweeping. Mouthpart mashing was accompanied by claw picking and occurred when the endognaths of the third or outer maxillipeds were repeatedly separated and brought together.

Both males and females without eggs did flap or wave the abdomen especially after the sternum and abdomen had been cleaned by claw picking but egg grooming and egg ventilation were, of course, performed only by ovigerous females. The eggs were carried on the abdomen which was flapped to ventilate them. Egg grooming accompanied, preceded, or followed egg ventilation and was performed by the chelae, which picked through the eggs and brought eggs to the mouth. The eggs were discarded and not consumed (Wright, 1966). Hiatt (1948) described similar egg grooming behavior in Pachygrapsus crassipes.

Foam bathing, which occurred in all the Grapsidae studied by Wright (1966), has had suggested for it other functions besides cleaning. Wright believed the spreading of the foam over the body by the chelae spread a chemical over the body that acted as a signal during walking leg contact. Characterization of the sex pheromone of Pachygrapsus crassipes led Takahashi (1974) to believe that the chemotactile signal he found releasing courtship behavior was a pheromone spread over the crab's body during foam bathing. Because foam bathing was done by both sexes, its function was probably not limited to just transmission of a sex pheromone by the female. Altevogt (1968) believed foam bathing, Schaumbaden, was definitely not a cleaning function but most probably a temperature regulatory mechanism during air exposure because it was seen in the field during periods of strong isolation, intense dessication,

and/or strong increase in body temperature.

Both antennule flicking and scaphognathite beating occurred almost constantly in submerged crabs. Rhythmical scaphognathite beating served to bring about water movement over the gills, and was described by Burrows and Willows (1969) for Hemigrapsus nudus.

Appendix II gives photographs of some of the behavioral units. Still photographs, of course, do not capture the movement but only the positioning of the body and its appendages. Also, little is seen of the context of the act that is so important to discerning its meaning and subsequently its behavioral category.

B. THE ACTIVITY BUDGET

Materials and Methods

The behavioral repertoire defined the activities to be timed for the budgets. The amount of time individual crabs marked with iridescent nail polish spent in 56 behavioral units was measured using an electronic metronome, modified after Wiens et al (1970), that gave an audible tone every 5 sec. The observer watched a single crab and upon hearing a tone recorded letter codes for the behavioral units seen during the 5 sec interval. Summing the number of letter codes in a given observational period gave the time spent in the various behaviors.

In accord with Enright's (1970) insight that knowledge of an organism's rhythmicity should lead to more appropriate designs for behavioral observations, the schedule for observing crabs was based on the lunar day (24.8 hours). During each 62 min lunar hour the six crabs in a habitat replica were observed in a random order, and each crab's activities were timed for 7 min. These hourly observation periods began exactly at low tide and continued for two full tidal cycles. The order in which the replicas were observed was also randomized, but the schedule was such that at the end of 8 lunar days each crab in every replica had been observed at every hour of the lunar day. Dividing the number of 5 sec intervals spent in each behavioral unit by the total number of

intervals that a crab was observed over the 8 lunar day sampling period estimated the proportion of the lunar day the crab spent in each behavior. The observations on the 56 behavioral units were later grouped into 20 higher-level categories of shelter use, posture, and activities as indicated in Table 3. A listing of the time spent by the crabs in each of these categories constituted the activity budget.

There were three crabs of each sex in each of the eight habitat replicas. Because the replica was the experimental unit in the statistical sense (Cox, 1958), the means for the replicas, not the measurements on individual crabs, appeared in the budgets and formed the basic measurement for statistical analysis.

All crabs observed under both ordinary and exposed conditions were collected at low tide at Coquille Point, Newport, Oregon, and were held 2 weeks in the replicas before observations commenced. During the 8 lunar day observation period, a crab that died was replaced within one tidal cycle by another of the same sex and similar size so that social density within each habitat replica was maintained.

At low tide following each lunar day's observations, 1 g of crushed commercial shrimp pellets was sprinkled over the sand in each replica.

The activity budget for ordinary conditions was compiled from 8 lunar days of observations when no PCBs were present in any of the eight habitat replicas. The procedures described above for obtaining an activity budget were also followed, except where noted, in the experiments where some replicas received PCBs contaminated sand.

Results and Discussion

Under ordinary conditions the activity budgets for male and female crabs differed as shown in Figure 2 and Appendices III and IV. Male crabs were unsheltered over three quarters of the lunar day while females spent less than one half the day unsheltered. Also males displayed and fought more than females even though the sexes did not differ in the amount of walking leg contact.

Female crabs spent about twice as much time engaging in prefeeding

TABLE 3. Behavioral repertoire of Hemigrapsus oregonensis with the 20 activities categories into which the behavioral units were grouped. The abbreviation code is used in subsequent tables and appendices.

| BEHAVIORAL UNIT | ACTIVITY CATEGORY | ABBREVIATION CODE |
|--------------------|-------------------|-------------------|
| <u>Shelter Use</u> | | |
| 1 Unsheltered | 1 Unsheltered | UNSH |
| 2 Sheltered | 2 Sheltered | SHEL |
| 3 Perched | 3 Perched | PERC |
| 4 Buried | 4 Buried | BURD |
| <u>Posture</u> | | |
| 5 Mating | 5 Mating | MATP |
| 6 Display | 6 High | HIGH |
| 7 High | 6 High | HIGH |
| 8 Low | 7 Low | LOWP |
| 9 Huddled | 8 Huddled | HUDP |
| <u>Locomotion</u> | | |
| 10 Standing | 9 Standing | STAN |
| 11 Walking | 10 Walking | WALK |
| 12 Climbing | 11 Climbing | CLIM |
| 13 Running | 12 Fast Movement | FAST |
| 14 Fleeing | 12 Fast Movement | FAST |
| 15 Chasing | 12 Fast Movement | FAST |
| 16 Swimming | * | |

TABLE 3. Continued

| BEHAVIORAL UNIT | ACTIVITY CATEGORY | ABBREVIATION CODE |
|--|---------------------------|-------------------|
| <u>Social Behavior</u> | | |
| 17 High Intensity Lateral Merus Displaying | 13 Displaying | DISP |
| 18 Mid Intensity Lateral Merus Displaying | 13 Displaying | DISP |
| 19 Low Intensity Lateral Merus Displaying | 13 Displaying | DISP |
| 20 Claw Shuddering | 13 Displaying | DISP |
| 21 Hemigrapsus Displaying | 13 Displaying | DISP |
| 22 Walking Leg Contacting | 14 Walking Leg Contacting | WLCN |
| 23 Piling Up | * | |
| 24 Lunging | 15 Fighting | FIGH |
| 25 Striking | 15 Fighting | FIGH |
| 26 Pinching | 15 Fighting | FIGH |
| 27 Pushing | 15 Fighting | FIGH |
| <u>Prefeeding</u> | | |
| 28 Claw Probing | 16 Prefeeding | PREF |
| 29 Dactyl Searching | 16 Prefeeding | PREF |
| 30 Maxilliped Sweeping Out | 16 Prefeeding | PREF |
| <u>Feeding</u> | | |
| 31 Maxilliped Sweeping Substrate | 17 Feeding | FEED |
| 32 Claw Feeding | 17 Feeding | FEED |
| 33 Scraping Feeding | 17 Feeding | FEED |
| 34 Claw Tearing | 17 Feeding | FEED |
| 35 Spitting | * | |

TABLE 3. Continued

| BEHAVIORAL UNIT | ACTIVITY CATEGORY | ABBREVIATION CODE |
|-----------------------------------|-------------------|-------------------|
| <u>Environmental Manipulation</u> | | |
| 36 Digging | 18 Digging | DIG |
| 37 Claw Shovelling | 18 Digging | DIG |
| 38 Bulldozing | 18 Digging | DIG |
| 39 Sand Scraping | 18 Digging | DIG |
| 40 Lifting | 18 Digging | DIG |
| 41 Ice Tonging | * | |
| <u>Sexual Behavior</u> | | |
| 42 Grabbing | 19 Sex | SEX |
| 43 Embracing | 19 Sex | SEX |
| 44 Struggling | 19 Sex | SEX |
| 45 Copulating | 19 Sex | SEX |
| <u>Body Maintenance</u> | | |
| 46 Eye Bobbing | 20 Cleaning | CLEN |
| 47 Claw Picking | 20 Cleaning | CLEN |
| 48 Dactyl Picking | 20 Cleaning | CLEN |
| 49 Claw Rubbing | 20 Cleaning | CLEN |
| 50 Leg Rubbing | 20 Cleaning | CLEN |
| 51 Claw Sweeping | 20 Cleaning | CLEN |
| 52 Eye Sweeping | 20 Cleaning | CLEN |

TABLE 3. Continued

| BEHAVIORAL UNIT | ACTIVITY CATEGORY | ABBREVIATION CODE |
|-----------------------------------|-------------------|-------------------|
| <u>Body Maintenance</u> Continued | | |
| 53 Antennule Sweeping | 20 Cleaning | CLEN |
| 54 Mouthpart Mashing | 20 Cleaning | CLEN |
| 55 Abdomen Flapping | 20 Cleaning | CLEN |
| 56 Egg Ventilating | 20 Cleaning | CLEN |
| 57 Egg Grooming | 20 Cleaning | CLEN |
| 58 Foam Bathing | 20 Cleaning | CLEN |
| 59 Antennule Flicking | * | |
| 60 Scaphognathite Beating | * | |
| 61 Molting | * | |
| 62 Defecating | * | |

* These behavioral units were identified for this repertoire but were not used in the construction of the activities budgets.

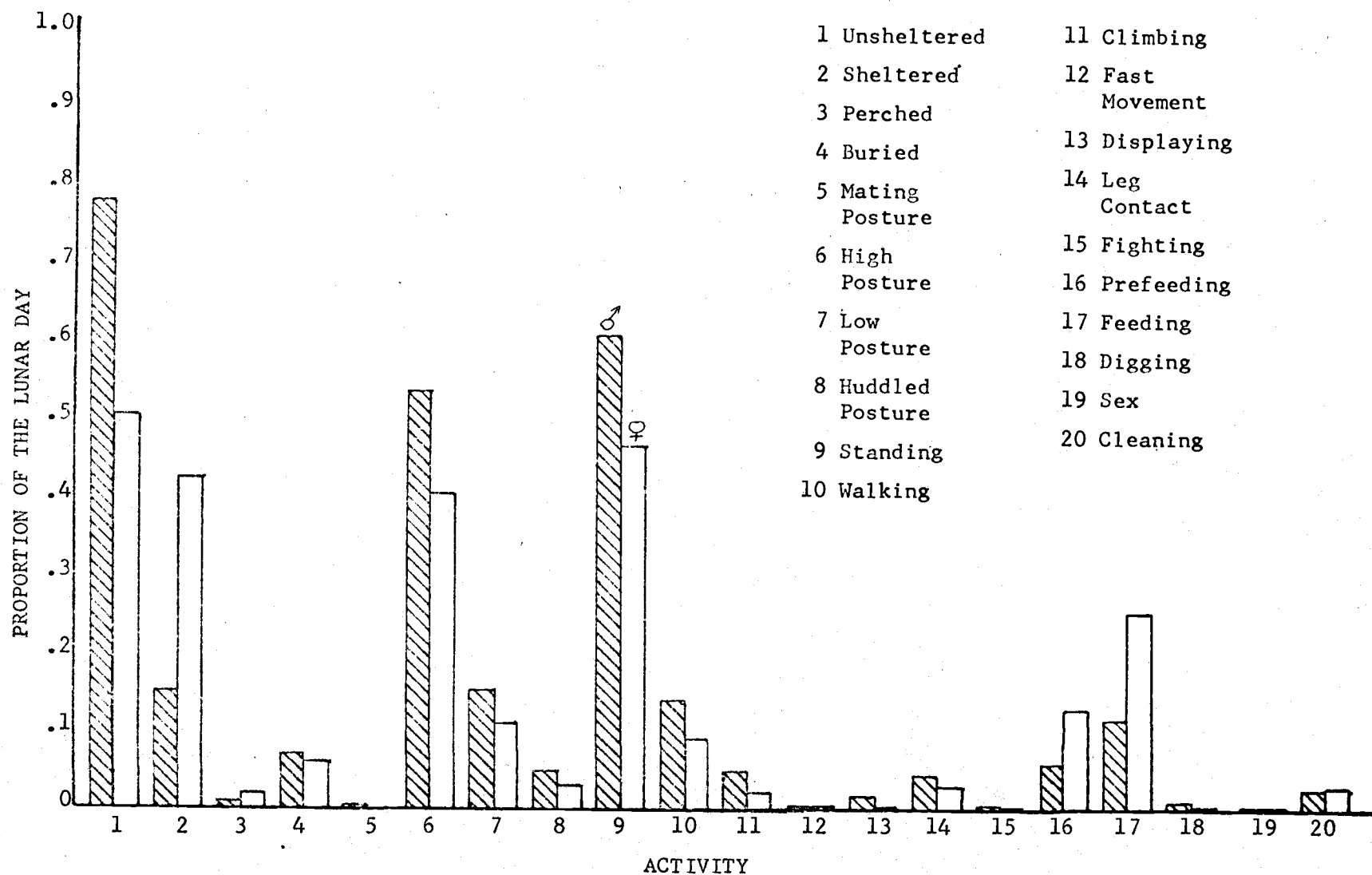


Figure 2. Activity budgets of male and female Hemigrapsus oregonensis under ordinary conditions.

and feeding than did males. Valiela et al (1974) found a similar variation in feeding time in Uca and ascribed it to the male crab's having a disproportionally larger claw than the female. A larger claw gathers more food per unit effort and given similar metabolic demands for both sexes the males' greater food gathering efficiency allows the same metabolic demands to be met with less time engaged in feeding. Because Hemigrapsus oregonensis males also had disproportionally larger claws than females, it is plausible that a greater efficiency allowed H. oregonensis males to meet their food requirements in less time than could females.

In most activities the males were less variable than the females as evidenced by the coefficients of variation in Appendices III and IV. Only in sheltered, buried, and mating posture were the males more variable, and the variability in both feeding and prefeeding for both sexes was about the same.

The size of a crab in relation to that of others within the same habitat influenced its behavior due to the development of a dominance hierarchy based on size. The clearest consequence of the hierarchy was that the larger males generally spent more time unsheltered than did the smaller males (Table 4). The hierarchy was not as evident among the females as among the males. Another consequence of the hierarchy was that the variability of behavior among individual crabs within a replica was greater than the variability among replicas.

Dominance hierarchies based on size have been found in other crustaceans. Cobb and Tamm (1975) found that larger lobsters, Homarus americanus, dominated smaller ones and molted before the subordinates. Lowe (1956) found that crawfish, Cambarellus shufeldtii, established dominance hierarchies of four ranks in the laboratory with larger individuals dominant over smaller ones. Larger groups of crawfish also established dominance orders but the lower ranks were often unclear. Loss of a claw influenced rank with crawfish. The dominant crawfish spent more time actively moving in the open and readily displaced lower ranked crawfish. While Table 4 indicates that the larger Hemigrapsus oregonensis also spent most of their time in the open, this study does

TABLE 4. The proportion of the lunar day male and female Hemigrapsus oregonensis spent unsheltered.

| <u>Males</u> | | | <u>Females</u> | | |
|--------------------------------|-----------------|----------------|--------------------------------|-----------------|----------------|
| Proportion of time unsheltered | | Carapace width | Proportion of time unsheltered | | Carapace width |
| Individual | Replica Average | (mm) | Individual | Replica Average | (mm) |
| .885 | | 28.4 | .739 | | 25.5 |
| .870 | .869 | 24.0 | .577 | .589 | 21.2 |
| .849 | | 25.1 | .451 | | 21.1 |
| 1.000 | | 28.7 | .654 | | 21.5*** |
| .629 | .739 | 24.4* | .458 | .491 | 23.9 |
| .589 | | 23.6 | .360 | | 19.1 |
| .958 | | 30.5 | .662 | | 24.1 |
| .907 | .829 | 24.1 | .473 | .532 | 20.5 |
| .623 | | 24.4 | .461 | | 20.6 |
| .998 | | 30.0 | .479 | | 20.5 |
| .875 | .892 | 24.7 | .462 | .407 | 22.0 |
| .803 | | 24.6 | .281 | | 21.5 |
| .868 | | 29.5 | .476 | | 19.5 |
| .642 | .700 | 24.5 | .326 | .371 | 24.5 |
| .591 | | 26.0 | .310 | | 21.4 |
| .753 | | 23.6 | .912 | | 23.5 |
| .745 | .708 | 25.5 | .626 | .623 | 20.5 |
| .626 | | 28.5** | .330 | | 21.4*** |
| .916 | | 25.5 | .796 | | 23.0 |
| .756 | .774 | 26.0 | .638 | .642 | 20.1 |
| .649 | | 24.6 | .494 | | 22.5 |
| .766 | | 24.2 | .540 | | 20.0 |
| .688 | .680 | 26.8 | .405 | .357 | 21.5 |
| .606 | | 24.2** | .127 | | 21.5 |
| Mean | .774 | 25.9 | .502 | .502 | 21.7 |
| STD DEV | .136 | 2.2 | .178 | .113 | 1.6 |

* Crab lost both claws.

** Crab lost one claw.

*** Female crab became ovigerous

not address the question of dominant crabs displacing subordinates from shelter as no systematic win/loss records were kept on each crab. Another failing is that throughout this study only crabs above 5 g were used so that there would be adequate tissue amount for the chemical analysis of PCBs content. This restriction to crabs in the upper size range of H. oregonensis probably influenced the development of the hierarchy. The hierarchy appeared clearer in replicas where the crabs differed more in carapace width.

Male crabs not only spent a greater part of their time displaying, but also gave different kinds of displays (Figure 3). Both sexes gave lateral merus displays of mid and low intensity most of the time, but in accord with Symons (1970) only the male gave the claw shuddering display, which was usually given in high intensity interactions. Females typically gave the Hemigrapsus display described by Wright (1966) in such intense situations, while males rarely did.

C. TIDAL PATTERNING OF ACTIVITIES

Because it became increasingly evident that certain activities predominated at certain tidal stages, the data from the hourly observations used to construct the activities budget were treated in a different manner in order to examine the occurrence of certain activities at points in the tidal cycle. For each lunar hour of the tidal cycle the number of 5 sec intervals spent in certain activities was summed over the 24 crabs of each sex in all replicas. Dividing the resulting total by the total number of intervals observed estimated the proportion of time spent in several activities at each hour of the tidal cycle. Separating day from night observations allowed investigation of any photoperiod effects on the occurrence of activities. Because the photoperiod was 16L:8D, there were twice as many daylight observations as dark ones.

For both sexes several activities were most prevalent at certain stages of the tide (Appendices V and VI). Shortly after submergence on a rising tide crabs emerged to begin feeding, walking, and climbing. There was usually a dip in feeding just before high tide, a rise at high

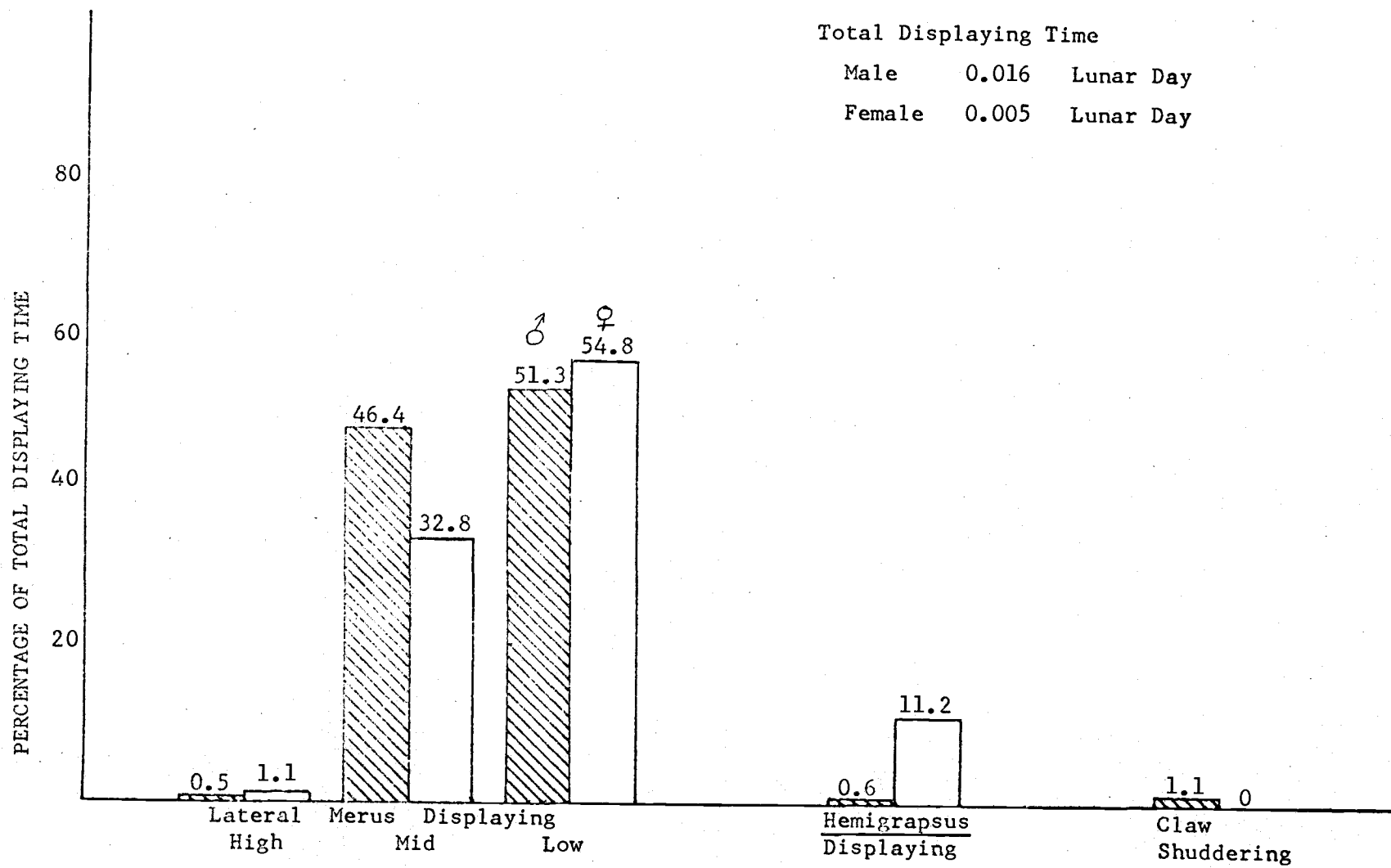


Figure 3. The distribution among various displays for Hemigrapsus oregonensis.

tide, and then a decline to little or no feeding when the tide fell to bring aerial exposure. While males spent about the same amount of time feeding at night as they did during the day, females spent more time feeding during the day than the night.

Although both sexes display more during the day than at night, the occurrence of displaying in the tidal cycle differed for the sexes. During the day males increased the time spent displaying with the rising tide, decreased displaying at high tide, increased after high tide, and decreased to little or no displaying during exposure at low tide. At night males exhibited about the same level of displaying until after high tide when with the falling tide a sharp rise was followed by a decline. Females showed a peak in displaying shortly after submergence both night and day and a second peak in the falling tide during the day but not at night.

The tidal pattern of digging activity was similar for both sexes. A small amount of digging occurred upon submergence, but most digging occurred just before the tide went out. Digging on the falling tide commenced earlier during the day than at night.

During daylight aerial exposure, the crabs buried or sheltered themselves. During nocturnal exposure crabs often stood quietly in the open with almost no movement as long as four hours. The crabs generally remained sheltered or quiescent until water flooded the replica, and then the cycle of activities began again.

Field observations indicated the general pattern of activities in nature had a timing similar to that seen in the laboratory replicas. Crabs in the intertidal were sheltered under rocks during daylight exposure but were observed in the open during nocturnal exposure. Shortly after submergence during the day crabs were seen walking from rock to rock but were not evident at high tide.

In comparing the results from the replicas to the field situation one should remember that the replicas were not as harsh as the intertidal. The replica lacked hot sun, dessicating wind, and predators. The milder conditions probably allowed the crabs to spend more time unsheltered than they would have in the natural situation. It is also

possible that the quality of the shelter within the replicas was less than that in the intertidal and contributed to the crab's being more unsheltered in replicas than in field.

If a decline in displaying at daytime high tides serves to lessen conspicuousness to predators, then the question is why there is not more displaying at night than during the day. Little is known of the color or low light vision of crabs, but it is plausible that visual signalling may be ineffectual at night because another animal and/or its display are not visible. Wright(1966) offered as evidence for the visual nature of grapsoid displays the coloring and shading of the anatomical structures, especially the chelae, that make the structures and displays highly conspicuous to the human eye. Another explanation of the reduced displaying at night is that if one assumes less need for shelter at night, it follows that there is less need for displaying over shelter. The smaller nocturnal amount of digging partly supports the assumption of lower nocturnal shelter needs.

If one is tempted to compare the activity patterns observed in the replicas with conventional rhythmicity studies, one should consider that tilting box actographs give a narrow view of an animal's behavior. Actographs indicate the level of locomotor activity from which can be discerned any predisposition of the animal to be active at certain times but do not indicate the character of such activity. In contrast the approach here gave the crab a periodically varying environment with which it could and did interact and allowed the kinds of activities that were rhythmic to become evident.

With the above discussion it is not surprising that the replica results differed from Batie's (1974) finding that Hemigrapsus oregonensis held in tilting boxes showed an activity peak at high tide. The replica results were more in accord with those of Williams (1969) for Hemigrapsus edwardsi which had its peak activity between 1.3 and 2.4 hours before high tide.

PCBs EXPOSURE AND THE BEHAVIOR
OF HEMIGRAPsus OREGONENSIS

Three experiments examined the behavior of Hemigrapsus oregonensis exposed to PCBs (Aroclor[®] 1260). The first two experiments intended to discern any shift in the activity budget with PCBs exposure. In Experiment I, from 18 to 30 June 1974, batches of sand contaminated with two levels of PCBs were added to the habitat replicas. Experiment II, from 22 August to 11 September 1974, had similar goals but an improved method of contaminating the sand. The results of the first experiments indicated that feeding behavior needed further study. In mid-September 1975, Experiment III offered the crabs a variety of food types in order to reveal any shift to foods other than PCBs-contaminated sand.

Placing the crabs on PCBs-contaminated sand was thought to be a natural exposure method because Hemigrapsus oregonensis readily ingests sand and accumulates PCBs from sediment as does Uca minax (Nimmo, 1971). Because PCBs occur in low concentrations in water but in high ones in sediment (Duke et al, 1970), exposure to contaminated sediment was considered to be the best approximation of the crab's real world exposure to PCBs.

Although these experiments were not primarily designed to investigate PCBs accumulation, whole body concentrations of PCBs were determined as a supplement.

A. EXPOSURE EXPERIMENTS - MATERIALS AND METHODS

The habitat replicas described under Ordinary Behavior were used in all three experiments. In Experiments I and II 48 marked crabs were held in 8 replicas while 24 marked crabs in 4 replicas constituted their own controls in the last experiment. Social density and hierarchies within a replica were preserved by replacing within one tidal cycle dead individuals with another of the same size and sex. Seven crabs were replaced in the first experiment; three in the second; none in the

third. Unsuccessful ecdysis and cannibalism following molting accounted for most deaths.

The procedures and conditions for constructing time budgets of activities described under Ordinary Behavior remained the same for the exposure experiments except that in Experiment III the time spent feeding on different food types was also measured, the various behavioral units of feeding were not combined, and the observation schedule was abbreviated. The crabs were allowed 2 weeks on clean sand to adjust to the tidal regime of the habitat replicas before imposition of experimental conditions. The amounts and PCBs concentration of sand added to the replicas appear in Table 5. In Experiments I and III on a daylight low tide after the adjustment period, the crabs were removed from the replicas just long enough to spread the contaminated or control sand over the clean sand already present. The observer during Experiment II was ignorant of the treatments given to the replicas. Two tidal cycles after sand introduction 8 lunar days of observation began on a schedule such that every crab in every replica was timed in its activities at every hour of the lunar day. The observational days were 12.4 hours apart in Experiment I and 37.2 hours apart in Experiment II. In Experiment III after the adjustment period 1.0 kg of acetone treated control sand replaced 1.0 kg of the clean sand already present in the 4 replicas. Observations began two tidal cycles later and continued for four days when 1.0 kg of sand was replaced by an equal amount of PCBs-contaminated sand. Another four days of observation followed the second sand replacement. During each of the four days of observation each replica was watched for one lunar hour of the four lunar hours between the time the replicas began to be flooded (low tide + 2 lunar hours) and the high tide (low tide + 6 lunar hours). The four hours before high tide were selected for observation because although they constitute a third of the tidal cycle, 60% of the feeding done by males and 56% of that done by females occurs during these hours under ordinary conditions. Also prefeeding and feeding behaviors are the most conspicuous activities in the time between submergence and high tide. The order of observing the replicas was randomized but at the end of four

TABLE 5. The PCBs concentrations and amounts of contaminated sand added to the habitat replicas for the exposure experiments.

PCBs concentrations (ppm) in sand of the replicas

| Replicas | First Experiment | | | | |
|----------|------------------|----------------------|-----------------|-----------------|--------------|
| | A Predicted | B Before Addition | C At 17 Days | D At 31 Days | E Average |
| 1 | 0 | .0005 | .032 | .002 | .013 |
| 2 | 400 | 597 | 506 | 173 | 425 |
| 3 | 200 | 3.9 | 27 | 104 | 45 |
| 4 | 800 | 256 | 41 | 127 | 141 |
| 5 | 400 | 363 | 209 | 53 | 208 |
| 6 | 200 | - | 1.0 | 30 | 15 |
| 7 | 800 | 132 | 626 | 27 | 262 |
| 8 | 0 | .028 | .022 | .032 | .027 |

Amount of clean sand
initially in replica

1.0 kg

Amount added or replaced

1.0 kg added

Size of replaced batches

1.0 kg

Sorption efficiency

40 ⁺ 36%
- 36%

TABLE 5. Continued

PCBs concentrations (ppm) in sand of the replicas

| Replicas | Second Experiment | | | Third Experiment | | |
|---|-------------------|-----------------|------------|------------------|-----------------|-----------|
| | F | G | H | I | J | K |
| | Predicted | Before Addition | At 23 Days | Predicted | Before Addition | At 4 Days |
| 1 | 0 | .002 | .001 | | | |
| 2 | 0 | .002 | .002 | | | |
| 3 | 800 | 553 | 365 | | | |
| 4 | 800 | 553 | 376 | | | |
| 5 | 800 | 553 | 469 | 742 | 560 | 367 |
| 6 | 800 | 553 | 478 | 742 | 560 | 298 |
| 7 | 0 | .002 | .002 | 742 | 560 | 327 |
| 8 | 0 | .002 | .001 | 742 | 560 | 138 |
| Amount of clean sand initially in replica | | 2.0 kg | | 4.0 kg | | |
| Amount added or replaced | | 2.0 kg added | | 1.0 kg replaced | | |
| Size of replaced batches | | 8.0 kg | | 4.0 kg | | |
| Sorption efficiency | | 69% | | 75% | | |

days every crab in every replica had its activities timed at every one of the four hours.

The feeding schedule for the adjustment and exposure periods of Experiments I and II was the same. One gram of crushed shrimp pellets was sprinkled over the sand in each replica after each lunar day's observations. In Experiment III food was added every day to the replicas at low tide, 2 lunar hours before observations began, and remained untouched until the crabs emerged with the flooding tide. The food added each day consisted of 0.5 g of crushed shrimp pellets, 1 crushed blue mussel broken into pieces, and 2 isopods (Idothea baltica) cut into thirds. In the replicas rocks with barnacles, attached algae, and 8 live mussels were maintained and a mat of diatoms was allowed to develop on the rocks, oyster shells, and two of the glass walls.

The methods for sorbing the PCBs (Aroclor[®] 1260) to the sand improved with each successive experiment. Fine sand skimmed to a depth of 2 to 3 cm from the surface of Idaho Flats, Yaquina Bay, Oregon, was dried for several days at 80°C before being mixed with an acetone solution of PCBs and exposed to a stream of air to evaporate the acetone. The mixture rate was 1.0 kg of sand per 1.0 l of PCB-acetone solution. Table 5 gives the levels of PCBs sought and those actually attained in the replicas. For Experiment I hand stirring single 1.0 kg batches of sand and PCBs solution for 1 day gave irregular results. For Experiments II and III stirring large batches with paddle stirrers for 2 days and then allowing the sand-solution mixture to stand for an additional 2 days improved the consistency of the PCBs sorption to sand. Occasional stirring while the acetone was evaporating prevented layering of sand size fractions. Control sand in the second and third experiments was treated in the same manner as experimental sand except that no PCBs were added to the acetone. Columns E, H, and K in Table 5 were taken as the exposure levels in subsequent analyses.

Whole body concentrations of PCBs were determined on all the crabs observed in the exposure experiments. In Experiment I at the end of the observation period (17 days of exposure) 2 crabs were removed from each replica for chemical analysis and replaced by fresh crabs. The fresh

and previously exposed crabs remained under exposure for another 14 days. The crab replacement and continued exposure were done to give some indication of PCBs accumulation as a function of time. In Experiment II all the crabs were removed for chemical analysis at the end of the behavioral observations (23 days of exposure). Crabs dying during the experiments were also retained for chemical analysis. Individual whole crabs were washed with distilled water, wiped with tissue, washed again, wrapped in aluminum foil and frozen. While crabs were individually analyzed in the first two experiments, the three crabs of each sex from each replica were pooled for the analysis in the third experiment.

Chemical analysis for PCBs was performed in the Pesticide Analysis Laboratory of the Oregon State University Department of Agricultural Chemistry using methods described by Haines (1976). For all three experiments 25 g sand samples from each replica underwent Soxhlet extraction before lipid separation, alumina clean up and gas chromatographic analysis. The crabs were ground with dry ice before undergoing the same lipid separation and subsequent procedures as the sand.

To discover in which behaviors the activity budgets of control and exposed conditions differed, the activity budgets underwent stepwise discriminant analysis using the BIOMED program of the OSU Computer Center which was designed to pick the most parsimonious discriminant function. This discriminant function, in turn, can be used to indicate in which activities the budgets for control and exposed conditions differ as well as to classify newly measured budgets as belonging to one or the other of the conditions. A classification matrix indicating how correctly a discriminant function classifies cases already known to be of one category is often used to evaluate the effectiveness of a discriminant function. Essentially the BIOMED program answers the question: If one were to pick n number of activities from the 20 available for a discriminant function, which particular activities would combine to give the discriminant function? The program selects the variables stepwise, i.e., one at a time, on the basis of the variables with the largest F-value. To enter the discriminant function

a variable needs an F-value exceeding that for the 0.01 significance level.

B. ACCUMULATION OF PCBs BY CRABS EXPOSED TO PCBs-CONTAMINATED SAND

Results

Table 6 gives the mean whole body burdens of Aroclor® 1260 found in crabs exposed to contaminated sand during Experiments I and II. Under a variety of exposure conditions the body burdens of PCBs were two to four orders of magnitude greater than under control conditions, but because measurements of the sediment concentration of PCBs varied greatly, the relation between body burden and exposure level could not be precisely evaluated. Female crabs generally had the higher body burdens, and a female exhibited the maximum concentration found in either experiment, 190 ppm PCBs. After 31 days at the low exposure in Experiment I, whole body concentrations averaged 13 ± 2.1 ppm for males and 78 ± 56 ppm for females. At the moderate exposure males concentrated an average of 16 ± 1.1 ppm PCBs and females 57 ± 11 ppm PCBs. In Experiment II the average whole body burden was 36 ± 7.8 ppm PCBs for males and 78 ± 12 ppm PCBs for females.

In Experiment II the whole body burden of PCBs increased with increasing proportion of time spent in feeding with the rate of increase being greater for the females (Figure 4). The simplest model to describe the accumulation of PCBs as a function of time spent feeding would be a straight line through the origin with a slope equal to the ratio of the mean body burden to the mean feeding time. The model chosen to describe the relationship seen in Figure 4 was modified from the simplest model by taking the point ($Y=12$) to be the origin but still having the line pass through the ratio of the means. The following equations result:

$$Y = 12.0 + 407.938X \quad \text{for males}$$

$$Y = 12.0 + 662.024X \quad \text{for females}$$

where Y is the whole body burden of PCBs in ppm and X is the proportion

TABLE 6. The mean whole body burdens of PCBs for Hemigrapsus oregonensis exposed to PCBs contaminated sand.

| | Mean Exposure | Duration | Mean PCBs Burden | | | Maximum PCBs Burden |
|-------------------|---------------|----------|------------------|------------------|--------|---------------------|
| | ppm | days | ppm | + Standard Error | | ppm |
| Experiment I | | | | | | |
| Control | .027 | 14* | .238 | + .076 | (2)** | .315 |
| | | 17 | .44 | + .036 | (4)** | .148 |
| | | 31 | .096 | + .065 | (4)** | .287 |
| Low Exposure | 30 | 14* | 53.4 | + 41.4 | (4)** | 177 |
| | | 17 | 2.0 | + 1.6 | (5)** | 8.3 |
| | | 31 | 41.0 | + 24.9 | (7)** | 190 |
| Moderate Exposure | 259 | 14* | 42.6 | + 12.8 | (7)** | 106 |
| | | 17 | 12.3 | + 3.1 | (6)** | 20.5 |
| | | 31 | 36.6 | + 7.7 | (16)** | 118 |

TABLE 6. Continued

| | Mean Exposure ppm | Duration days | Mean PCBs Burden ppm ⁺ Standard - Error | Maximum PCBs Burden ppm |
|----------------|----------------------|------------------|--|----------------------------|
| Experiment II | | | | |
| Control | .0012 | 23 | .029 ⁺ - .007 | (24)** .13 |
| Exposure | 422 | 23 | 57.9 ⁺ - 8.3 | (24)** 147 |
| Experiment III | | | | |
| Exposure | 282 | 4 | 13.9 ⁺ - 1.7 | (8)*** 20.6 |

* In Experiment I, 2 crabs per replica were replaced after 17 days and then the replacements were exposed for 14 days.

** The number of individuals

*** Pooled samples of 3 crabs

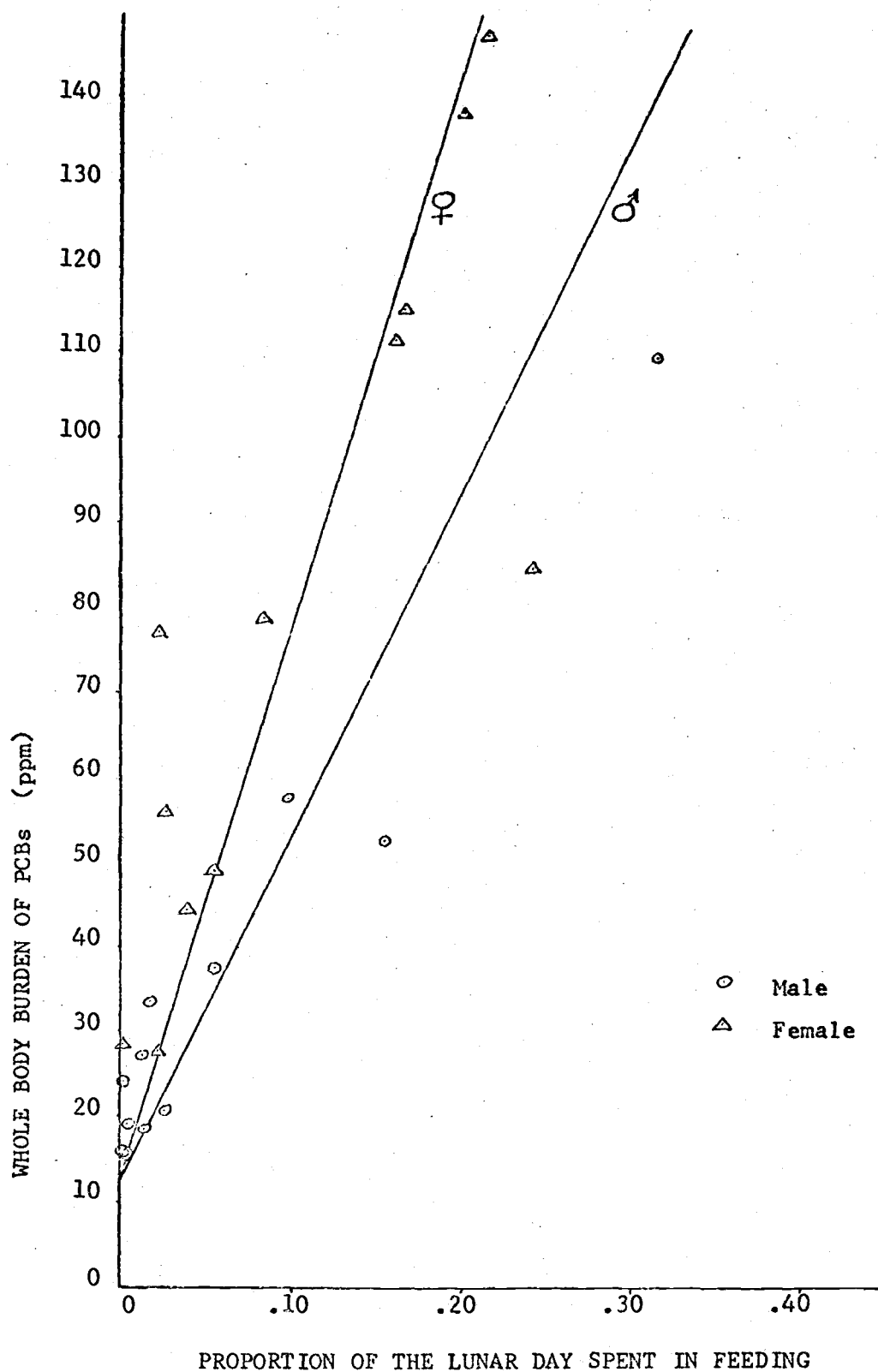


Figure 4. The whole body burden of PCBs and the time spent in feeding for Experiment II.

of the lunar day spent in feeding taken from the activity budget data.

Discussion

The results indicate that Hemigrapsus oregonensis readily accumulates PCBs from contaminated sand when held under simulated natural conditions. The values for whole body burden were the same order of magnitude as those found by Nimmo et al (1971) for the fiddler crab, Uca minax, which accumulated an average of 80^{+25} ppm Aroclor[®] 1254 when held for 30 days over sediment with 61 ppm PCBs. Because U. minax and H. oregonensis feed upon detritus, PCBs were taken up from both food and water and neither this study nor Nimmo's can adequately discern the relative importance of the two pathways. Another Brachyuran, the blue crab, Callinectes sapidus, accumulated similar whole body residues (23 ppm PCBs) when exposed only to contaminated water (5.0 ppb Aroclor[®] 1254) for 20 days (Duke et al, 1970). A whole body burden of such magnitude as that of C. sapidus indicates the PCBs uptake from the water cannot be considered negligible in comparison to uptake from food. In both Nimmo's study and this one, leaching of PCBs from the sediment did occur so that the opportunity for uptake from the water cannot be denied.

When considering the question of whether food or water is the main pathway for PCBs uptake in Hemigrapsus oregonensis and then learning that increased feeding time brings increased body burdens, the temptation is to weigh the food pathway more heavily. Unfortunately greater time spent feeding also means a greater intimacy with the sediment and consequently a presumably greater opportunity for uptake via the gills from the water. The crab in feeding often produces clouds of resuspended sediment increasing the possibility of PCBs leaching into the water. In the present experiments the two pathways both exist and undoubtedly operate but their relative importance cannot be judged.

This study agrees with those of Duke et al (1970) and Nimmo et al (1971) in that at high body burdens (about 10^2 ppm PCBs) no mortality or grossly obvious disability can be attributed to PCBs accumulation.

In contrast other chlorinated hydrocarbons have produced damage at body burdens 2 to 3 orders of magnitude lower than that for PCBs considered above. DDT accumulated from marsh sediments by Uca pugnax produced disequilibrium and impaired escape behavior at 0.885 ppm DDT in the muscle tissue (Odum et al, 1969). Dieldrin impaired escape behavior and reduced field populations in U. pugnax at tissue levels between 0.3 and 0.4 ppm Dieldrin (Krebs et al, 1974).

The likelihood of PCBs exposure at the levels utilized in this study is suggested by two studies, one of a PCBs spill at Escambia Bay, Florida (Duke et al, 1970) and the other of an ocean dumping site for sewage sludge near the Firth of Clyde, Great Britain (Halcrow et al, 1975). In sediment down bay of the spill Duke found a maximum of 486 ppm PCBs, a concentration slightly above the maximum (478 ppm) in Experiments I and II and less than that (560 ppm) of Experiment III. In the firth of Clyde PCBs concentrations in the sediment were 2890 ppb at the sludge disposal site and still as high as 26 ppb 11 km away. Present evidence indicates that the PCBs levels used in this study are comparable to those probable in a PCBs spill. The lower levels in Experiment I could possibly be attained in sediment on and about areas of chronic sewage sludge dumping.

Although this study did not specifically investigate the chemistry of the sorption of PCBs to sand, the experience of preparing experimental sand indicated a heterogeneous distribution of sorbed PCBs. After the Escambia Bay spill, the PCBs appeared to be evenly distributed through the size fractions of the sediment (Nimmo et al, 1971). The fact that in Experiment I batches of sand seemed only to sorb a maximum amount of PCBs no matter how much was applied suggests that the sediment may have possessed a limited number of binding sites for PCBs. The correlation of PCBs concentration with organic content of the sediment found by Halcrow et al (1975) and the known high solubility of PCBs in lipids enhances the conjecture that organic content may limit the PCBs sorption capacity of sediment.

In the first experiment the heterogeneous sorption of the PCBs to the sand and the leaching of PCBs from the sand in the replicas produced

variation in the measurements of sediment concentrations of PCBs large enough to preclude precise assessment of the exposure levels actually experienced by the crabs. Without measurements of exposure of greater precision than those of the body burden, the relationship between body burden and exposure level can not be determined. The improved preparation of contaminated sand in the second and third experiments, however, produced exposure conditions uniform enough to examine the influence of sex and extent of feeding upon uptake.

The simplest accumulation model, a straight through the origin and the ratio of the means, was modified after examination of Figure 4 showed a cluster of individuals with low feeding rates and body burdens above 15 ppm PCBs. Such a cluster would occur if individuals feeding infrequently had their feeding rate underestimated. Because the estimates of feeding time were based on observations of individual crabs for a short part of the lunar day over many days, individual crabs spending less than 3% of the lunar day in feeding probably did have their feeding rate underestimated. Adjustment of the intercept to a point slightly below the lowest observed body burden was done in order to compensate for the underestimation of low feeding rates, and the modified models more adequately described the uptake of PCBs as a function of time spent in feeding and indicated that uptake rate of female crabs was higher than that of males.

The higher rate of PCBs accumulation can in part be accounted for by variations in the chemical composition of the body which are known to be considerable over the course of the female sexual cycle (Vonk, 1960). Female crabs maturing eggs during the PCBs exposure would have a higher lipid content than males and consequently a higher capacity for uptake and storage of the lipidophilic PCBs. The facts that a small percentage of female crabs did come into berry during the exposure experiments and that the highest body burdens for experiments I and II were observed in ovigerous female crabs support the explanation that the higher PCBs accumulation rate was a consequence of chemical changes in the female crabs associated with the reproductive cycle.

C. ACTIVITY BUDGETS UNDER PCBs EXPOSURE - EXPERIMENTS I AND II

Results

The activity budgets for Hemigrapsus oregonensis exposed to PCBs-contaminated sand differed primarily in prefeeding and feeding activities (Figures 5 to 8; Appendices VII to X). In Experiment I lowly exposed males showed no difference from control males in the activities budget while lowly exposed females exhibited more time sheltered and less time prefeeding than controls. With moderate exposure both sexes sheltered more and prefed less. In Experiment II both sexes again exhibited a depression in time spent prefeeding and feeding under exposure, but a change in shelter use was not clear. Exposed males did not use shelter for a differing amount of time than control males while exposed females exhibited a trend of shelter use opposite to that of Experiment I in that females sheltered less.

Examination of the coefficients of variation in Appendices VII to X reveals that the females were generally more variable in their behavior than the males under exposed conditions just as under ordinary conditions. No obvious pattern of variability appeared consistently through all experiments except that the variability of prefeeding and feeding by females increased with PCBs exposure.

Table 7 gives the discriminant functions resulting from the multivariate analysis, Stepwise BIOMED. Prefeeding or feeding behavior was the first selection for both sexes and both experiments. A posture category appeared in the discriminant functions for both sexes and both experiments. For males in both experiments the discriminant functions contained a locomotor category. For females in both experiments the functions contained a category of shelter use and a category involving contact with the sediment. For both experiments only one or two variables for male crabs were needed to correctly classify all cases while four variables were necessary for female crabs for correct classification of all cases.

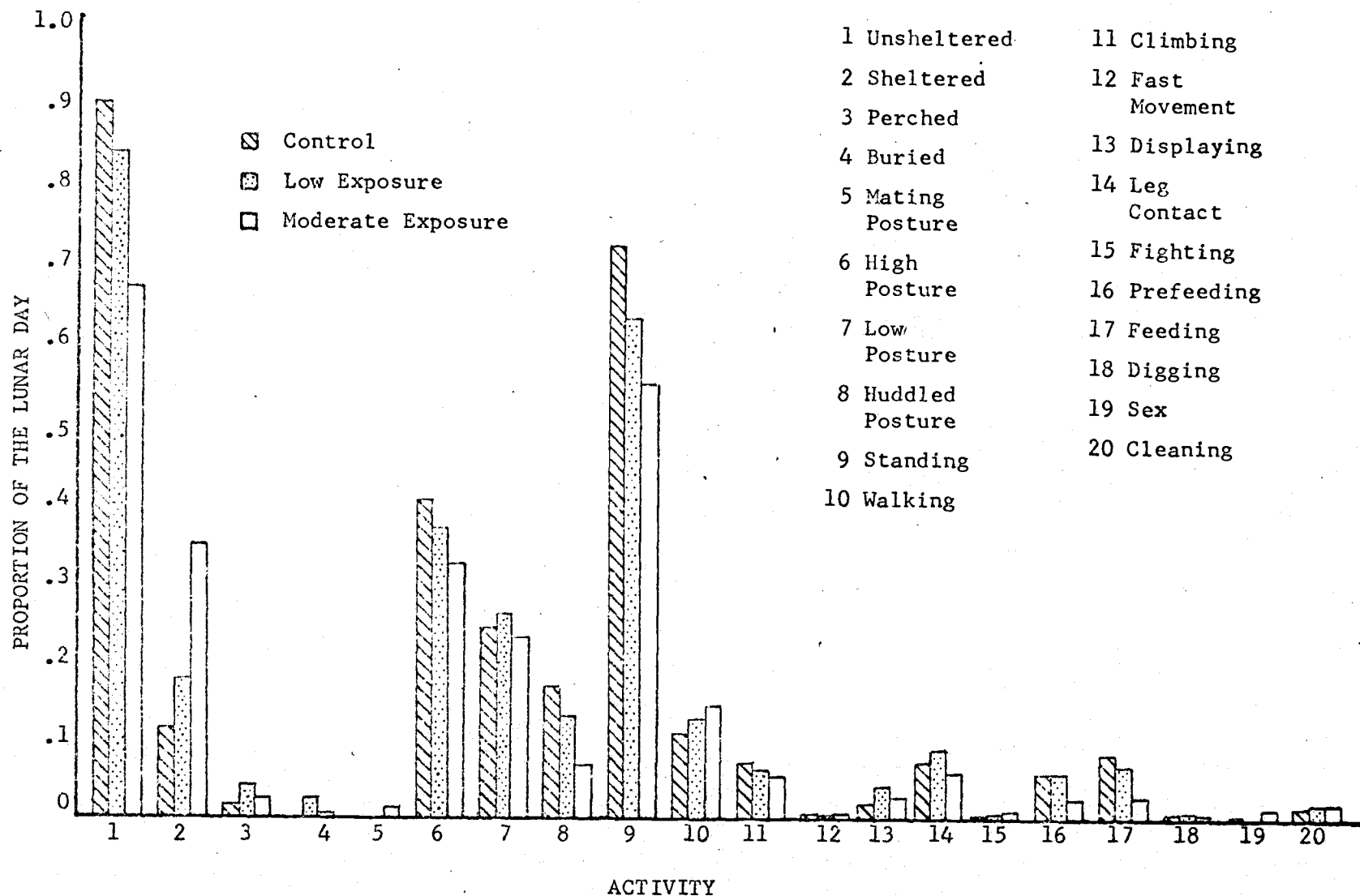


Figure 5. Activity budgets for male Hemigrapsus oregonensis in Experiment I.

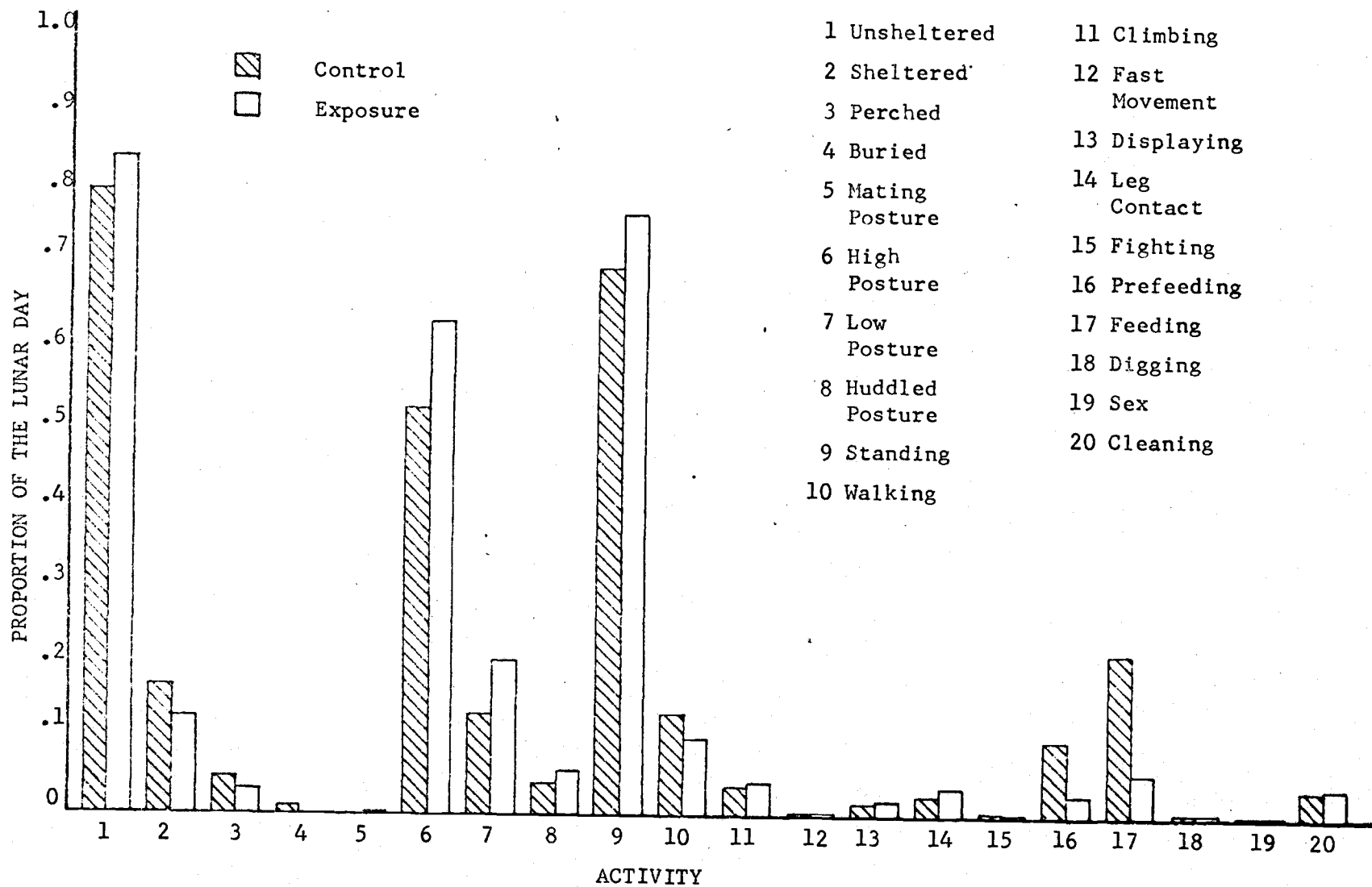


Figure 6. Activity budgets for male Hemigrapsus oregonensis in Experiment II.

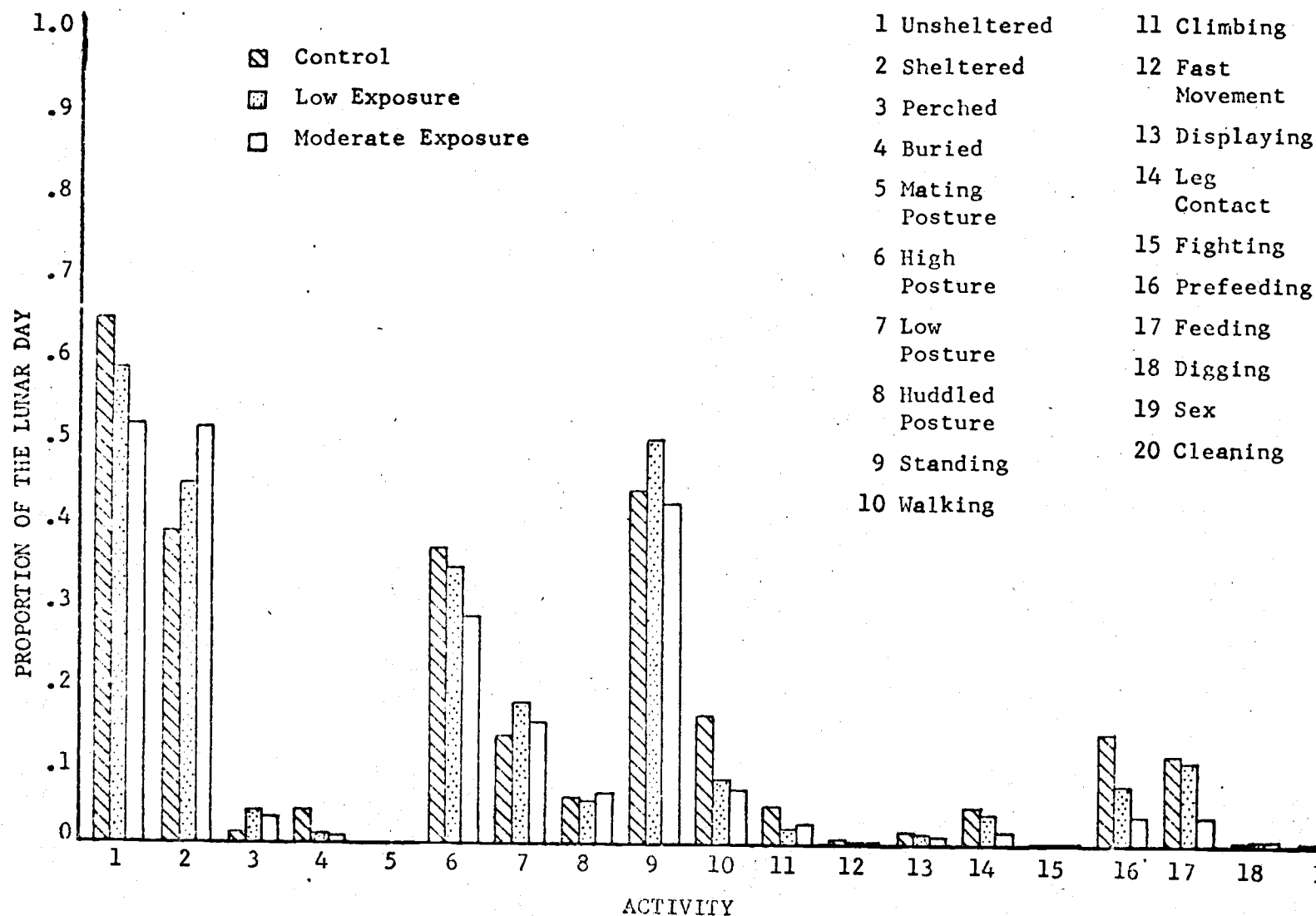


Figure 7. Activity budgets for female Hemigrapsus oregonensis in Experiment I.

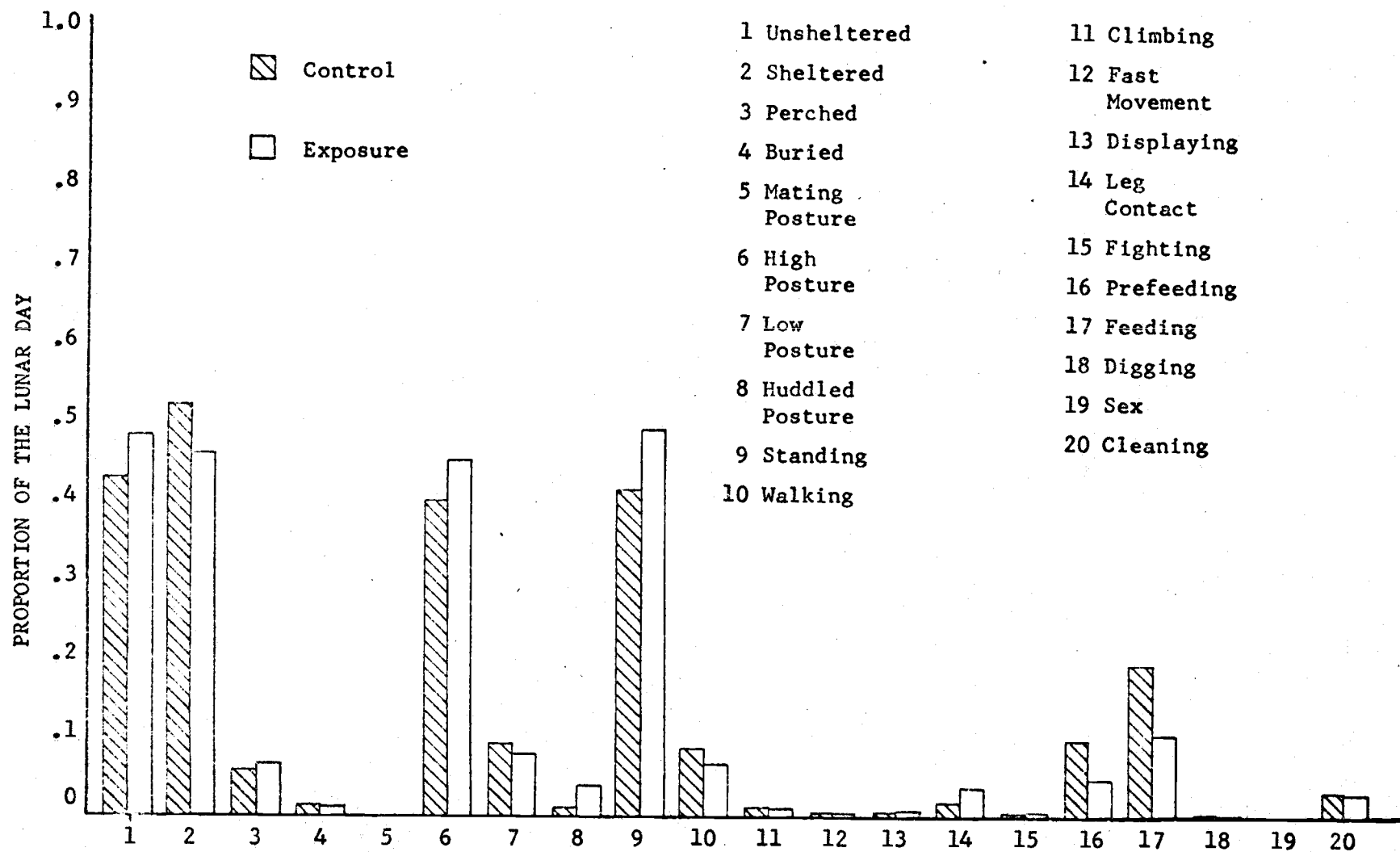


Figure 8. Activity budgets for female *Hemigrapsus oregonensis* in Experiment II.

TABLE 7. Discriminant functions resulting from stepwise analyses with the activity categories given in the order of their selection.

| First Experiment | 1 | 2 | 3 | 4 | 5 | 6 |
|-------------------|------------|-------------|----------------|-----------------|---------------|-------------|
| Males | Feeding | Climbing* | Mating Posture | Huddled Posture | Fast Movement | |
| Females | Prefeeding | Buried | High Posture | Sex* | Sheltered | |
| Second Experiment | | | | | | |
| Males | Feeding* | Walking | Cleaning | Huddled Posture | Displaying | Perched |
| Females | Prefeeding | Low Posture | Digging | Cleaning* | Feeding | Unsheltered |

* With the addition of this variable the discriminant function correctly classified all cases.

Discussion

The results of the multivariate analyses can be viewed in several ways, and several criteria exist to help in their evaluation. There are, however, no standard, generally accepted methods for making definite decisions using multivariate analyses. What should inform our judgement is an understanding of the animal's situation and behavior and of how the BIOMED program manipulates the data, not one index number's being less or more than another.

The BIOMED procedure considers the question what n variables distinguish the budgets of one condition from another. The choosing of only five or six variables out of the 20 available can be taken to mean that the budgets of exposed and control conditions differ only in part and not throughout their full extent. Next one can look to the identity of the variables and to their order of selection. Using the selection order as a measure of importance one compares the selection orders among sexes and experiments seeking any regular pattern. Thus the consistent first selection of prefeeding or feeding for both sexes in both experiments indicates that feeding behaviors are the best measures for distinguishing the behavior of crabs under PCBs exposure from that of crabs under control conditions, and for the males of Experiment II examination of the classification matrices shows that feeding behavior alone is an adequate discriminator between exposed and control conditions. The fact that female crabs require more variables for correct classification does not necessarily mean, however, that PCBs exposure influences more behaviors in the female than male crabs.

In the attempt to discern patterns in the order of selection consideration is given to not only the specific identity of the chosen variables but also the higher level categories from which they derive. For example, climbing and walking, the second selections for male crabs in Experiments I and II respectively, are both types of locomotion. In both experiments male crabs are affected in their feeding, locomotion, and posture, and female crabs in their prefeeding, contact with the sediment (digging and buried), posture, and shelter use. Now one

returns to the original data to find the direction in which these general activities have changed upon exposure. For males feeding and locomotion decrease under exposure; for females prefeeding and contact with the sediment decrease. The effects of exposure upon posture and shelter use are more difficult to interpret because the direction of change reverses from one experiment to the other.

In Experiment I crabs showed a trend of increasing time in shelter with increasing exposure level while in Experiment II crabs under exposure sheltered less. The reversal in shelter use from one experiment to the other is difficult to explain but probably derives from differences in the quality of shelter within the replicas. The sand, rocks, and oyster shells were replaced between the experiments and could well have varied in their quality as shelter. The fact that crabs under control conditions in the second experiment sheltered less than control crabs in the first experiment indicates some variation between experiments in shelter use derived from changes in the crabs, changes in shelter quality, or both.

The appearance of the rare behaviors, e.g. sex and cleaning, in the discriminant functions raises the question of whether their selection is based on their rarity or on some real effect of exposure. The problem of rare behaviors is akin to that of rare species in community analysis where multivariate techniques are used to rank or classify communities. The difficulty is that for the rarer behaviors or species a considerably greater sampling effort is required to achieve estimates of the same accuracy and precision as that for common behaviors or species. In both situations, however, the rarer behavior or rarer species is often the best indicator for the classification of an activity budget or species assemblage.

Both systematic scrutiny and multivariate analysis indicate that exposure to PCBs-contaminated sand reduces the time spent in prefeeding and feeding by both sexes. To a lesser extent and consistency PCBs exposure influences sheltering and close contact with the sediment. The bulk of the activity budgets differ little between perturbed and ordinary conditions. Such findings lead to the reasonable argument

that the main portion of the activity budget is conserved under PCBs exposure by the avoidance of presumably debilitating body burdens of PCBs brought about by reduced feeding. The ability to avoid high body burden by decreasing feeding can be surmised from the relationship of body burden and feeding shown in Figure 4. Qualitative observations not reflected in the quantitative behavioral data encourage the argument that decreasing feeding is adaptive to the perturbed conditions. The crabs shifted from feeding on sediment and particles in the sediment under ordinary conditions to feeding by scraping the algal growth from the chamber walls and rocks under exposed conditions. The possibility of a shift in food type or feeding method under exposure led to Experiment III in which the crabs were given greater choice of food types.

D. THE FEEDING BEHAVIOR OF HEMIGRAPSUS OREGONENSIS UNDER PCBs EXPOSURE - EXPERIMENT III

Results

Under control conditions male Hemigrapsus oregonensis spent more time in prefeeding and feeding behaviors than did females and also differed from females in the distribution of time spent feeding upon various foods (Figure 9 and Appendix XI). Males spent 87% of their total feeding time consuming mussels and isopods and only 12% directly feeding upon sediment. Females spent less of their total feeding time on mussels and isopods, 50%, but more on sand, 35%, and other foods not utilized by the males. Among the prefeeding and feeding behaviors males devoted about the same proportion of prefeeding time to dactyl searching but less of their prefeeding time to probing the sediment (Figures 10 and 11; Appendix XII). Food holding and sweeping out with the maxillipeds constituted about 12% of the prefeeding of females and 42% of that of males. Tearing up food for ingestion took up most (83%) of feeding time of males while females allotted their feeding time more evenly to claw feeding, tear feeding, and sweeping sand to the mouth (30, 40, and 25% respectively).

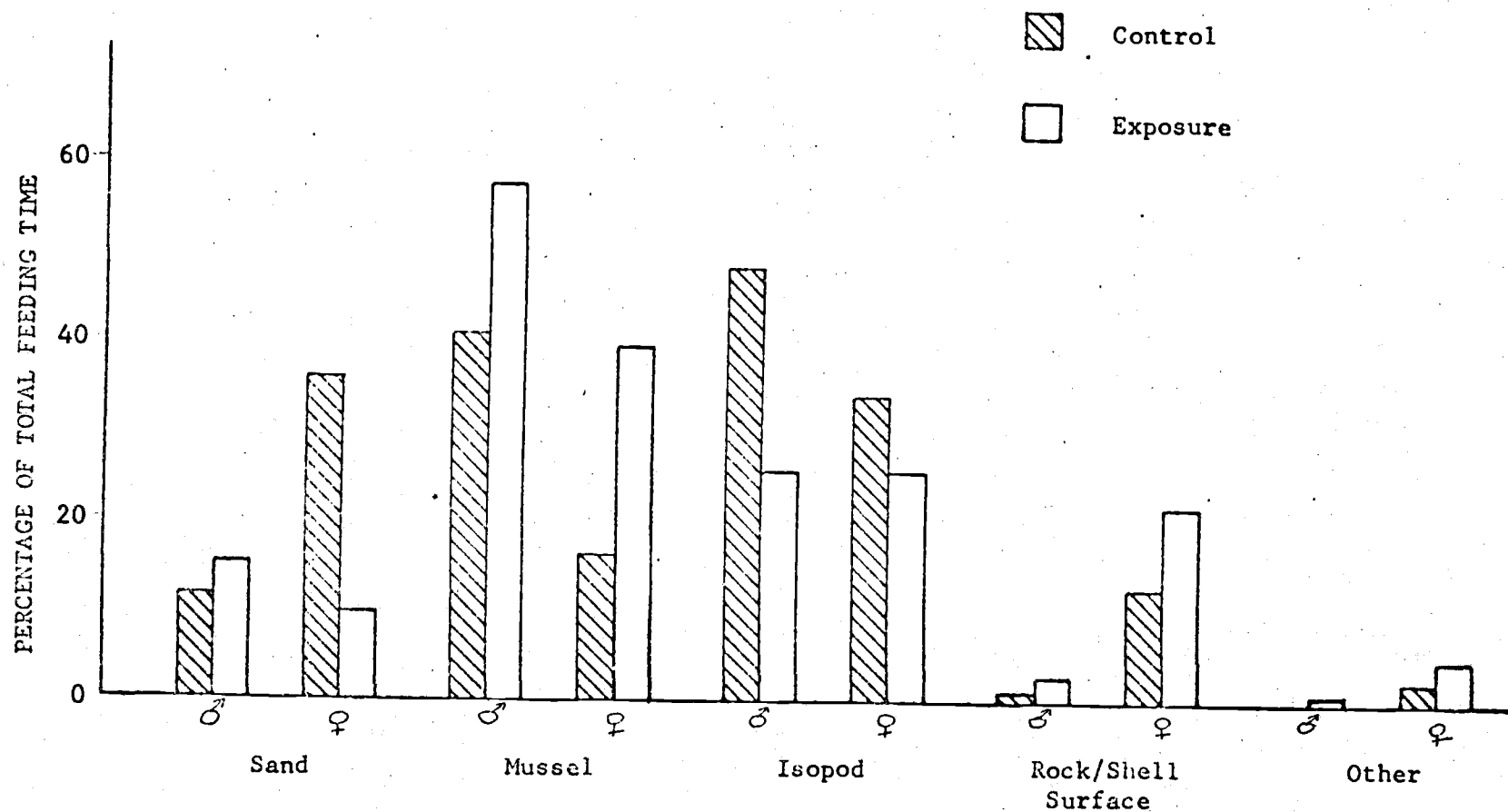


Figure 9. The distribution of feeding among various food for male and female Hemigrapsus oregonensis in Experiment III.

Upon exposure to PCBs-contaminated sand the only substantial change in total prefeeding and feeding times was that total feeding time for females dropped from 0.152 to 0.106 of the total observed time. In contrast to the total prefeeding and feeding time, food type and feeding style did show a shift, especially for females. Exposed males decreased the portion of their feeding time devoted to isopods and increased it for mussels. Exposed females decreased the portion of their feeding time allotted to feeding upon sand from 35 to 10 % and showed complimentary increases in the time apportioned to feeding upon mussels and the surfaces of rocks and shells. For males exposed conditions brought an increase in probing and a decrease in holding food; for females, decreases in claw feeding and sweeping the sand and increases by more than a factor of two in scrape feeding and tear feeding.

The average whole body burden of PCBs was the same for both sexes, $14.8^{+3.5}$ ppm PCBs for males and $13.0^{+0.6}$ ppm PCBs for females. The body burden increased with increasing time spent feeding upon sand for the males but such a relationship was not as clear for the females (Figure 12). Fitting the simples model yields the following equations:

$$Y = 388.158X \quad \text{for males}$$

$$Y = 1298.00X \quad \text{for females}$$

where Y equals the whole body burden (ppm PCBs) and X equals the proportion of time spent in feeding upon the sand.

Discussion

The third experiment demonstrates that under control conditions the sexes differ in their food preferences and that given choices other than sediment alone male Hemigrapsus oregonensis will spend as long or longer in prefeeding and feeding behaviors as will females. The males concentrate their feeding upon the larger food items, mussels and isopods, while the females distribute their feeding time more evenly among the available options. The feeding style, i.e. what particular feeding behaviors predominate, follows from the particular predominant food. For example, males expend 87% of their total feeding time on mussels and isopods and,

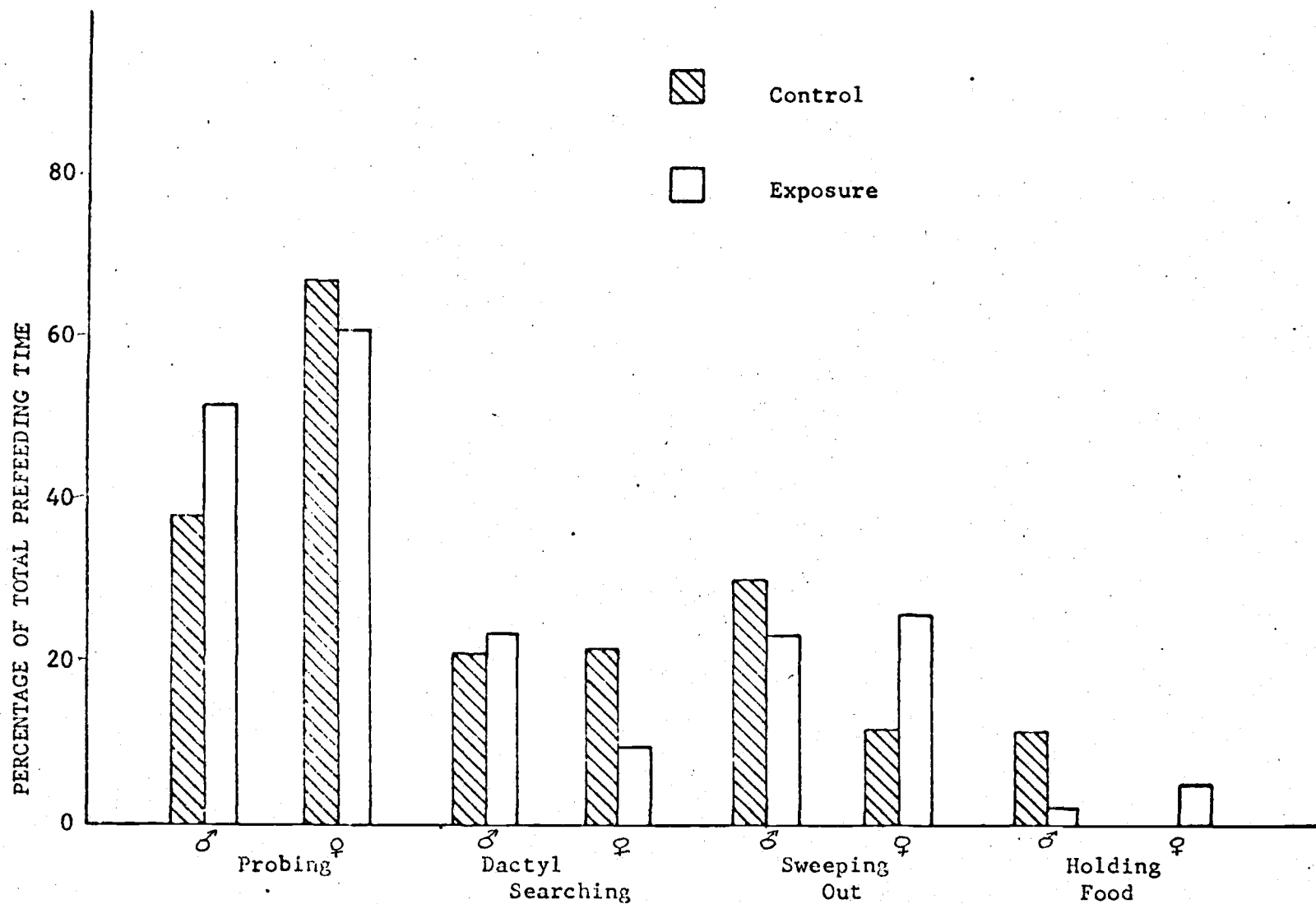


Figure 10. The distribution of prefeeding behaviors for Hemigrapsus oregonensis in Experiment III.

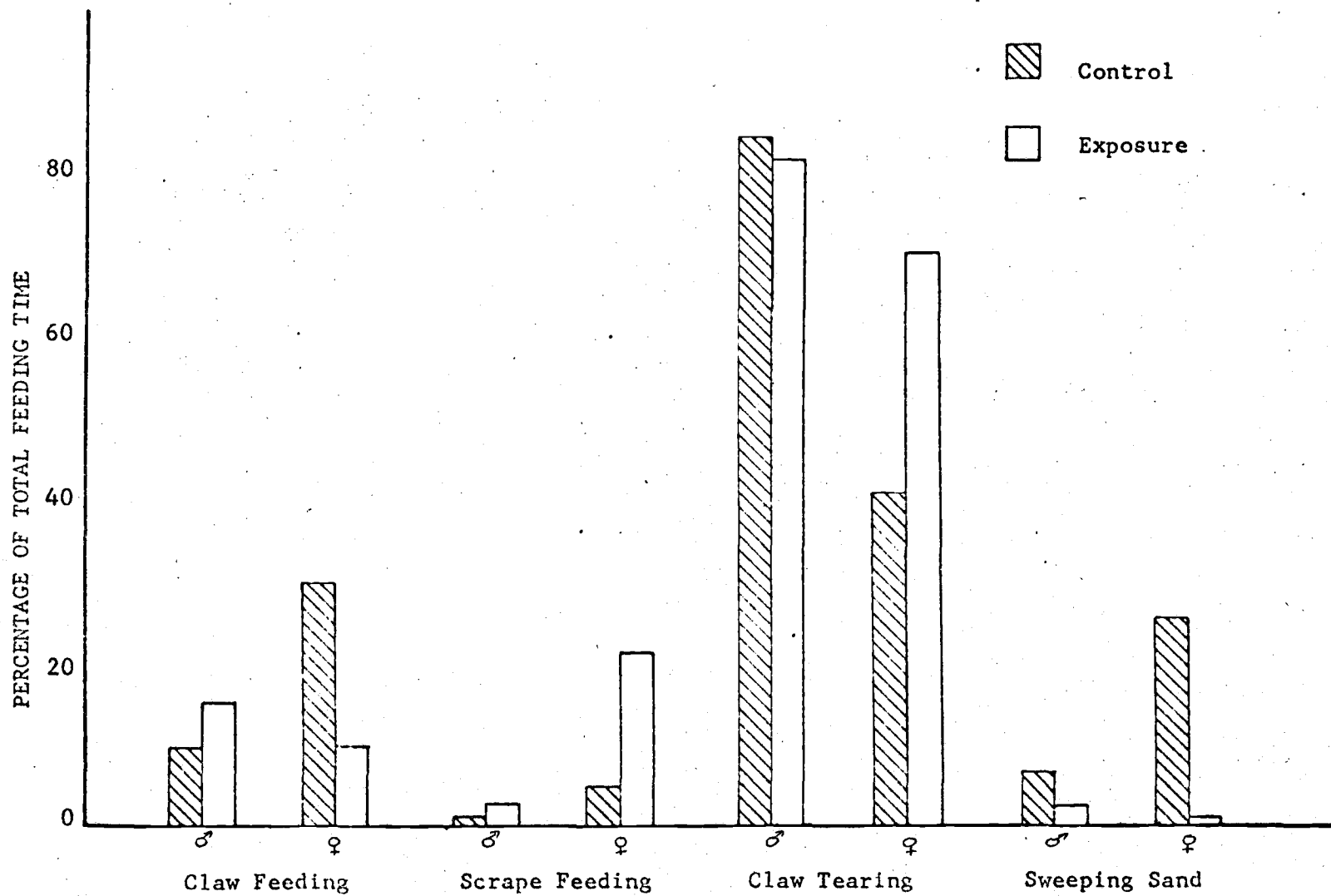


Figure 11. The distribution of feeding behaviors in Hemigrapsus oregonensis in Experiment III.

consequently, 83% of their feeding time in the behavioral unit tear feeding. The sex difference in food preferences can be explained as a consequence of the male's larger size and more than proportionately larger claws. Larger size confers dominance which presumably earns the larger animal a disproportionately greater share of the choicer food items. Larger claws confer the ability to manipulate the larger, tougher food that smaller crabs cannot tear up. The greater total feeding time of the males in Experiment III contrasts with the female's greater feeding time in the previous experiment and is a consequence of the availability of more food items and the longer handling time required for consumption.

Females modify their feeding behavior under PCBs exposure to a greater extent than do males. Males under exposure show no decrease in the total prefeeding and feeding times and little shift in food preference, continuing to feed on sediment at the same rate. Females under exposure show a decrease in total feeding time and, more importantly, shift feeding from PCBs-contaminated sand to mussels and the surfaces of rocks, shells and glass. Thus the shift from contaminated to uncontaminated food hypothesized from the results of the first two experiments does occur.

The predictions of body burden in Table 8 are derived from the relationships shown in Figures 4 and 12 and provide evidence that the food shift under exposure functions to avoid high PCBs body burdens. The body burden is clearly related to the amount of time spent feeding on the sediment. The predictions of Table 8 show that if feeding continued under exposure at the same rate as under control conditions the PCBs body burdens would have been considerably higher than those actually achieved.

The relationship between body burden and sediment feeding time was not as clear for the females as for the males because the females in Experiment III almost completely stopped sediment feeding. Because of their higher uptake rate, the females presumably reached the body burden at which sediment feeding ceased much more quickly than the males. Unfortunately these experiments can not evaluate the presumption that

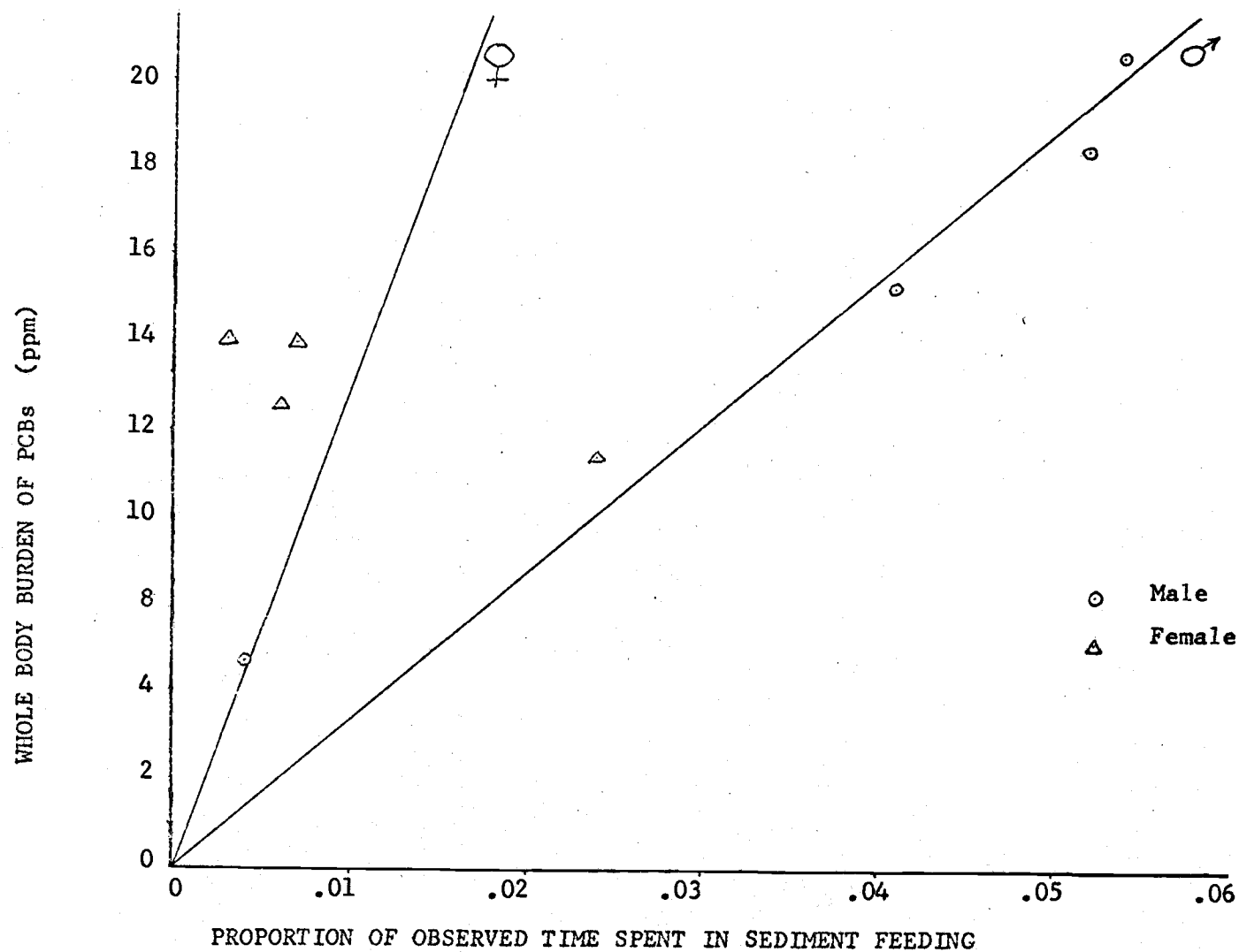


Figure 12. The whole body burden of PCBs and the time spent in sediment feeding for Experiment III.

TABLE 8. PCBs body burdens predicted using the models describing body burden as a function of feeding time.

| | | |
|----------------|--|-------|
| Experiment II | Models on p. 46 | |
| Males | with feeding at control average (0.203) | 82.8 |
| | with feeding at exposed average (0.056) | 22.8 |
| Females | with feeding at control average (.190) | 125.8 |
| | with feeding at exposed average (0.102) | 67.5 |
| Experiment III | Models on p. 64 | |
| Males | with feeding at control average (0.032) | 12.4 |
| | with feeding at exposed average (0.038) | 14.8 |
| Females | with feeding at control average (0.042) | 54.5 |
| | with feeding at exposed average (0.010) | 13.0 |

the crabs feed upon the contaminated sand until the achievement of some threshold body burden where a shift to other food occurs. The alternative explanation for cessation of sediment feeding is that the PCBs-contaminated sediment has an unpleasant taste and is only eaten when other more attractive food is unavailable. The experiments to discover the pathways leading to the shift in feeding under PCBs exposure remain to be done.

If the females of Experiment III stop sediment feeding and shift to other foods, why don't the males do so? Perhaps the males with their larger size and lack of the need to produce eggs can tolerate higher tissue residues, and a shift in feeding would have been seen when higher body burdens were reached. Another possible explanation is that because the PCBs accumulation rate of the males was lower than that of the females, the experiment of 4 days length did not allow enough time for the body burdens to reach the level at which cessation of sediment feeding would have occurred. The shift in food is so dramatic in females because the sediment normally comprises a larger part of their diet than that of males.

The nature of the adaptive feeding shift to other available foods allows us to predict that winter and early spring, when little food other than sediment and detritus exists for Hemigrapsus oregonensis, could become more stressful with the presence of PCBs in the sediment and detritus. The amount of feeding and, consequently, the magnitude of the PCBs body burdens would probably be determined by the energy requirements and reserves of the crab population. The cessation of sediment feeding with the possible accompaniment of shifting to other food leaves the nutrient content and pollutant load of that otherwise utilized sediment either to the consumption of another organism less discerning than H. oregonensis or to some other fate.

CONCLUSIONS

Under ordinary conditions Hemigrapsus oregonensis differs between sexes in the time apportioned to various activities with certain activities prevailing at certain stages of the tidal cycle. Under perturbed conditions, exposure to PCBs-contaminated sediment, both sexes modify their activities with females doing so to the greater extent. The crabs actively mitigate their exposure and presumably its consequences by shifting to uncontaminated food when available or by decreasing sediment feeding when no alternate foods exist. Because the crabs readily accumulate PCBs in proportion to the amount of sediment feeding, stopping feeding or shifting to other foods serves to lessen the PCBs body burden from what it would otherwise be if feeding continued as under ordinary conditions. H. oregonensis successfully adapts to the perturbed conditions by a behavioral change, but the nature of the success, no less than its alternative, failure, has implications for the energy flow and pollutant cycling in the crab's ecosystem.

The general approach of exposing crabs to PCBs under simulated natural conditions proves fruitful because the habitat replicas provide opportunity for the innovative behavior that mitigates exposure and its consequences. As one limits the organism's opportunities, one lessens the probability of observing successful adaption to perturbation and the strategies used to achieve it. Combining PCBs accumulation data with behavioral observations also allows the demonstration of how other factors besides the traditional ones of dose and time influence accumulation.

The results of the multivariate analyses demonstrate the need for a wide perspective in pollutant - behavioral effects studies. If behaviors other than the five or six appearing in the discriminant functions had been initially chosen for observation, the conclusions drawn from the identical experimental events could have been far different. To widen the perspective of this study, observations of interactions between animals could have been more closely observed and

led to conclusions about dominance relationships. The need is to view the organism in the broadest terms and resist the temptation to focus one's vision down to a few aspects of behavior.

The habitat replica experiments are of the greatest value in indicating the ranking of the organism's requirements. Because the activity budgets reflect the synchrony of the crab's activities with the tidal cycle, the dominant event of the organism's environment, the conservation of the activity budget under PCBs exposure may be a consequence of the crab's overriding need to remain in tidal synchrony. If the organism is minimizing the stakes, as Slobodkin and Rapoport (1974) believe, decreased growth due to less feeding may be the price of maintaining tidal synchrony. The strategy of delaying feeding until the next tide that will probably bring a new food situation probably has proven less costly than that of prolonging food searching and feeding with its certain increase in dessication and predation. Understanding of the organism's natural strategies derived from the habitat replica studies enables one to ask the pertinent questions about pollutant effects and to design appropriate experiments for their answers.

BIBLIOGRAPHY

- Altevogt, R. 1968. Das 'Schaumbaden' brachyurer Crustaceen als Temperaturregulator. Zool. Anz. 181:398-402.
- Atema, J., S. Jacobson, J. Todd and D. Boylan. 1973. The importance of chemical signals in stimulating behavior of marine organisms: Effects of altered environmental chemistry on animal communication, p. 177-197. In: Gary E. Glass (ed.) Bioassay techniques and environmental chemistry. Ann Arbor Science Publishers, Inc., Ann Arbor, Mich.
- Atkinson, R. J. A. 1974. Behavioral ecology of the mud-burrowing crab Goneplax rhomboides. Mar. Biol. 25:239-252.
- Batie, R. E. 1974. Population structure of the intertidal shore crab Hemigrapsus oregonensis (Brachyura, Grapsidae) in Yaquina Bay, a central Oregon coast estuary. Ph.D. Thesis. Oregon State Univ., Corvallis. 138p. Univ. Microfilms. Ann Arbor, Mich. (Diss. Abstr. 34(07):3345-B).
- Beckner, M. 1959. The biological way of thought. Univ. California Press, Berkeley. 200p.
- Bertalanffy, L. von. 1950. The theory of open systems in physics and biology. Science 111:23-29.
- Bertalanffy, L. von. 1968. General system theory. George Braziller, New York. 289p.
- Booolootian, R. A., A. C. Giese, A. Farmanfarmaian and J. Tucker. 1959. Reproductive cycles of five west coast crabs. Physiol. Zool. 32:213-220.
- Bovbjerg, R. V. 1960a. Behavioral ecology of the crab, Pachygrapsus crassipes. Ecology 41:668-672.
- Bovbjerg, R. V. 1960b. Courtship behavior of the lined shore crab, Pachygrapsus crassipes Randall. Pac. Sci. 14:421-422.
- Briggs, M. H. 1961. Visual pigment of grapsoid crabs. Nature 190:784-786.
- Burrows, M. and A. O. D. Willows. 1969. Neuronal coordination of rhythmic maxilliped beating in Brachyuran and Anomuran Crustacea. Comp. Biochem. Physiol. 31:121-135.
- Cobb, J. S. and G. R. Tamm. 1975. Dominance status and molt order in lobsters (Homarus americanus). Mar. Behav. Physiol. 3:119-124.

- Cox, D. R. 1958. Planning of experiments. John Wiley & Sons, New York. 308p.
- De Blok, J. W. 1964. An apparatus to generate tidal fluctuations and a modification to render constant flow. *Neth. J. Sea Res.* 2:186-188.
- Dehnel, P. A. 1960. Effect of temperature and salinity on the oxygen consumption of two intertidal crabs. *Biol. Bull.* 118:215-249.
- Dimick, R. E., G. Egland and J. B. Long. 1941. Native oyster investigations of Yaquina Bay, Oregon, July 4, 1939 to September 30, 1941. *Ore. Agr. Exp. Sta. Prog. Rep.* 11. (Oregon State Univ., Corvallis, Ore.).
- Duke, T. W., J. I. Lowe and A. J. Wilson, Jr. 1970. A polychlorinated biphenyl (Aroclor[®] 1254) in the water, sediment and biota of Escambia Bay, Florida. *Bull. Env. Contam. Toxicol.* 5:171-180.
- Emery, F. E. 1969. Introduction, p. 7-13. In: F. E. Emery (ed.) *Systems thinking*. Penguin Books, Baltimore. 398p.
- Enright, J. T. 1970. Ecological aspects of endogenous rhythmicity. *Ann. Rev. Ecol. Syst.* 1:221-238.
- Evans, F. 1964. A tide generating machine for laboratory use. *Neth. J. Sea Res.* 2:183-185.
- Feibleman, J. K. 1969. Knowledge, adaptive responses, and the ecosystem. *Tulane Stud. Phil.* 18:17-49.
- Fernandez, H. R. 1973. Spectral sensitivity and visual pigment of the compound eye of the galatheid crab Pleuroncodes planipes. *Mar. Biol.* 20:148-153.
- Goldsmith, T. H. and H. R. Fernandez. 1968. Comparative studies of crustacean spectral sensitivity. *Z. vergl. Physiol.* 60:156-175.
- Grosch, D. S. 1973. Reproduction tests: the toxicity for Artemia of derivatives from non-persistent pesticides. *Biol. Bull.* 145:340-351.
- Haines, V. E. 1976. Effects of polychlorinated biphenyls (PCBs) on the respiration of the speckled sand dab (Citharichthys stigmaeus). M.S. Thesis. Oregon State Univ. 57p.
- Halcrow, W., O. W. MacKay and J. Bogan. 1974. PCB levels in Clyde marine sediments and fauna. *Mar. Poll. Bull.* 5(9):134-136.
- Hartnoll, R. G. 1971. The occurrence, methods and significance of swimming in the Brachyura. *Anim. Behav.* 19:35-50.

- Hiatt, R. W. 1948. The biology of the lined shore crab, Pachygrapsus crassipes Randall. Pac. Sci. 2:135-213.
- Hull, D. 1974. Philosophy of biological science. Prentice-Hall, Englewood Cliffs. 148p.
- Jones, A. C. 1962. The biology of the euryhaline fish Leptocottus armatus armatus Girard (Cottidae). Univ. Calif. Pub. Zool. 67:321-368.
- Knudsen, J. W. 1964. Observations of the reproductive cycles and ecology of the common Brachyura and crablike Anomura of Puget Sound, Washington. Pac. Sci. 18:3-33.
- Koestler, A. 1967. The ghost in the machine. Henry Regnery Co., Chicago. 384p.
- Krebs, C. T., I. Valiela, G. R. Harvey and J. M. Teal. 1974. Reduction of field populations of fiddler crabs by uptake of chlorinated hydrocarbons. Mar. Poll. Bull. 5:140-142.
- Kuris, A. M. 1971. Population interactions between a shore crab and two symbionts. Ph.D. Thesis. Univ. Calif., Berkeley. 345p.
- Lorenz, K. Z. 1974. Analog as a source of knowledge. Science 185:229-234.
- Low, C. J. 1970. Factors affecting the distribution and abundance of two species of beach crab, Hemigrapsus oregonensis and H. nudus. M.S. Thesis. Univ. British Columbia, Vancouver. 70p.
- Lowe, M. E. 1956. Dominance-subordinance relationships in the crawfish Cambarellus shufeldtii. Tulane Stud. Zool. 4(5):139-170.
- McLarney, W. O., D. G. Engstrom and J. H. Todd. 1974. Effects of increasing temperature on social behavior in groups of yellow bullheads (Ictalurus natalis). Env. Poll. 7:111-120.
- Naughton, C. C. 1969. Setae on chelae of shore crabs, Hemigrapsus: Function. N. W. Sci. 44:253-257.
- Nimmo, D. R., P. D. Wilson, R. R. Blackman and A. J. Wilson, Jr. 1971. Polychlorinated biphenyls absorbed from sediments by fiddler crabs and pink shrimp. Nature 231:50-52.
- Odum, W. E., G. M. Woodwell and C. F. Wurster. 1969. DDT residues absorbed from organic detritus by fiddler crabs. Science 164:576-577.
- Powers, W. T. 1973. Feedback: Beyond behaviorism. Science 179:351-356.

- Rathbun, M. J. 1918. The grapsoid crabs of America. Bull. U. S. Nat. Mus. 97:1-461.
- Rice, A. L. and C. J. Chapman. 1971. Observations on the burrows and burrowing behavior of two mud-dwelling crustaceans, Nethrops norvegicus and Goneplax rhomboides. Mar. Biol. 10:330-342.
- Russell, E. S. 1938. The behavior of animals. Edward Arnold Co., London. 184p.
- Slobodkin, L. B. 1968. Toward a predictive theory of evolution, p. 187-205. In: R. C. Lewontin (ed.) Population biology and evolution. Syracuse Univ. Press, Syracuse, New York.
- Slobodkin, L. B. and A. Rapoport. 1974. An optimal strategy of evolution. Q. Rev. Biol. 49:181-200.
- Sparks, R. E., W. T. Waller and J. Cairns, Jr. 1972. Effects of shelters on the resistance of dominant and submissive bluegills (Lepomis macrochirus) to a lethal concentration of zonc. J. Fish. Res. Board Can. 29:1356-1358.
- Steen, W. J. van der and J. C. Jager. 1971. Biology, causality and abstraction, with illustrations from a behavioral study of chemoreception. J. Theor. Biol. 33:265-278.
- Symons, P. E. K. 1964. Behavioral responses of the crab Hemigrapsus oregonensis to temperature, diurnal light variation and food stimuli. Ecology 45:580-591.
- Symons, P. E. K. 1970. Claw - shuddering behavior of the shore crab, Hemigrapsus oregonensis. Can. Field Natur. 84:55-56.
- Takahashi, F. T., Jr. 1974. Chemical communication and chemoreception in the Dungeness crab, Cancer magister, and the lined shore crab, Pachygrapsus crassipes. Ph.D. Thesis. Oregon State Univ., Corvallis. 119p.
- Tinbergen, N. 1951. The study of instinct. Clarendon Press, Oxford. 228p.
- Todd, J. H., D. Engstrom, S. Jacobson and W. D. McLarney. 1972. An introduction to environmental ethology: A preliminary comparison of sublethal thermal and oil stresses on the social behavior of lobsters and fishes from a freshwater and a marine ecosystem. Progress report to the U. S. A. E. C. AT(11-1)-3567. Unpublished manuscript. Woods Hole Oceanographic Instit. 104p.
- Underwood, A. J. 1972. Sinusoidal tide models: Design, construction and laboratory performance. J. Exp. Mar. Biol. Ecol. 8:101-111.

- Valiela, I., D. F. Babiec, W. Atherton, S. Seitzinger and C. Krebs.
1974. Some consequences of sexual dimorphism: Feeding in male and female fiddler crabs, Uca pugnax (Smith). Biol. Bull. 147:652-660.
- Vonk, H. J. 1960. Digestion and metabolism, p. 291-316. In: T. H. Waterman (ed.) The physiology of crustacea, Vol. II. Academic Press, New York.
- Wares, P. G. 1968. Biology of the pile perch (Rhacochilus vacca). M.S. Thesis. Oregon State Univ., Corvallis. 73p.
- Waterman, T. H. 1961. Light sensitivity and vision, p. 1-64. In: T. H. Waterman (ed.) The physiology of crustacea, Vol. II. Academic Press, New York.
- Wiens, J. A. 1969. An approach to the study of ecological relationships among grassland birds. Ornith. Monogr. No. 8. 93p.
- Wiens, J. A., S. G. Martin, W. R. Holthaus and F. A. Iwen. 1970. Metronome timing in behavioral ecology studies. Ecology 51:350-352.
- Williams, B. G. 1969. The rhythmic activity of Hemigrapsus edwardsii (Hilgendorf). J. Exp. Mar. Biol. Ecol. 3:215-223.
- Wright, H. O. 1966. Comparative studies of social behavior in grapsoid crabs. Ph.D. Thesis. Univ. Calif., Berkeley. 227p. Univ. Microfilms. Ann Arbor, Mich. (Diss. Abstr. 27:4184-4185B).
- Wright, H. O. 1968. Visual displays in Brachyuran crabs: Field and laboratory studies. Amer. Zool. 8:655-665.
- Yaldwyn, J. C. 1966. Observation on copulation in the New Zealand grapsid crab Hemigrapsus crenulatus (M. Edw.). Pac. Sci. 20:384-385.

APPENDICES

APPENDIX I.

The average water height, temperature and salinity within the replicas at each hour of the tidal cycle given with the 95% confidence limits.

| Hour of Tidal Cycle | Water Height cm | Water Temperature C | | | |
|------------------------|--------------------|------------------------|---------------------|----------------------|---------------------|
| | | Ordinary Conditions | First Experiment | Second Experiment | Third Experiment |
| 1 | 0 | 13.5 \pm 0.4 | 11.4 \pm 0.5 | 14.0 \pm 0.4 | |
| 2 | 0 | 13.7 \pm 0.4 | 11.8 \pm 0.5 | 14.3 \pm 0.3 | |
| 3 | 5.8 \pm 1.6 | 13.8 \pm 0.5 | 12.2 \pm 0.6 | 14.5 \pm 0.3 | 12.0 \pm 1.3 |
| 4 | 13.1 \pm 1.1 | 13.5 \pm 0.6 | 12.2 \pm 0.7 | 14.7 \pm 0.3 | 12.4 \pm 0.6 |
| 5 | 19.9 \pm 1.0 | 12.8 \pm 0.6 | 11.8 \pm 0.7 | 14.6 \pm 0.3 | 12.3 \pm 0.6 |
| 6 | 22.5 \pm 1.1 | 12.2 \pm 0.5 | 11.2 \pm 0.7 | 14.3 \pm 0.2 | 12.2 \pm 0.4 |
| 7 | 20.0 \pm 1.4 | 11.7 \pm 0.5 | 11.0 \pm 0.8 | 13.9 \pm 0.3 | |
| 8 | 14.2 \pm 2.0 | 11.6 \pm 0.5 | 10.6 \pm 0.8 | 13.7 \pm 0.4 | |
| 9 | 6.2 \pm 1.6 | 11.8 \pm 0.4 | 10.5 \pm 0.7 | 13.5 \pm 0.4 | |
| 10 | 0.6 \pm 0.7 | 12.2 \pm 0.4 | 10.4 \pm 0.6 | 13.4 \pm 0.5 | |
| 11 | 0 | 12.5 \pm 0.3 | 10.8 \pm 0.7 | 13.6 \pm 0.5 | |
| 12 | 0 | 13.1 \pm 0.4 | 11.2 \pm 0.6 | 13.8 \pm 0.5 | |
| Total Cycle | | 12.7 \pm 0.5 | 11.2 \pm 0.4 | 14.0 \pm 0.3 | 12.2 \pm 0.2 |

APPENDIX I.

Continued

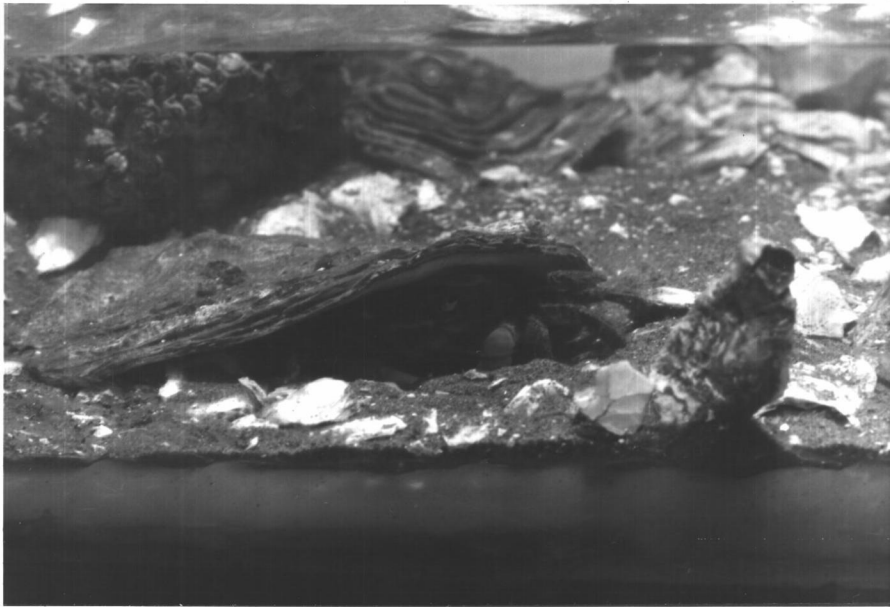
Hour of
Tidal Cycle

Salinity ‰

Ordinary
ConditionsFirst
ExperimentSecond
ExperimentThird
Experiment

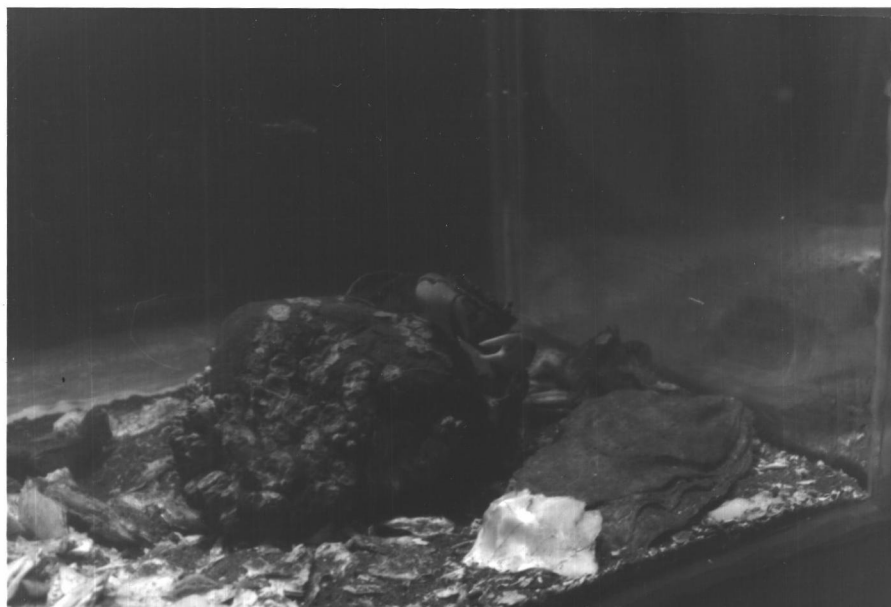
| | | | | |
|-------------|------------|------------|------------|------------|
| 1 | 31.5 ± 0.5 | 32.1 ± 0.9 | 32.7 ± 0.3 | |
| 2 | 31.6 ± 0.3 | 31.6 ± 0.7 | 32.5 ± 0.3 | |
| 3 | 31.6 ± 0.4 | 31.2 ± 0.8 | 32.5 ± 0.2 | 29.5 ± 2.2 |
| 4 | 31.6 ± 0.4 | 31.3 ± 1.0 | 32.5 ± 0.3 | 28.8 ± 2.2 |
| 5 | 32.0 ± 0.4 | 31.6 ± 1.1 | 32.5 ± 0.3 | 29.2 ± 2.1 |
| 6 | 32.1 ± 0.5 | 32.2 ± 1.2 | 32.6 ± 0.3 | 29.7 ± 1.8 |
| 7 | 32.4 ± 0.6 | 32.6 ± 1.3 | 32.6 ± 0.3 | |
| 8 | 32.3 ± 0.6 | 32.9 ± 1.2 | 32.8 ± 0.2 | |
| 9 | 32.3 ± 0.6 | 33.3 ± 0.9 | 32.8 ± 0.3 | |
| 10 | 32.1 ± 0.6 | 33.3 ± 1.1 | 32.8 ± 0.3 | |
| 11 | 31.9 ± 0.5 | 33.0 ± 1.0 | 32.7 ± 0.4 | |
| 12 | 31.8 ± 0.4 | 32.8 ± 0.9 | 32.7 ± 0.3 | |
| Total Cycle | 31.9 ± 0.2 | 32.3 ± 0.5 | 32.6 ± 0.1 | 29.4 ± 0.5 |

APPENDIX II. Photographs of some behavioral units in the repertoire
of Hemigrapsus oregonensis.



Hemigrapsus oregonensis sheltering under an oyster shell

APPENDIX II. Continued



A male Hemigrapsus oregonensis perching upon a rock

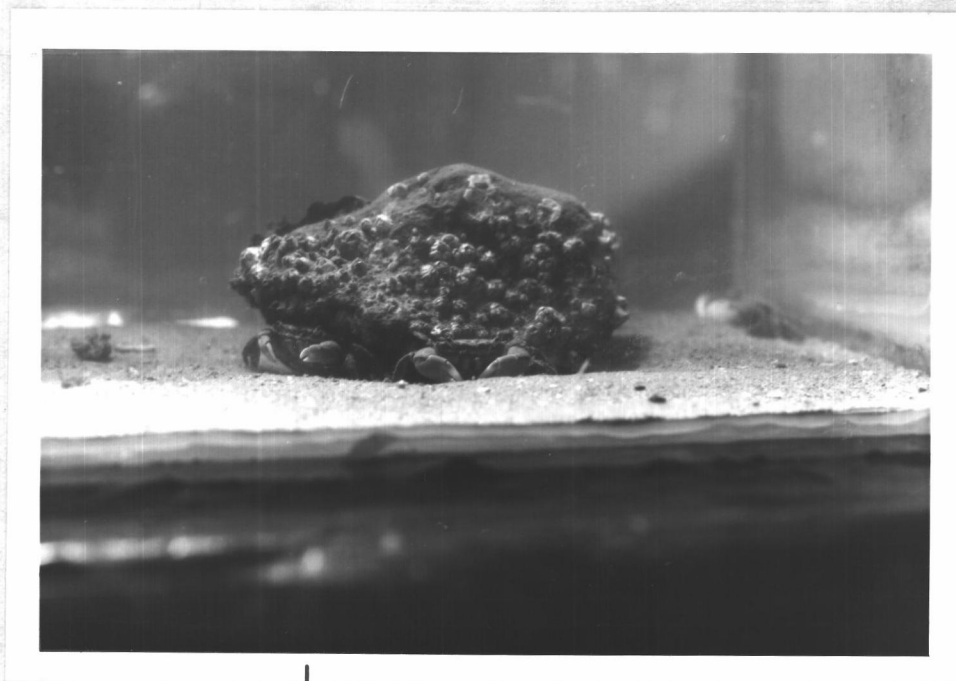
APPENDIX II. Continued



Hemigrapsus oregonensis digging into the sand

APPENDIX II.

Continued



Male and female Hemigrapsus oregonensis in walking leg contact
with the female on the left giving a mid intensity lateral
merus display with one claw

APPENDIX III. The proportion of the lunar day spent by male Hemigrapsus oregonensis in various activities under ordinary conditions.

| | UNSH | SHIEL | PERC | BURD | MATP | HIGH | LOWP | HUDP | STAN | WALK |
|----------------------------|------|-------|------|------|------|------|------|------|------|------|
| <u>Replica</u> | | | | | | | | | | |
| 1 | .868 | .039 | .003 | .089 | 0 | .638 | .161 | .048 | .707 | .128 |
| 2 | .739 | .243 | .018 | 0 | 0 | .633 | .067 | .008 | .569 | .154 |
| 3 | .829 | .141 | .023 | .006 | 0 | .551 | .191 | .078 | .682 | .139 |
| 4 | .892 | .024 | .001 | .083 | .003 | .558 | .241 | .042 | .736 | .113 |
| 5 | .700 | .238 | .008 | .054 | 0 | .458 | .191 | .058 | .575 | .136 |
| 6 | .708 | .177 | .006 | .110 | 0 | .450 | .137 | .053 | .510 | .129 |
| 7 | .774 | .180 | .006 | .041 | 0 | .562 | .115 | .029 | .522 | .184 |
| 8 | .680 | .173 | .003 | .144 | 0 | .417 | .124 | .115 | .528 | .127 |
| Mean | .774 | .152 | .008 | .066 | .001 | .533 | .153 | .054 | .604 | .139 |
| Standard Error | .029 | .029 | .003 | .018 | .001 | .029 | .019 | .011 | .032 | .008 |
| Coefficient of Variation % | 10.5 | 53.9 | 100. | 75.8 | 300. | 15.5 | 35.3 | 59.2 | 15.1 | 15.8 |

APPENDIX III. Continued

| | CLIM | FAST | DISP | WLCN | FIGH | PREF | FEED | DIG | SEX | CLEN |
|----------------------------------|------|-------|------|------|-------|------|------|-------|--------|------|
| <u>Replica</u> | | | | | | | | | | |
| 1 | .040 | .001 | .023 | .040 | .004 | .118 | .197 | .010 | 0 | .029 |
| 2 | .052 | .003 | .009 | .025 | .003 | .061 | .112 | .0007 | .0002 | .035 |
| 3 | .043 | .0005 | .013 | .055 | .003 | .038 | .048 | .007 | 0 | .044 |
| 4 | .047 | .001 | .022 | .042 | .002 | .051 | .093 | .001 | 0 | .040 |
| 5 | .031 | .002 | .011 | .014 | .003 | .085 | .196 | .005 | 0 | .013 |
| 6 | .076 | .003 | .014 | .068 | .002 | .042 | .083 | .009 | 0 | .025 |
| 7 | .069 | .002 | .032 | .093 | .003 | .058 | .100 | .003 | 0 | .007 |
| 8 | .034 | .001 | .012 | .022 | .0003 | .032 | .100 | .011 | 0 | .010 |
| Mean | .049 | .002 | .017 | .045 | .002 | .061 | .116 | .006 | .00002 | .025 |
| Standard Error | .006 | .0004 | .003 | .009 | .0004 | .010 | .019 | .001 | .00002 | .005 |
| Coefficient of Variation % | 32.6 | 50.0 | 47.0 | 57.8 | 50.0 | 45.9 | 45.7 | 66.7 | 300. | 56.0 |

APPENDIX IV.

The proportion of the lunar day spent by female Hemigrapsus oregonensis in various activities under ordinary conditions.

| | UNSH | SHEL | PERC | BURD | MATP | HIGH | LOWP | HUDP | STAN | WALK |
|----------------------------|------|------|------|------|------|------|------|------|------|------|
| <u>Replica</u> | | | | | | | | | | |
| 1 | .589 | .302 | .013 | .096 | 0 | .413 | .216 | .006 | .577 | .079 |
| 2 | .491 | .418 | .098 | .068 | 0 | .405 | .075 | .018 | .400 | .096 |
| 3 | .532 | .439 | .015 | .013 | 0 | .399 | .115 | .032 | .536 | .061 |
| 4 | .407 | .509 | .017 | .066 | 0 | .350 | .094 | .026 | .402 | .069 |
| 5 | .371 | .548 | .026 | .055 | 0 | .336 | .097 | 0 | .343 | .091 |
| 6 | .623 | .292 | .008 | .076 | 0 | .516 | .115 | .004 | .489 | .193 |
| 7 | .642 | .297 | .018 | .043 | 0 | .473 | .106 | .071 | .562 | .086 |
| 8 | .357 | .535 | .025 | .083 | 0 | .270 | .091 | .036 | .376 | .068 |
| Mean | .502 | .418 | .018 | .062 | 0 | .395 | .114 | .030 | .460 | .093 |
| Standard Error | .040 | .038 | .010 | .009 | 0 | .028 | .015 | .011 | .032 | .015 |
| Coefficient of Variation % | 22.5 | 26.1 | 161. | 41.9 | 0 | 19.7 | 37.7 | 103. | 19.8 | 45.2 |

APPENDIX IV. Continued

| | CLIM | FAST | DISP | WLCN | FIGH | PREF | FEED | DIG | SEX | CLEN |
|----------------------------------|------|-------|------|------|-------|------|------|-------|-------|------|
| <u>Replica</u> | | | | | | | | | | |
| 1 | .028 | .002 | .005 | .016 | 0 | .137 | .248 | .001 | 0 | .064 |
| 2 | .027 | .002 | .003 | .007 | .0002 | .159 | .325 | .002 | .005 | .006 |
| 3 | .002 | .001 | .003 | .064 | 0 | .032 | .053 | .0005 | 0 | .050 |
| 4 | .032 | .001 | .002 | .009 | 0 | .229 | .452 | .004 | 0 | .008 |
| 5 | .008 | .004 | .004 | .006 | .002 | .148 | .327 | 0 | 0 | .029 |
| 6 | .036 | .001 | .012 | .066 | 0 | .134 | .282 | .004 | 0 | .020 |
| 7 | .043 | .001 | .005 | .052 | 0 | .082 | .141 | .002 | 0 | .019 |
| 8 | .008 | .001 | .008 | .028 | .0002 | .097 | .204 | .0008 | 0 | .023 |
| Mean | .023 | .002 | .005 | .031 | .0003 | .127 | .254 | .002 | .0006 | .027 |
| Standard Error | .008 | .0004 | .001 | .009 | .0002 | .020 | .043 | .0007 | .001 | .007 |
| Coefficient of Variation % | 104. | 50.0 | 60.0 | 83.9 | 233. | 45.7 | 48.4 | 100. | 667. | 77.8 |

APPENDIX V.

The proportion of observed time male Hemigrapsus oregonensis spent in various activities at each hour of the tidal cycle (12.4 hours) under ordinary conditions.

| Lunar hour after low tide | Buried and Sheltered | | Walk and Climb | | Feeding | | Displaying | | Digging | |
|---------------------------------|-------------------------|------|-------------------|------|---------|------|------------|------|---------|-------|
| | Night | Day | Night | Day | Night | Day | Night | Day | Night | Day |
| 1 | .203 | .398 | .011 | .014 | 0 | 0 | .004 | .014 | 0 | 0 |
| 2 | .217 | .525 | .074 | .008 | 0 | 0 | .015 | 0 | 0 | .0004 |
| 3 | .111 | .222 | .288 | .254 | .129 | .268 | .009 | .023 | .004 | .002 |
| 4 | .003 | .108 | .438 | .310 | .182 | .397 | .013 | .023 | .002 | .0004 |
| 5 | .046 | .180 | .416 | .292 | .235 | .097 | .014 | .040 | 0 | .002 |
| 6 | .112 | .128 | .166 | .321 | .172 | .165 | .016 | .020 | 0 | .004 |
| 7 | .051 | .126 | .313 | .254 | .223 | .220 | .031 | .046 | .0006 | .002 |
| 8 | .089 | .072 | .360 | .278 | .117 | .177 | .026 | .035 | .001 | .011 |
| 9 | .048 | .168 | .263 | .232 | .123 | .185 | .020 | .017 | 0 | .021 |
| 10 | .062 | .559 | .056 | .070 | .018 | .021 | .022 | .001 | .027 | .008 |
| 11 | .214 | .519 | .008 | .016 | 0 | 0 | 0 | .003 | 0 | .016 |
| 12 | .167 | .343 | .065 | .002 | 0 | 0 | .009 | 0 | 0 | .018 |

APPENDIX VI.

The proportion of observed time female Hemigrapsus oregonensis spent in various activities at each hour of the tidal cycle (12.4 hours) under ordinary conditions.

| Lunar hour after low tide | Buried and Sheltered | | Walk and Climb | | Feeding | | Displaying | | Digging | |
|---------------------------------|-------------------------|------|-------------------|------|---------|------|------------|-------|---------|-------|
| | Night | Day | Night | Day | Night | Day | Night | Day | Night | Day |
| 1 | .500 | .804 | .011 | .013 | 0 | 0 | 0 | 0 | 0 | .002 |
| 2 | .244 | .626 | .005 | .007 | 0 | 0 | 0 | .002 | 0 | .0003 |
| 3 | .188 | .439 | .266 | .120 | .136 | .378 | .006 | .013 | .008 | .0004 |
| 4 | .444 | .82 | .182 | .176 | .506 | .454 | .008 | .011 | 0 | 0 |
| 5 | .393 | .350 | .157 | .261 | .307 | .406 | .006 | .007 | 0 | .0008 |
| 6 | .272 | .284 | .242 | .087 | .495 | .629 | .002 | .005 | 0 | .001 |
| 7 | .440 | .364 | .129 | .179 | .338 | .492 | 0 | .020 | 0 | .003 |
| 8 | .220 | .486 | .167 | .101 | .296 | .492 | .002 | .017 | 0 | .002 |
| 9 | .426 | .427 | .141 | .142 | .373 | .338 | .002 | .011 | 0 | .009 |
| 10 | .209 | .795 | .061 | .111 | .001 | .120 | 0 | .0004 | .003 | .009 |
| 11 | .471 | .795 | .003 | .002 | 0 | 0 | .005 | 0 | 0 | 0 |
| 12 | .607 | .840 | .022 | .002 | .042* | 0 | 0 | 0 | 0 | .0004 |

* Feeding done while submerged in a puddle.

APPENDIX VII. The proportion of the lunar day spent by male Hemigrapsus oregonensis in various activities during Experiment I.

| | UNSH | SHEL | PERC | BURD | MATP | HIGH | LOWP | HUDP | STAN | WALK |
|----------------|------|------|------|------|------|------|------|------|------|------|
| <u>Replica</u> | | | | | | | | | | |
| Con 1 | .956 | .044 | .019 | 0 | 0 | .415 | .277 | .131 | .735 | .109 |
| 8 | .825 | .175 | .008 | 0 | 0 | .377 | .198 | .198 | .688 | .099 |
| Mean | .890 | .110 | .014 | 0 | 0 | .396 | .238 | .164 | .712 | .104 |
| Std Err | .066 | .066 | .006 | 0 | 0 | .019 | .040 | .033 | .023 | .005 |
| Co Var % | 10.4 | 84.5 | 57.1 | 0 | 0 | 6.8 | 23.5 | 28.6 | 4.6 | 6.7 |
| Low 3 | .783 | .217 | .015 | 0 | 0 | .371 | .285 | .130 | .689 | .098 |
| 6 | .873 | .127 | .030 | .080 | 0 | .349 | .221 | .124 | .553 | .151 |
| Mean | .28 | .172 | .040 | .022 | 0 | .360 | .253 | .127 | .621 | .124 |
| Std Err | .045 | .045 | .008 | .040 | 0 | .011 | .032 | .003 | .068 | .026 |
| Co Var % | 7.7 | 37.2 | 27.5 | 254. | 0 | 4.4 | 17.8 | 3.1 | 15.4 | 29.8 |
| Mod 2 | .832 | .168 | .012 | 0 | .003 | .464 | .267 | .067 | .671 | .111 |
| 5 | .488 | .512 | .003 | .014 | 0 | .214 | .181 | .070 | .414 | .318 |
| 4 | .811 | .189 | .002 | 0 | .002 | .375 | .257 | .083 | .655 | .067 |
| 7 | .509 | .492 | .006 | 0 | 0 | .212 | .194 | .039 | .420 | .064 |
| Mean | .660 | .340 | .022 | .004 | .012 | .316 | .225 | .065 | .540 | .140 |
| Std Err | .094 | .094 | .002 | .004 | .001 | .062 | .022 | .009 | .071 | .060 |
| Co Var % | 28.3 | 55.0 | 18.2 | 175. | 16.7 | 39.2 | 19.6 | 27.7 | 26.3 | 85.7 |

APPENDIX VII. Continued

| | CLIM | FAST | DISP | WLCN | FIGH | PREF | FEED | DIG | SEX | CLEN |
|----------------|------|-------|------|------|-------|------|------|-------|------|------|
| <u>Replica</u> | | | | | | | | | | |
| Con 1 | .111 | .002 | .030 | .101 | .001 | .045 | .065 | .003 | .005 | .019 |
| 8 | .029 | .003 | .008 | .038 | .005 | .066 | .095 | .008 | 0 | .007 |
| Mean | .070 | .002 | .019 | .070 | .003 | .056 | .080 | .006 | .002 | .013 |
| Std Err | .041 | .0005 | .011 | .031 | .002 | .011 | .015 | .003 | .003 | .006 |
| Co Var % | 82.8 | 35.0 | 84.2 | 62.8 | 100. | 26.8 | 26.2 | 66.7 | 200. | 61.5 |
| Low 3 | .041 | .001 | .045 | .109 | .005 | .046 | .070 | .006 | 0 | .032 |
| 6 | .078 | .001 | .034 | .064 | .003 | .065 | .062 | .008 | 0 | .004 |
| Mean | .060 | .001 | .040 | .086 | .004 | .056 | .066 | .007 | 0 | .018 |
| Std Err | .018 | 0 | .006 | .023 | .0007 | .009 | .004 | .0007 | 0 | .014 |
| Co Var % | 43.3 | 0 | 20.0 | 37.2 | 25.0 | 23.2 | 9.1 | 14.3 | 0 | 111. |
| Mod 2 | .042 | .004 | .025 | .035 | .002 | .031 | .034 | .002 | .003 | .028 |
| 5 | .019 | .001 | .003 | .039 | .003 | .021 | .027 | .001 | 0 | .014 |
| 4 | .088 | .002 | .063 | .142 | .008 | .017 | .022 | .008 | 0 | .016 |
| 7 | .055 | .0008 | .016 | .006 | .026 | .014 | .016 | .008 | .053 | .012 |
| Mean | .051 | .002 | .027 | .056 | .010 | .021 | .025 | .005 | .014 | .018 |
| Std Err | .014 | .0007 | .013 | .030 | .006 | .004 | .004 | .002 | .013 | .004 |
| Co Var % | 56.9 | 70.0 | 96.3 | 107. | 110. | 33.3 | 32.0 | 80.0 | 186. | 33.9 |

APPENDIX VIII. The proportion of the lunar day spent by male Hemigrapsus oregonensis in various activities during Experiment II.

| | UNSH | SHEL | PERC | BURD | MATP | HIGH | LOWP | HUDP | STAN | WALK |
|----------------|------|------|------|------|-------|------|------|------|------|------|
| <u>Replica</u> | | | | | | | | | | |
| Con 1 | .723 | .211 | .065 | 0 | 0 | .631 | .123 | .031 | .646 | .138 |
| 2 | .769 | .213 | .018 | 0 | 0 | .058 | .133 | .007 | .626 | .129 |
| 7 | .785 | .131 | .069 | .014 | 0 | .701 | .101 | .031 | .725 | .108 |
| 8 | .847 | .086 | .040 | .028 | 0 | .651 | .142 | .093 | .752 | .133 |
| Mean | .781 | .160 | .048 | .010 | 0 | .510 | .125 | .040 | .687 | .127 |
| Std Err | .026 | .031 | .012 | .006 | 0 | .152 | .009 | .018 | .030 | .006 |
| Co Var % | 6.5 | 39.0 | 50.0 | 130. | 0 | 59.4 | 14.4 | 92.5 | 8.9 | 10.2 |
| Exp 3 | .819 | .116 | .065 | 0 | 0 | .721 | .126 | .015 | .751 | .081 |
| 4 | .993 | 0 | .007 | 0 | 0 | .632 | .244 | .029 | .817 | .113 |
| 5 | .740 | .254 | .006 | 0 | 0 | .492 | .207 | .149 | .736 | .082 |
| 6 | .754 | .199 | .047 | 0 | .002 | .627 | .197 | .035 | .701 | .109 |
| Mean | .826 | .122 | .031 | 0 | .0005 | .618 | .194 | .057 | .751 | .096 |
| Std Err | .058 | .052 | .015 | 0 | .0005 | .047 | .024 | .031 | .024 | .008 |
| Co Var % | 14.0 | 85.2 | 96.8 | 0 | 200. | 15.2 | 25.2 | 109. | 6.4 | 17.7 |

APPENDIX VIII. Continued

| | CLIM | FAST | DISP | WLCN | FIGH | PREF | FEED | DIG | SEX | CLEN |
|----------------|------|-------|-------|------|-------|------|------|-------|-------|------|
| <u>Replica</u> | | | | | | | | | | |
| Con 1 | .034 | .002 | .047 | .016 | .009 | .083 | .191 | .001 | 0 | .036 |
| 2 | .054 | .002 | .008 | .014 | .004 | .067 | .143 | .002 | 0 | .034 |
| 7 | .036 | .001 | .010 | .054 | .0008 | .152 | .306 | .003 | 0 | .040 |
| 8 | .027 | .002 | .008 | .029 | .001 | .083 | .172 | .003 | .0002 | .039 |
| Mean | .038 | .002 | .018 | .028 | .004 | .096 | .203 | .002 | .0002 | .037 |
| Std Err | .006 | .0002 | .010 | .009 | .002 | .020 | .036 | .0005 | .0002 | .002 |
| Co Var % | 31.6 | 25.0 | 105.6 | 64.3 | 100. | 41.7 | 35.0 | 50.0 | 250. | 8.1 |
| Exp 3 | .039 | .0005 | .014 | .030 | .001 | .003 | .018 | .0005 | .001 | .047 |
| 4 | .087 | .004 | .024 | .056 | .003 | .023 | .031 | 0 | 0 | .027 |
| 5 | .017 | .0007 | .014 | .012 | .001 | .036 | .062 | .002 | 0 | .052 |
| 6 | .025 | .001 | .026 | .040 | .003 | .047 | .113 | .007 | 0 | .028 |
| Mean | .042 | .002 | .020 | .034 | .002 | .027 | .056 | .002 | .0002 | .038 |
| Std Err | .016 | .0005 | .003 | .009 | .0005 | .010 | .021 | .002 | .0002 | .009 |
| Co Var % | 73.8 | 50.0 | 30.0 | 52.9 | 50.0 | 70.4 | 75.0 | 150. | 250. | 34.2 |

APPENDIX IX. The proportion of the lunar day spent by female Hemigrapsus oregonensis in various activities during Experiment I.

| | UNSH | SHEL | PERC | BURD | MATP | HIGH | LOWP | HUDP | STAN | WALK |
|----------------|------|------|------|------|------|------|------|-------|------|------|
| <u>Replica</u> | | | | | | | | | | |
| Con 1 | .671 | .329 | .006 | .013 | 0 | .334 | .167 | .099 | .472 | .199 |
| 8 | .589 | .423 | .019 | .067 | 0 | .377 | .092 | .015 | .374 | .107 |
| Mean | .630 | .376 | .012 | .040 | 0 | .356 | .130 | .057 | .423 | .153 |
| Std Err | .041 | .047 | .006 | .027 | 0 | .021 | .037 | .042 | .049 | .046 |
| Co Var % | 9.2 | 17.6 | 75.0 | 95.0 | 0 | 8.4 | 40.8 | 103.5 | 16.3 | 42.5 |
| Low 3 | .825 | .175 | .031 | .015 | 0 | .396 | .282 | .094 | .685 | .115 |
| 6 | .313 | .687 | .050 | .004 | 0 | .263 | .057 | .010 | .289 | .041 |
| Mean | .569 | .431 | .040 | .010 | 0 | .330 | .170 | .052 | .487 | .078 |
| Std Err | .256 | .256 | .009 | .006 | 0 | .066 | .112 | .042 | .199 | .037 |
| Co Var % | 63.6 | 84.0 | 32.5 | 80.0 | 0 | 28.4 | 93.5 | 114. | 57.5 | 66.7 |
| Mod 2 | .530 | .470 | .055 | 0 | 0 | .255 | .177 | .067 | .404 | .099 |
| 5 | .490 | .510 | .020 | .007 | 0 | .199 | .150 | .101 | .406 | .048 |
| 4 | .463 | .537 | .031 | .014 | 0 | .309 | .114 | .052 | .407 | .041 |
| 7 | .526 | .473 | .013 | .014 | 0 | .326 | .130 | .030 | .419 | .072 |
| Mean | .502 | .498 | .030 | .009 | 0 | .272 | .143 | .062 | .409 | .065 |
| Std Err | .016 | .016 | .009 | .004 | 0 | .028 | .136 | .015 | .004 | .013 |
| Co Var % | 6.3 | 6.4 | 60.0 | 77.7 | 0 | 21.0 | 190. | 48.4 | 1.7 | 40.0 |

APPENDIX IX. Continued

| | CLIM | FAST | DISP | WLCN | FIGH | PREF | FEED | DIG | SEX | CLEN |
|----------------|------|-------|-------|------|-------|------|------|-------|-------|-------|
| <u>Replica</u> | | | | | | | | | | |
| Con 1 | .058 | .009 | .023 | .078 | .0002 | .169 | .090 | .001 | .0007 | .015 |
| 8 | .035 | .004 | .010 | .013 | 0 | .100 | .126 | 0 | 0 | .002 |
| Mean | .047 | .007 | .016 | .046 | .0005 | .134 | .108 | .0005 | .0005 | .008 |
| Std Err | .011 | .003 | .006 | .032 | .0005 | .035 | .018 | .0005 | .0005 | .006 |
| Co Var % | 35.6 | 57.1 | 56.2 | 100. | 140. | 36.6 | 23.1 | 140. | 140. | 112.5 |
| Low 3 | .033 | .002 | .027 | .070 | .0003 | .088 | .159 | .0003 | .001 | .014 |
| 6 | .005 | .001 | .002 | .002 | 0 | .056 | .036 | .003 | 0 | .012 |
| Mean | .019 | .002 | .014 | .036 | .0005 | .072 | .098 | .002 | .0005 | .013 |
| Std Err | .014 | .0007 | .013 | .034 | .0005 | .016 | .062 | .0007 | .0005 | .0007 |
| Co Var % | 105. | 50.0 | 128.6 | 133. | 140. | 31.9 | 88.8 | 50.0 | 140. | 7.7 |
| Mod 2 | .041 | .005 | .009 | .023 | .0002 | .037 | .053 | .0003 | 0 | .026 |
| 5 | .025 | .002 | .022 | .031 | 0 | .021 | .024 | .008 | 0 | .003 |
| 4 | .022 | .0007 | .004 | .002 | 0 | .023 | .035 | 0 | 0 | .011 |
| 7 | .025 | .002 | .003 | .006 | 0 | .057 | .019 | .001 | .065 | .050 |
| Mean | .023 | .002 | .010 | .016 | .0003 | .034 | .033 | .002 | .016 | .022 |
| Std Err | .008 | .001 | .004 | .007 | .0002 | .008 | .008 | .002 | .016 | .010 |
| Co Var % | 69.6 | 100. | 90.0 | 87.5 | 167. | 50.0 | 45.5 | 200. | 200. | 95.4 |

APPENDIX X.

The proportion of the lunar day spent by female Hemigrapsus oregonensis in various activities during Experiment II.

| | UNSH | SHEL | PERC | BURD | MATP | HIGH | LOWP | HUDP | STAN | WALK |
|----------------|------|------|------|------|------|------|------|------|------|------|
| <u>Replica</u> | | | | | | | | | | |
| Con 1 | .477 | .448 | .074 | 0 | 0 | .387 | .157 | .002 | .448 | .084 |
| 2 | .275 | .681 | .030 | .014 | 0 | .307 | .010 | .002 | .267 | .052 |
| 7 | .561 | .325 | .100 | .014 | 0 | .531 | .100 | .037 | .557 | .110 |
| 8 | .412 | .552 | .021 | .015 | 0 | .353 | .094 | .003 | .359 | .091 |
| Mean | .431 | .512 | .056 | .011 | 0 | .394 | .090 | .011 | .408 | .084 |
| Std Err | .060 | .074 | .018 | .004 | 0 | .048 | .030 | .008 | .062 | .012 |
| Co Var % | 28.1 | 28.9 | 66.1 | 63.6 | 0 | 24.6 | 66.7 | 154. | 30.4 | 28.6 |
| Exp 3 | .691 | .252 | .043 | .014 | 0 | .548 | .158 | .072 | .689 | .046 |
| 4 | .406 | .448 | .137 | .010 | 0 | .482 | .053 | .035 | .502 | .054 |
| 5 | .341 | .622 | .023 | .014 | 0 | .340 | .055 | 0 | .345 | .050 |
| 6 | .465 | .483 | .052 | 0 | 0 | .412 | .046 | .045 | .397 | .105 |
| Mean | .476 | .451 | .064 | .010 | 0 | .446 | .078 | .038 | .483 | .064 |
| Std Err | .076 | .076 | .025 | .004 | 0 | .045 | .026 | .015 | .076 | .014 |
| Co Var % | 31.9 | 33.9 | 78.1 | 70.0 | 0 | 20.2 | 67.9 | 78.9 | 31.5 | 43.8 |

APPENDIX X.

Continued

| | CLIM | FAST | DISP | WLCN | FIGH | PREF | FEED | DIG | SEX | CLEN |
|----------------|------|-------|------|------|-------|------|------|-------|-----|------|
| <u>Replica</u> | | | | | | | | | | |
| Con 1 | .022 | .002 | .001 | .021 | .0002 | .071 | .149 | .0002 | 0 | .037 |
| 2 | .001 | .0008 | .005 | .002 | 0 | .099 | .223 | 0 | 0 | .026 |
| 7 | .012 | .002 | .006 | .040 | .0002 | .093 | .177 | .001 | 0 | .042 |
| 8 | .008 | .002 | .008 | .007 | 0 | .110 | .213 | .002 | 0 | .022 |
| Mean | .011 | .002 | .005 | .018 | .0005 | .093 | .190 | .001 | 0 | .032 |
| Std Err | .004 | .0002 | .002 | .008 | .0003 | .008 | .017 | .0005 | 0 | .004 |
| Co Var % | 81.8 | 25.0 | 60.0 | 94.4 | 120. | 17.2 | 17.9 | 100. | 0 | 28.1 |
| Exp 3 | .012 | .0007 | .015 | .091 | .0005 | .022 | .026 | .0007 | 0 | .027 |
| 4 | .006 | .002 | .003 | .024 | .0003 | .092 | .192 | .0007 | 0 | .057 |
| 5 | .004 | .0003 | .006 | .002 | .0008 | .035 | .071 | 0 | 0 | .017 |
| 6 | .016 | .002 | .005 | .019 | 0 | .043 | .121 | 0 | 0 | .015 |
| Mean | .010 | .002 | .007 | .034 | .001 | .048 | .102 | .0005 | 0 | .029 |
| Std Err | .003 | .0002 | .002 | .020 | .0002 | .015 | .036 | .0003 | 0 | .010 |
| Co Var % | 60.0 | 25.0 | 71.4 | 115. | 50.0 | 62.5 | 69.6 | 120. | 0 | 65.5 |

APPENDIX XI.

The time spent feeding upon various types of food as a proportion of the total observed time during Experiment III.

| | SAND | MUSSEL | ISOPOD | ROCK/SHELL SURFACE | OTHER FOOD |
|----------------|------|--------|--------|-----------------------|------------|
| MALES | | | | | |
| <u>Control</u> | | | | | |
| Mean | .032 | .111 | .131 | .003 | 0 |
| Std Dev | .022 | .067 | .098 | .004 | 0 |
| Co Var % | 68.8 | 60.4 | 74.8 | 133. | 0 |
| <u>Exposed</u> | | | | | |
| Mean | .038 | .143 | .064 | .007 | .002 |
| Std Dev | .023 | .068 | .066 | .008 | .0035 |
| Co Var % | 60.5 | 47.6 | 103. | 114. | 175. |
| FEMALES | | | | | |
| <u>Control</u> | | | | | |
| Mean | .042 | .019 | .040 | .015 | .003 |
| Std Dev | .040 | .015 | .037 | .015 | .0038 |
| Co Var % | 95.2 | 78.9 | 92.5 | 100. | 127. |
| <u>Exposed</u> | | | | | |
| Mean | .010 | .040 | .026 | .022 | .005 |
| Std Dev | .009 | .026 | .041 | .021 | .010 |
| Co Var % | 90.0 | 65.0 | 158. | 95.4 | 200. |

APPENDIX XII.

The time spent in various prefeeding and feeding behaviors as a proportion of the total observed time during Experiment III.

| | PROBING | DACTYL SEARCHING | SWEEPING OUT | HOLDING FOOD | TOTAL PREFEEDING |
|----------------|---------|---------------------|-----------------|-----------------|---------------------|
| MALES | | | | | |
| <u>Control</u> | | | | | |
| Mean | .078 | .043 | .062 | .024 | .207 |
| Std Dev | .049 | .022 | .045 | .038 | .146 |
| Co Var % | 62.8 | 51.1 | 72.6 | 158. | 70.5 |
| <u>Exposed</u> | | | | | |
| Mean | .116 | .053 | .052 | .005 | .226 |
| Std Dev | .043 | .012 | .016 | .005 | .071 |
| Co Var % | 37.1 | 22.6 | 30.8 | 100. | 31.4 |
| FEMALES | | | | | |
| <u>Control</u> | | | | | |
| Mean | .113 | .037 | .020 | 0 | .170 |
| Std Dev | .051 | .004 | .014 | 0 | .059 |
| Co Var % | 45.1 | 10.8 | 70.0 | 0 | 34.7 |
| <u>Exposed</u> | | | | | |
| Mean | .100 | .016 | .043 | .008 | .166 |
| Std Dev | .046 | .010 | .036 | .010 | .079 |
| Co Var % | 46.0 | 62.5 | 83.7 | 125. | 47.6 |

APPENDIX XII. Continued

| | CLAW FEEDING | SCRAPE FEEDING | CLAW TEARING | SWEEPING SAND | TOTAL FEEDING |
|----------------|-----------------|-------------------|-----------------|------------------|------------------|
| MALES | | | | | |
| <u>Control</u> | | | | | |
| Mean | .027 | .003 | .242 | .018 | .290 |
| Std Dev | .023 | .0036 | .071 | .013 | .063 |
| Co Var % | 85.2 | 120. | 29.3 | 72.2 | 21.7 |
| <u>Exposed</u> | | | | | |
| Mean | .038 | .007 | .206 | .006 | .257 |
| Std Dev | .024 | .008 | .070 | .006 | .062 |
| Co Var % | 63.2 | 114. | 34.0 | 100. | 24.1 |
| FEMALES | | | | | |
| <u>Control</u> | | | | | |
| Mean | .046 | .007 | .061 | .038 | .152 |
| Std Dev | .045 | .009 | .017 | .034 | .077 |
| Co Var % | 97.8 | 128. | 27.9 | 89.5 | 50.6 |
| <u>Exposed</u> | | | | | |
| Mean | .010 | .022 | .073 | .0008 | .106 |
| Std Dev | .008 | .020 | .031 | .00096 | .041 |
| Co Var % | 80.0 | 90.9 | 42.4 | 120. | 38.7 |