

AN ABSTRACT OF THE THESIS OF

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Title: POPULATION STRUCTURE OF THE INTERTIDAL SHORE  
CRAB *HEMIGRAPSUS OREGONENSIS* (BRACHYURA,  
GRAPSIDAE) IN YAQUINA BAY, A CENTRAL OREGON  
COAST ESTUARY

Abstract approved:

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Dr. ~~C. J. Dayne~~

The Hemigrapsus oregonensis population at Coquille Point in the Yaquina Bay Estuary on the Central Oregon Coast was studied from April, 1972 through May, 1973. The population was found to be vertically stratified from the 1 ft level to the 5 ft level. Population densities were found to be most dense in the upper regions. Greatest population density (about 20 crab/m<sup>2</sup>) was found to be in the 3-4 ft interval above MLLW (0.0 ft level).

The population sex ratio was biased in favor of the females (53.3%) and did not vary appreciably during the year. The reproductive season, as determined by the percentage of berried females, was from February through May with a peak (32.8%) during March. Brooding females were found every month during the study, indicating

a continuous, low level egg production throughout the year. A model for estimating potential egg production is given. The minimum carapace width of brooding females was found to be 0.86 cm.

Biomass values were determined from carapace width measurements. A conversion equation is given. Biomass values generally increased as tidal height increased. The average biomass value for the area was  $8.47 \text{ g/m}^2$ . The average dry weight per crab decreased as tidal height increased. The average dry weight per crab at each tidal height (about 0.5 g) did not significantly increase during the study, suggesting a stable population. The average monthly production showed an over-all negative rate of  $-1.23 \text{ g/m}^2$  per month. No significant differences were found between tidal heights. The net production rate at each tidal height could not be shown to be different from a zero net production rate, again suggesting a stable population.

Monthly distributional patterns indicated an high degree of population mobility. Crabs tested for locomotory activity patterns in the laboratory showed rhythms influenced by both the light regime and the tidal regime. Weak endogenous displays were found for a light component with increased activity during dark periods. Greatest activity generally occurred during dark-high tide periods. It is suggested that the locomotory activity patterns of H. oregonensis are influenced by both a tidal cycle and a light cycle.

Under constant experimental conditions, the endogenous rhythmicity decayed within 3-9 tidal cycles and resulted in more or less continuous random movements. Only about 50% of the tested crabs, however, displayed an endogenous locomotory rhythm.

Population Structure of the Intertidal Shore Crab Hemigrapsus  
oregonensis (Brachyura, Grapsidae) in Yaquina Bay,  
a Central Oregon Coast Estuary

by

Robert Edward Batie

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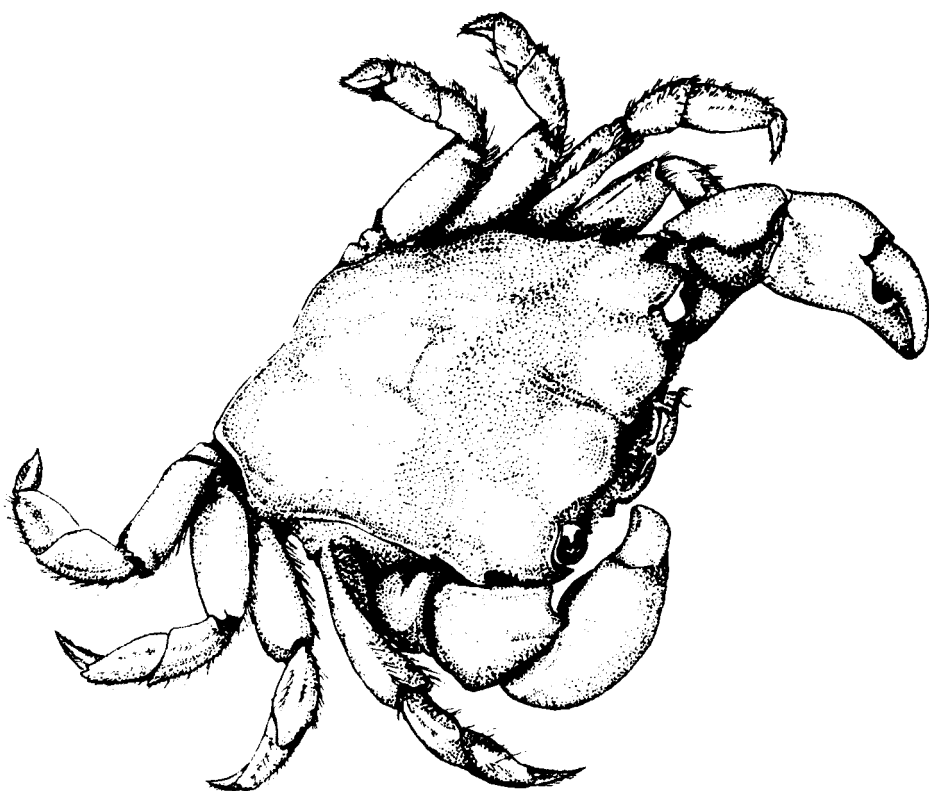
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POPULATION STRUCTURE OF THE INTERTIDAL SHORE  
CRAB HEMIGRAPSUS OREGONENSIS (BRACHYURA,  
GRAPSIDAE) IN YAQUINA BAY, A CENTRAL  
OREGON COAST ESTUARY

INTRODUCTION

The Yaquina Bay Estuary on the Central Oregon Coast is a multiple-use estuary supporting an industrial port, viable commercial fisheries, and active sport fisheries. It is a major port for the export of Northwest timber products to Japan. Other industrial activities include fish processing, log storage, and wood pulp manufacturing. Commercial fisheries based here include those for Dungeness crab, salmon, herring, pink shrimp, bottom fish, and oyster culture. In addition, Yaquina Bay is a major recreation site for charter boat fisheries and bay sport fisheries for salmon, perch, flounder, crab, and several species of clams.

If such a multiple-use resource is to be maintained in a productive state, it must be characterized and carefully monitored with respect to physical and biological changes. One of the first needs for proper estuarine management, then, is a full understanding of the biological processes in the estuary. This study was undertaken in an effort to contribute to this basic knowledge, using, as a test system, the population structure of the intertidal shore crab

Hemigrapsus oregonensis (Dana, 1851).

Yaquina Bay (Figure 1) is a semi-enclosed bay where oceanic water and fresh water run-off meet and, to some degree, mix, hence establishing a salinity gradient; thus Yaquina Bay is a true estuary. The estuary was formed from the drowned river mouth of the Yaquina River, which drains about 400 square miles (1036 km<sup>2</sup>) of the western slopes of the Coastal Mountain Range. The bay is Oregon's sixth largest with a surface area of 2700 acres (1093 hectares) at Mean High Water (MHW) and 1110 acres (449 hectares) at Mean Lower Low Water (MLLW) with 1600 to 1700 tideland acres (648 to 708 hectares) (Fish and Wildlife on Yaquina Bay, Oregon, 1968; Goodwin, Emmett, and Glenne, 1970; Wick, 1970).

The tidal regime in the bay is a mixed semi-diurnal tide, consisting of two high tides and two low tides of different amplitudes and duration per lunar day (24.8 h). At the Marine Science Center dock, 3 km from the collection site, the diurnal tidal range has been established as 8.8 ft (1 ft = 30.48 cm) with the mean tidal level at 4.58 ft above MLLW (Thum, 1972).

### Distribution

Hemigrapsus is a widely distributed genus of crab, occurring intertidally along the entire Pacific Rim from Alaska to Chile and from the USSR, Japan, Hawaii, China, and from New Zealand.

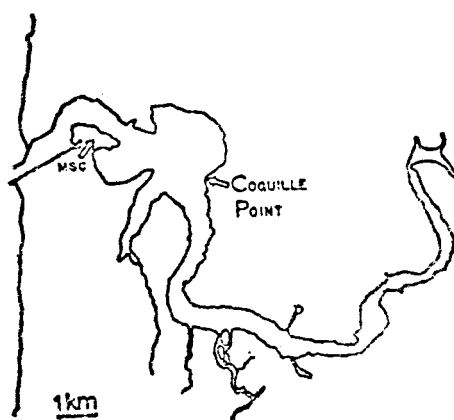
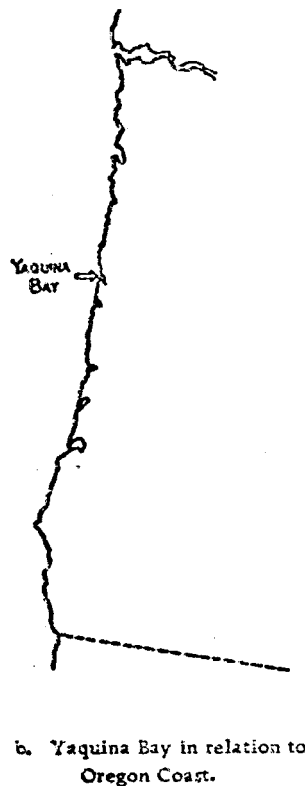
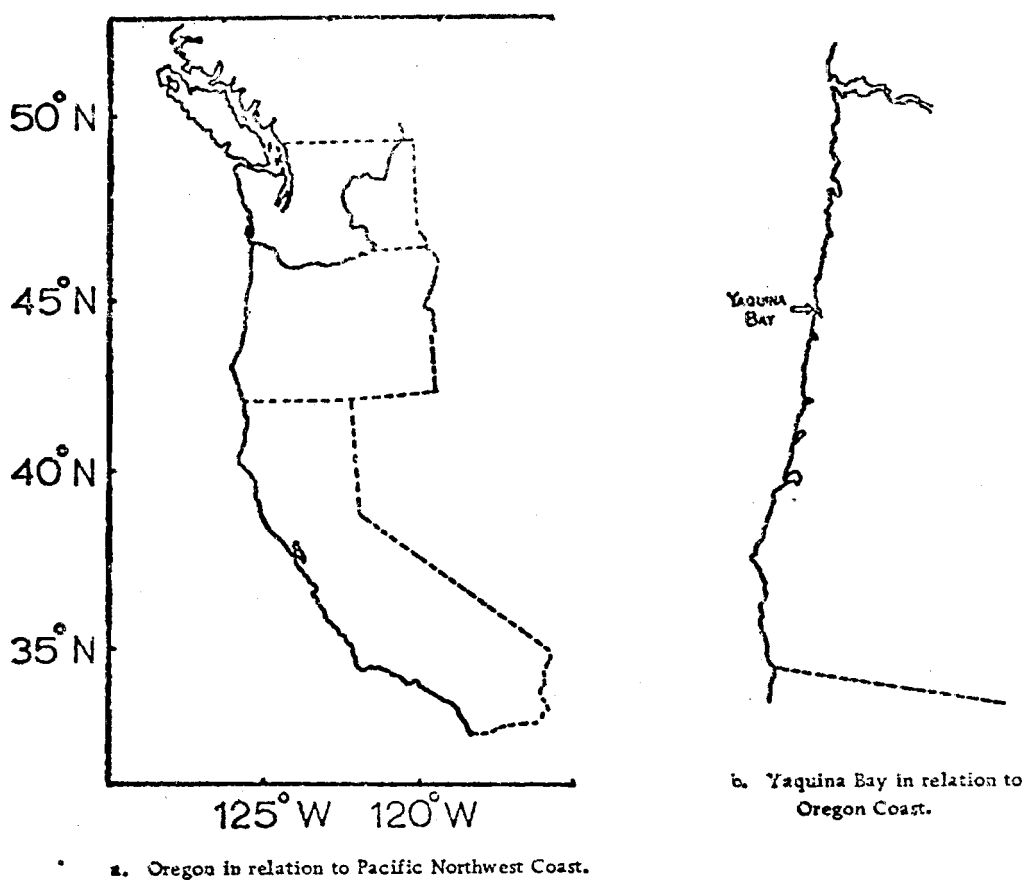


Figure 1. Yaquina Bay



Eleven species have been described within this genus. Along the North American Pacific shores, however, only two species of Hemigrapsus are found: H. nudus and H. oregonensis. Both range from Alaska to the Gulf of California (Schmidt, 1921; Hart, 1968). H. nudus is typically found in rocky outer coast areas with well-aerated, silt-free water. H. oregonensis, in contrast, is more common in regions with a higher silt load and, in general, is more typical of a muddy substratum (Way, 1917; MacKay, 1943; Hiatt, 1948; Knudsen, 1964-a; Low, 1970). Hiatt (1948) has indicated that where these two species overlap there is usually a gradation of substrate types from a muddy or silty lower region, dominated by H. oregonensis, to a gravelly, well-drained upper region inhabited by H. nudus. Overlapping populations in this type of habitat are thought to be approaching their limits of adaptations with respect to habitat suitability. At Coquille Point in the Yaquina Bay Estuary, these two species are found in such an overlapping distribution.

### Natural History

Hemigrapsus oregonensis is a brachyuran decapod crustacean in the family Grapsidae. The adult is a relatively small crab, measuring up to 3.5 cm in carapace width but averaging about 1.5 cm.

Although this species has been considered a scavenger, Knudsen (1964-a) has indicated that food consisted mainly of

diatoms and desmids obtained from scraping rocks with their chelae. Very few animal remains were found in gut analyses and Knudsen concluded that this species is mainly herbivorous.

The life cycle of this crab is similar to others in the family. However, no pre-copulatory behavior pattern seems to exist in Hemigrapsus as it does in some other brachyurans (Williamson, 1903; Churchill, 1918; Knudsen, 1960, 1964-b; Snow and Neilsen, 1966). The mating act, however, exhibits a rather stylized behavior pattern (Knudsen, 1964-a; Yaldwyn, 1966).

Knudsen (1964-a) reported that egg deposition in Puget Sound H. oregonensis began as early as February and was completed by late April, with an average of 7,650 eggs being produced per female per year. He reported that the reproductive season was from April through August. Hatching started in May and continued into July. A second egg brood may be deposited in August and would be hatched by late September. The largest number of berried females occurred in May (90% of the females) with the second brood peak in August (70% of females berried).

Newly deposited eggs are orange but within a week turn a brown to purple color. The eggs also increase in size during the brooding period from about 0.33 mm in diameter to about 0.40 mm (Hart, 1935) before they hatch. There is one pre-zoeal stage prior to hatching, five post-hatching zoeal stages, and one megalopa stage.

A planktonic life of 4 to 5 weeks is necessary for the first young crab stage to appear, which measures about 0.16 cm in carapace width. The time required between egg deposition and adult recruitment may thus vary from about 8 to 13 weeks.

### Investigation

The Hemigrapsus oregonensis population at Coquille Point has been studied in an attempt to answer several general questions:

i) Does the bay population represent a permanent, reproducing population? ii) Does the population structure vary vertically or seasonally and, if so, do these changes correlate with major environmental changes? iii) Is the locomotory activity of the crab influenced by a fluctuating tidal rhythm?

## METHODS AND MATERIALS

The study area at Coquille Point in the Yaquina Bay Estuary ( $44^{\circ} 37' \text{ N. Lat.}, 124^{\circ} 04' \text{ W. Long.}$ ) was marked out in a grid from the 0 ft tidal level to the +5 ft tidal level at 1 ft vertical intervals (Figure 2). At each vertical foot interval, lines were extended horizontally along the beach for 15 ft. Every 3 ft. along the horizontal lines a rod was placed to mark a subplot corner. Thus the total sample area contained 25 subplots, with 5 at each tidal height. Each of the subplots had an area of about  $3 \text{ m}^2$ . Each month during the spring tidal cycle, one subplot at each tidal height was sampled, using a complete population census, and all the crabs collected were sexed, determined if berried, measured, and returned to the same subplot from which they had been sampled. Sampling efficiency was estimated to be greater than 90% as fewer than 10 observed crabs per month escaped collection. Measurements of carapace width, taken at the second lateral carapace tooth (Figure 3), were made with an Almkvist excaliper and reported to the nearest one-hundredth of a centimeter.

Tidal level determinations were based on actual 0.0 ft datum readings obtained at the O. S. U. Marine Science Center from the continuous tidal level recorder. The time of the 0.0 ft level at the MSC plus 10 minutes was the time at which the 0.0 ft level occurred

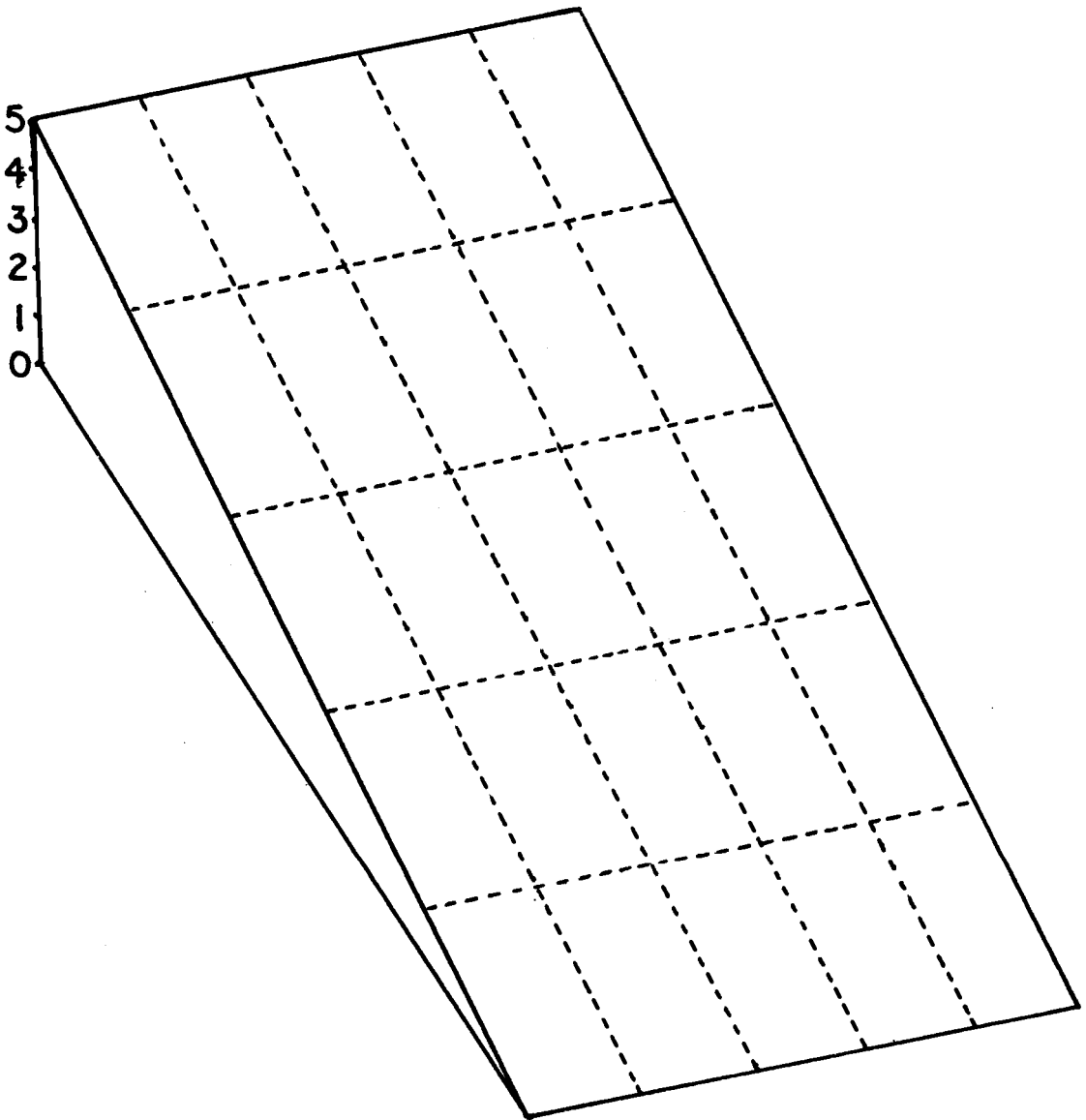


Figure 2. Representation of collection sampling grid used at Coquille Point.

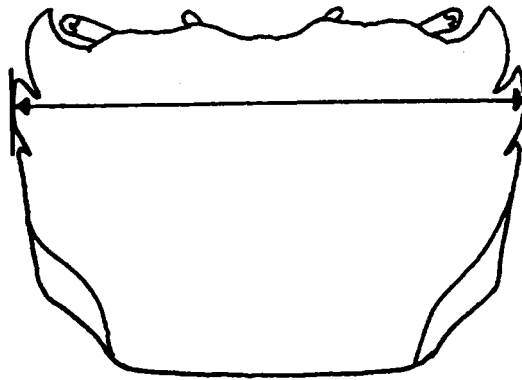


Figure 3. Dorsal view of carapace of Hemigrapsus oregonensis showing position where carapace width measurements were taken (edge of second lateral carapace tooth).

at the collection site. The vertical foot intervals were placed at the proper levels at the collection site by sighting along a yard stick at the water's edge with a hand held level. With the hand level at the 1, 2, or 3 ft level on the yard stick, the line of sight intersecting the beach gave the properly spaced vertical interval. Different tidal levels were marked by pushing metal rods into the substrate. The tidal levels and the grid were established for each collection period. A vertically stratified random sampling technique was used. One subplot at each tidal height was selected each month, having been chosen from a table of random numbers.

The tidal regime for Yaquina Bay was determined from daily predicted tidal levels at the O. S. U. Marine Science Center dock. Tidal predictions were computed by the National Ocean Survey, an agency of the U.S. Department of Commerce's National Oceanic and Atmospheric Administration and were listed in the 1972 and 1973 tide tables, Newport, Oregon. From these daily tidal levels, seven tidal variables were determined and analyzed for the period from April, 1972 through June, 1973.

All temperature measurements were taken with a mercury column thermometer graduated in half Celsius degree increments; estimates were made to the nearest tenth degree.

### Biomass and Production Estimates

A dry weight conversion equation was established from specimens killed and held in formalin for not longer than 48 h. The crabs were measured and dried in an oven at 85 C until constant weight was attained (usually within 24 h). The dry weight value of each crab was then regressed on several other variables using a step-wise multiple regression technique (Snedecor and Cochran, 1969). Having established a relationship between dry weight and carapace width (variable of best fit), biomass estimates were made for each tidal height from measurements of carapace width of each crab and from counts of numbers of crabs in each tidal height interval. Monthly biomass values ( $\text{g/m}^2$ ) were determined for each tidal level.

Production estimates were determined from the net loss or gain in biomass at each tidal height from one month to the next. Production estimates are reported as biomass fluctuations per unit time ( $\text{g/m}^2$  per month) and can be regarded as a measure of population stability (Warren, 1971). In this study, production was defined as a measure of standing crop fluctuation and was not meant to imply the inclusion of relative growth rate data. Hence, the terminology used here and throughout the thesis was somewhat different than that in current usage.



### Locomotory Activity

All activity experiments were carried out in a cold room maintained at a constant ( $\pm 1$  C) temperature of 10 C. The crabs were placed in an activity chamber (Figure 4), one per chamber, and their locomotory responses monitored for a period of up to 9 days. The animals were not fed during the experimental period. The test chambers were constructed of two circular pieces of plexiglass 5 cm high, one having a diameter of 15 cm and the other a diameter of 25 cm. The smaller diameter piece was placed into the larger piece and spaced evenly to give a circular runway. The floor of the chamber was fitted with filter paper saturated with salt water and a lid was placed over the chamber to prevent the crabs from escaping. The seal allowed gases to remain at atmospheric levels but evaporation was very much retarded. The chamber was suspended from a ball-bearing pivoted yoke and gimbal framework. Because the pivotal axes were at right angles to each other, the suspended activity chamber could be tilted in any direction. Micro-switches were placed under the movable frameworks and the displacement of either framework onto the switch would activate or deactivate the switch mechanism, depending on the position of the crab in the chamber. Hence, each time the crab crossed a quadrant of the chamber (rotational axis), the displacement of the chamber activated or deactivated a switch

Figure 4. Activity chamber used in locomotory analysis of Hemigrapsus oregonensis. Chamber was suspended from yoke and gimbal framework to allow displacement in any plane from the horizontal. Microswitches were activated when the crab crossed an axis of rotation. Microswitches were connected to an Esterline-Angus event recorder which allowed continuous activity monitoring. Activity events were recorded as vertical marks on the continuously moving chart and were tabulated as number of events per hour.

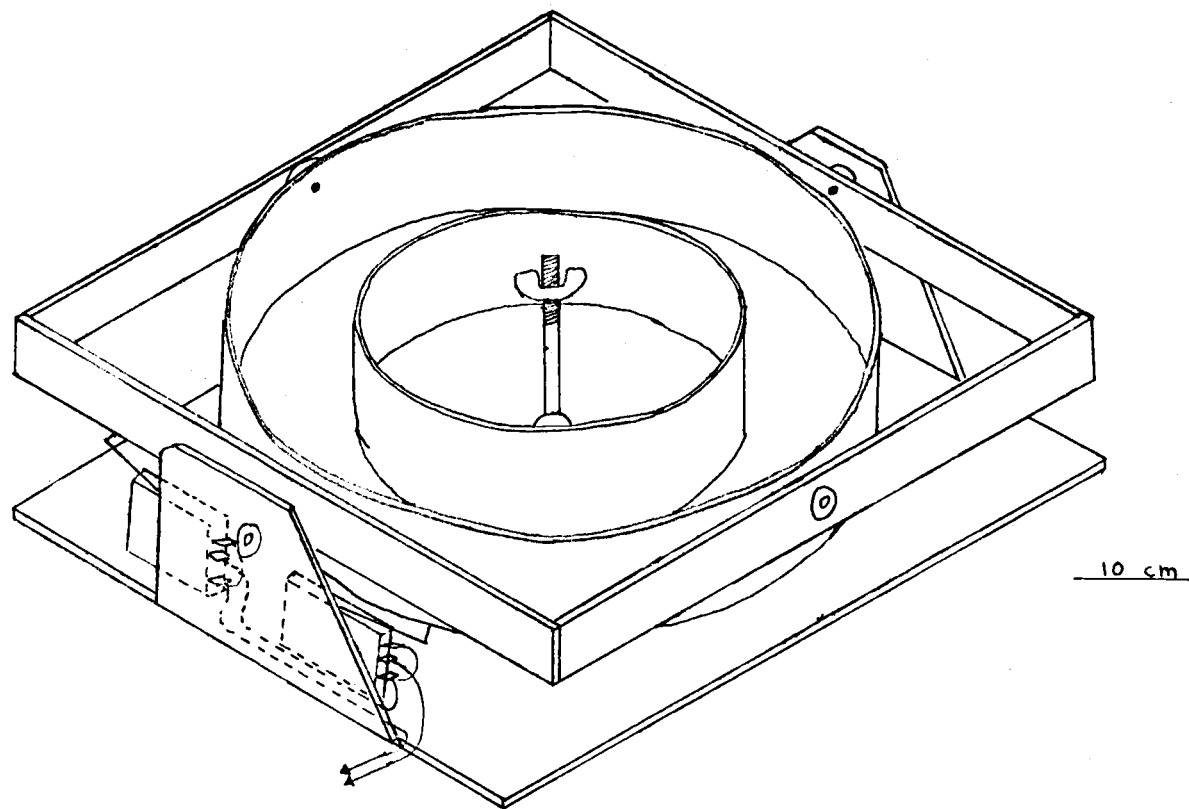


Figure 4.

mechanism. The switches were connected to an Esterline-Angus 12 volt D.C. series 80 M continuous recorder. Activity events, recorded as the number of vertical lines per hour, were counted and compared to the natural daylight hours and the tidal regime during the experimental period. The light regime in the experimental chamber was, early in the experiments, identical in length to the natural light period but was later reduced to a constant low level red light regime. The tidal regime during the study period was established by plotting the predicted tidal heights and then calculating the time during which the +5 ft level (from which the experimental crabs were collected) was covered and exposed both during natural daylight and night time periods. The number of tilts per hour were then compared between periods of light, dark, covered, exposed, and several combinations of these variables. Student's t-test between means was applied as a statistical test to determine if significant variations in activity patterns correlated with natural light or tidal cycles.

All data were transferred to IBM data cards and were analyzed with the aid of the O.S.U. Computer Center's CDC 3300 computer.

## RESULTS

### Habitat Characterization

The study area was on the bay side of an old abandoned artificial dike which had been constructed from dredge tailing. Small gravel, sandstone, and mudstone covered the dredge tailing. The substrate texture graded continuously from a fine, water-saturated mud at the 0 ft level to a pea-sized, well-drained gravel at the 5 ft level. Interspersed throughout the substrate were numerous shell fragments and larger rocks from 6 inches to 3 feet in diameter. The rocks were quite uniformly spaced from the 1 ft level to the 5 ft level, but at the 0 ft level the substrate consisted mainly of mud. The bay side of the dike extended for about 150 ft parallel to the estuary channel and had a uniform slope of about  $10^{\circ}$  from the 0 to the 5 ft level (Figure 5).

The surface water temperature at 10 cm (Figure 6) at the collection site was measured about an hour before the lower high tide. The period of warmest water was in June (18.0 C) and July (17.5 C) but then decreased continuously to a seasonal low during December (8.0 C), after which a general warming trend followed. The surface water temperature at the collection site followed the trend of the open ocean seasonal water temperatures (Figure 7) (Wyatt and Gilbert,



Figure 5. Habitat conformation at Coquille Point  
at low tide.

1972; Gilbert, 1973). Water temperatures at the collection site are determined by the interaction of the river water temperature, solar heat input onto the water surface and the adjacent mud flats, and the oceanic water temperature. Periods of warmest bay water (June, July) and ocean water (August) do not, however, coincide. Since the bay water was warmer than ocean water in the Spring and Summer, the heat input from the river water and from direct insolation are considerable. During November and December, however, bay water temperatures were lower than oceanic water temperatures. The bay thus experienced seasonal surface water temperatures which were greater in range (10.0 C) than the open ocean water (2.1 C) during the study period. This is in agreement with Frolander (1964) who stated that estuaries, due to their relatively shallow conditions, have little heat storage capacity and, hence, tend to experience a greater fluctuation in seasonal temperature ranges than does the open ocean. The result is that estuaries tend to have colder Winter water and warmer Summer waters than does the open ocean. Bay and outer coast crab populations may thus be under differing temperature regimes and as a result may be expected to show differences in various aspects of their biology as an adaptation to varying environmental conditions.

Microhabitat temperatures, taken in shaded area at the air-substrate interface (Figure 8), were much more variable than water

Figure 6. Surface water temperature at Coquille Point in Yaquina Bay Estuary, Oregon, from April, 1972 through May, 1973. Water Temperatures were taken with a mercury-column thermometer on the incoming tide about one hour before the lower high tide. Mean annual temperature at 13.2 C.



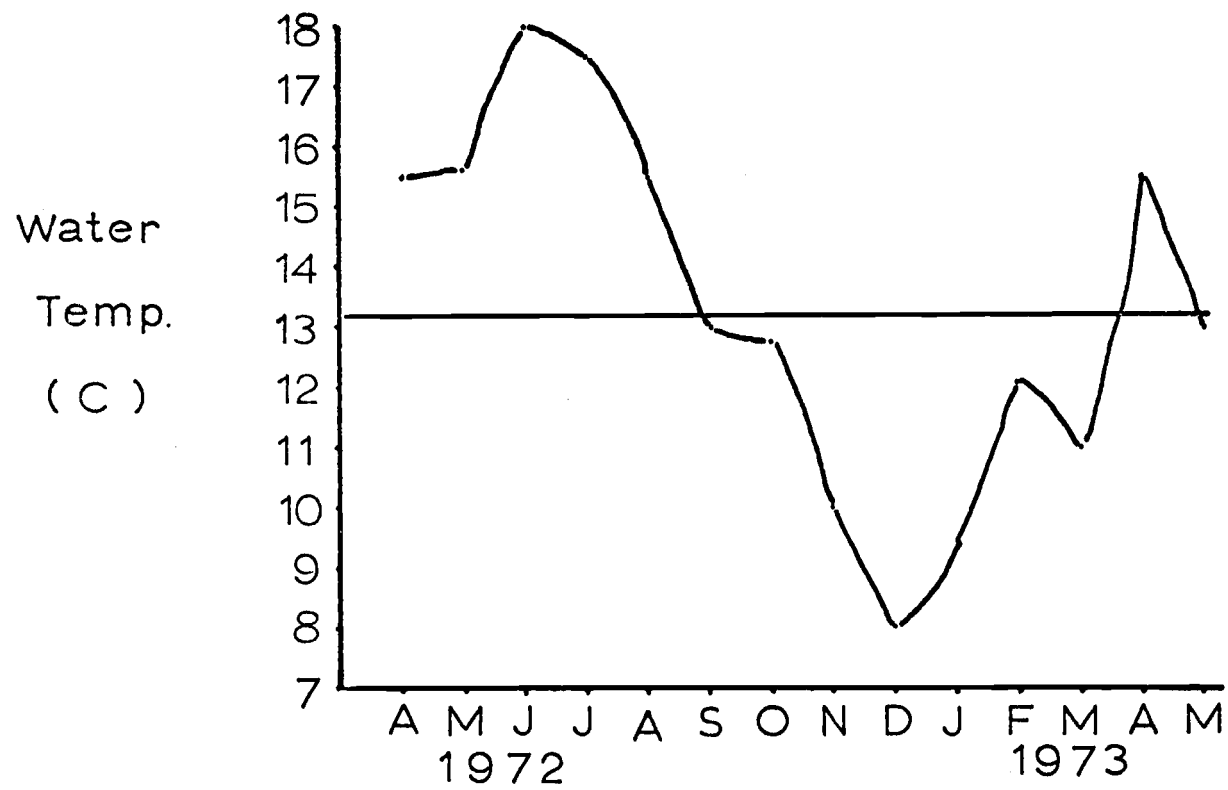


Figure 6.

Figure 7. Mean monthly open ocean surface water temperature at Newport, Oregon, from January, 1971 through December, 1972 (from Wyatt and Gilbert, 1972; Gilbert, 1973). Mean annual temperature at 10.5 C. Arrow indicates period of rapid water temperature drop due to coastal upwelling in 1971.

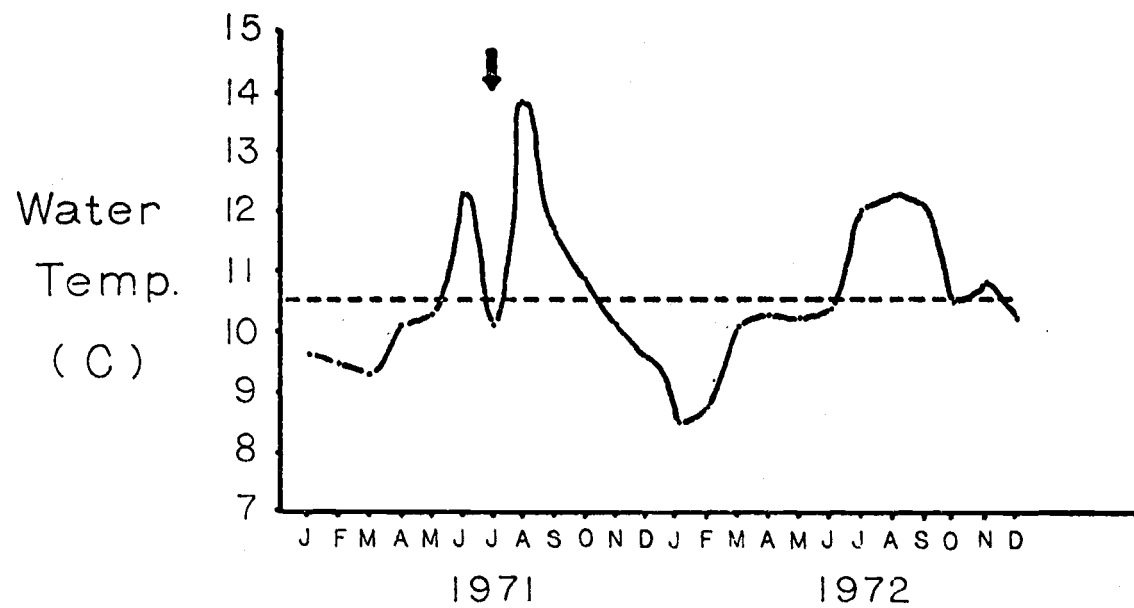


Figure 7.

Figure 8. Air-substrate interface temperature at the +5 ft level at Coquille Point from April, 1972 through May, 1973. Mean annual temperature was 13.8 C. Temperatures were taken in shaded areas.

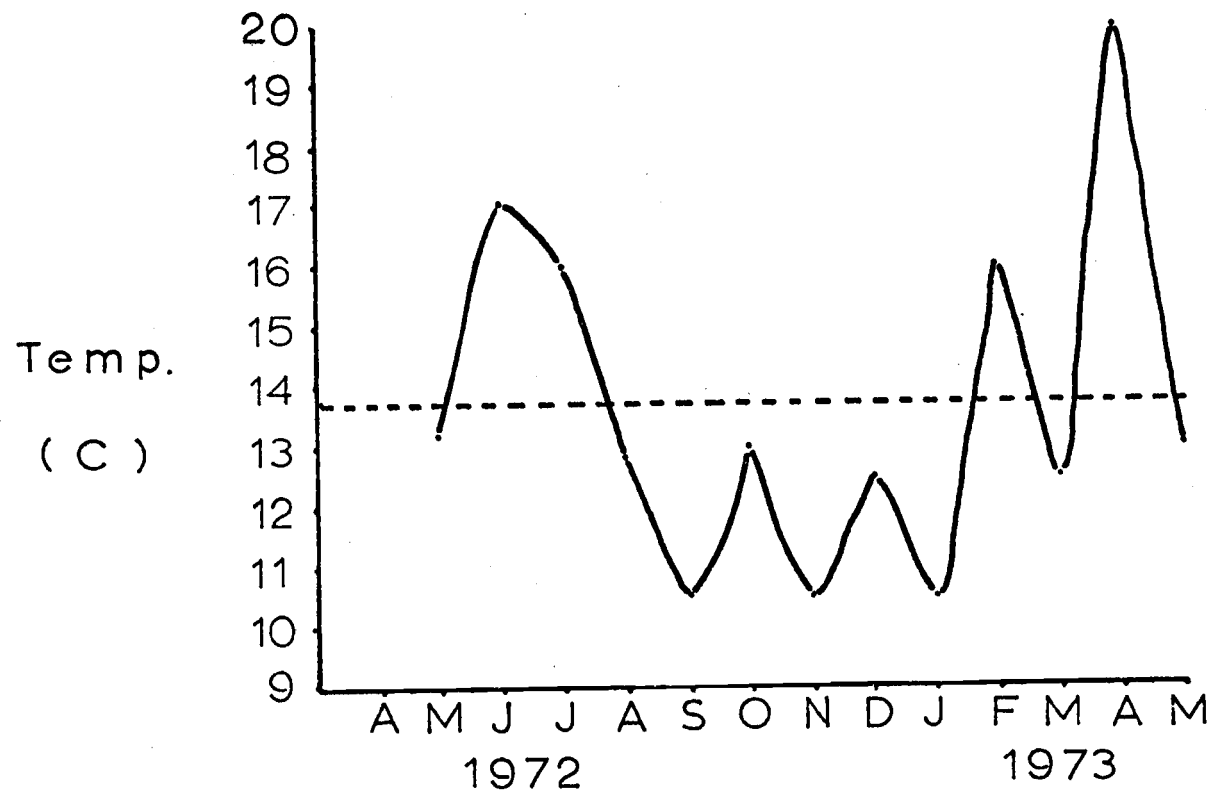


Figure 8.

temperatures. The general trend, however, follows that of the surface water temperatures: Spring and early Summer warming with Fall and Winter cooling. The annual temperature range was about 10 C. However, the greatest temperature change experienced by crabs, as interpreted from Figures 6 and 8, did not exceed 5 C (observed maxima at December = 4.5 C and April = 4.5 C).

### Tidal Regime

The tidal regime in Yaquina Bay is a mixed semidiurnal tide (Figure 9). Mean Lower Low Water (MLLW) had a monthly range of 1.2 ft during the study period. The lowest means occurred in the early Summer months (May, June, July) and the highest means during the late Winter months (January, February, March). The average MLLW was calculated to be -0.2 ft over the study period. Over the long run, however, this value by definition is the 0.0 ft datum level on the Pacific Coast.

The Mean Higher Low Water (MHLW) cycle had a slightly greater fluctuation range (1.4 ft) than the MLLW cycle. The average MHLW value was 2.8 ft. The Mean Low Water (MLW) values had a 1.0 ft seasonal range with the lowest values occurring in the Summer and the highest values occurring in the Winter. The average MLW value was 1.3 ft.

The higher tide cycles exhibited a similar seasonal trend.

Figure 9. Average monthly tidal height of seven tidal variables in Yaquina Bay from April, 1972 through June, 1973. MLLW = Mean Lower Low Water, MLW = Mean Low Water, MHLW = Mean Higher Low Water, MSL = Mean Sea Level, MLHW = Mean Lower High Water, MHW = Mean High Water, MHHW = Mean Higher High Water. Average Mean Lower Low Water (AMLLW) = -0.2 ft, Average Mean Low Water (AMLW) = 1.3 ft. Average Mean Higher Low Water (AMHLW) = 2.8 ft, Average Mean Sea Level (AMSL) = 4.3 ft, Average Mean Lower High Water (AMLHW) = 6.7 ft, Average Mean High Water (AMHW) = 7.4 ft, Average Mean Higher High Water (AMHHW) = 8.3 ft. The area between the dashed lines (0 to 5 ft level) indicates the boundaries of the study area.

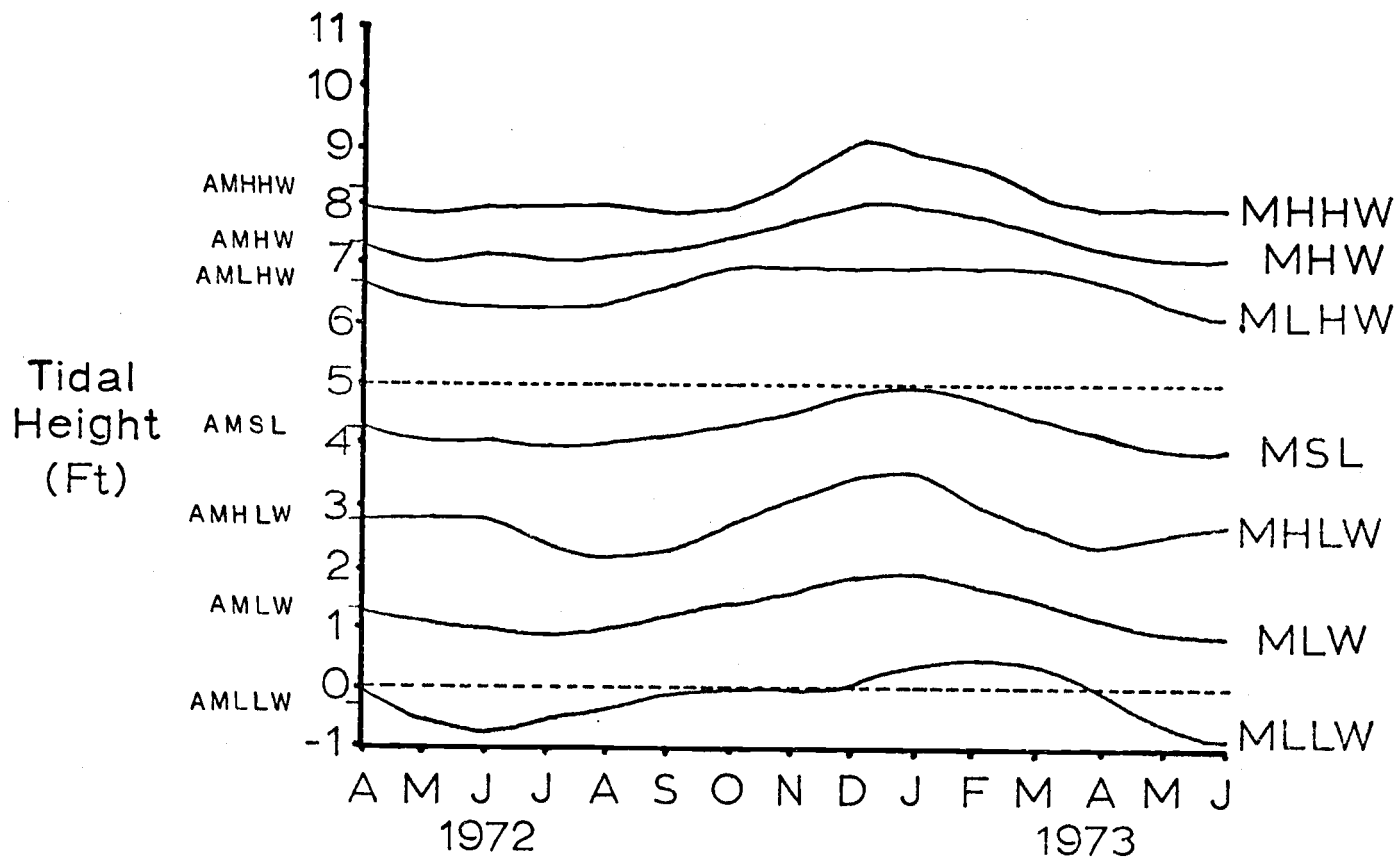


Figure 9.



The Mean Lower High Water (MLHW) values were lowest during the Summer and highest during the Winter. The seasonal tidal range of the MLHW, however, was only 0.8 ft with the average MLHW at 6.8 ft. The Mean Higher High Water (MHHW) values showed a rather constant lower limit at about 8.0 ft from April through October. A maximum was reached during December (9.1 ft) and then values decreased again to the 8.0 ft level. Maximum seasonal variation was 1.1 ft and occurred within a 4 month period (September to December). Mean High Water (MHW) variation was 1.0 ft with the average MHW at 7.4 ft.

The Mean Sea Level (MSL) value fluctuated seasonally up to 1.0 ft, with a minimum value in the Summer and a maximum during the Winter. The average MSL for the study period was 4.3 ft.

The variation between the MHHW and the MLHW for each month was, in all cases, less than the difference between the MHLW and the MLLW values. Thus, within the bay there was a greater difference between the tidal exposure heights for the lower tide series than the higher tide series. An exposure curve for the bay, based on the data obtained at the Marine Science Center's floating dock (Thum, 1972), gives the time that each tidal height is exposed to the air during a tidal cycle (Figure 10). The collection area (0 to 5 ft) had an exposure time range from 8 to 50%.

Figure 10. Exposure curve for the study area at Coquille Point. Percentage exposure as measurement of time each tidal height is exposed to the air during the year (adapted from Thum, 1972). Dotted lines indicate upper and lower boundaries of the study area.

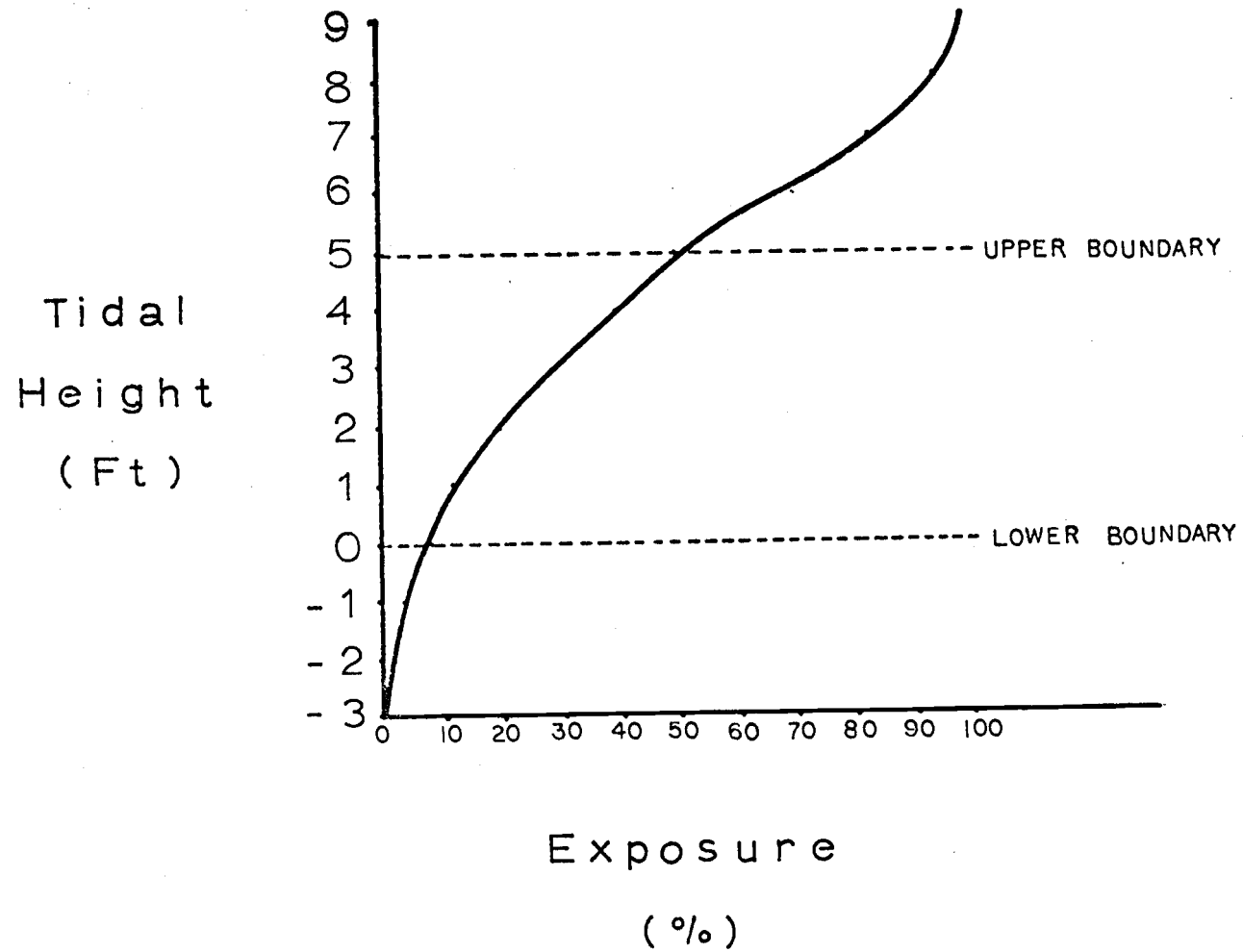


Figure 10.

### Population Distribution

At the collection site, many organisms in addition to Hemigrapsus were observed. Algae (mainly Zostera, Gigartina, Iridaea, Ulva and Fucus) were most abundant during the Spring and Summer months. In addition to the algae, other organisms frequently observed included small barnacles, blennies in the lower regions, snails (Thais), clams (Tresus), shrimp (Callinassa), ribbon worms (Paranemertes), and numerous isopods (Idothea).

The vertical distribution of the crab population during the collection period, however, can be seen in Figure 11. The upper two tidal intervals (3-4 ft and 4-5 ft) supported the most crabs (716 and 713, respectively). The 1-2 ft tidal interval supported the fewest crabs (220). The bulk of the population is thus concentrated in the upper regions.

Figure 12 shows the monthly population distribution. Although the majority of crabs are found in the upper regions, no apparent vertical population shift occurs during the year. It is of interest, however, to note that movements do occur. In comparing the monthly number of crabs present in the 3 to 4 ft interval from May, 1972 to August, 1972, large fluctuations in numbers are noted. The only explanation of the apparent gain or loss of crabs, which remains consistent with data presented later, is that of crab

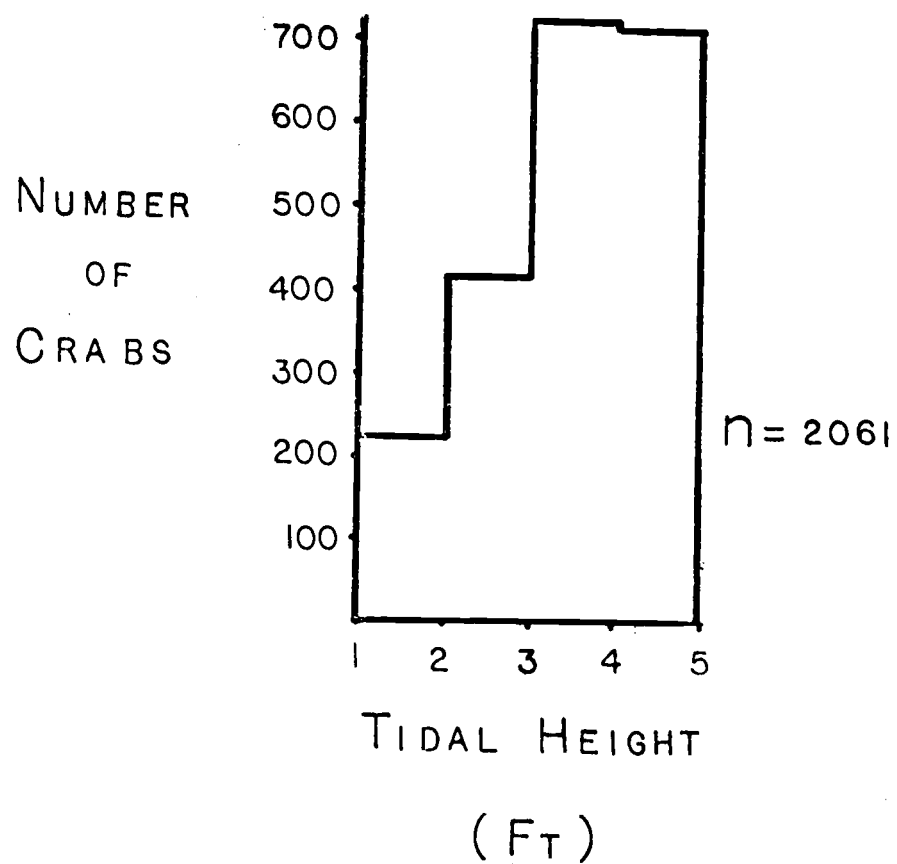


Figure 11. Histogram of number of crabs collected at each tidal height interval at Coquille Point from April, 1972 through May, 1973.

Figure 12. Histograms of total number of crabs collected monthly at each tidal height interval at Coquille Point from May, 1972 through May, 1973. Dotted lines (September, 1972; January, 1973; February, 1973) indicate estimates of crabs present based on average number of crabs sampled during the other months at this tidal height. These tidal heights were not sampled because of high water levels due to gale conditions.

TIDAL HEIGHT  
INTERVAL  
( $F_T$ )

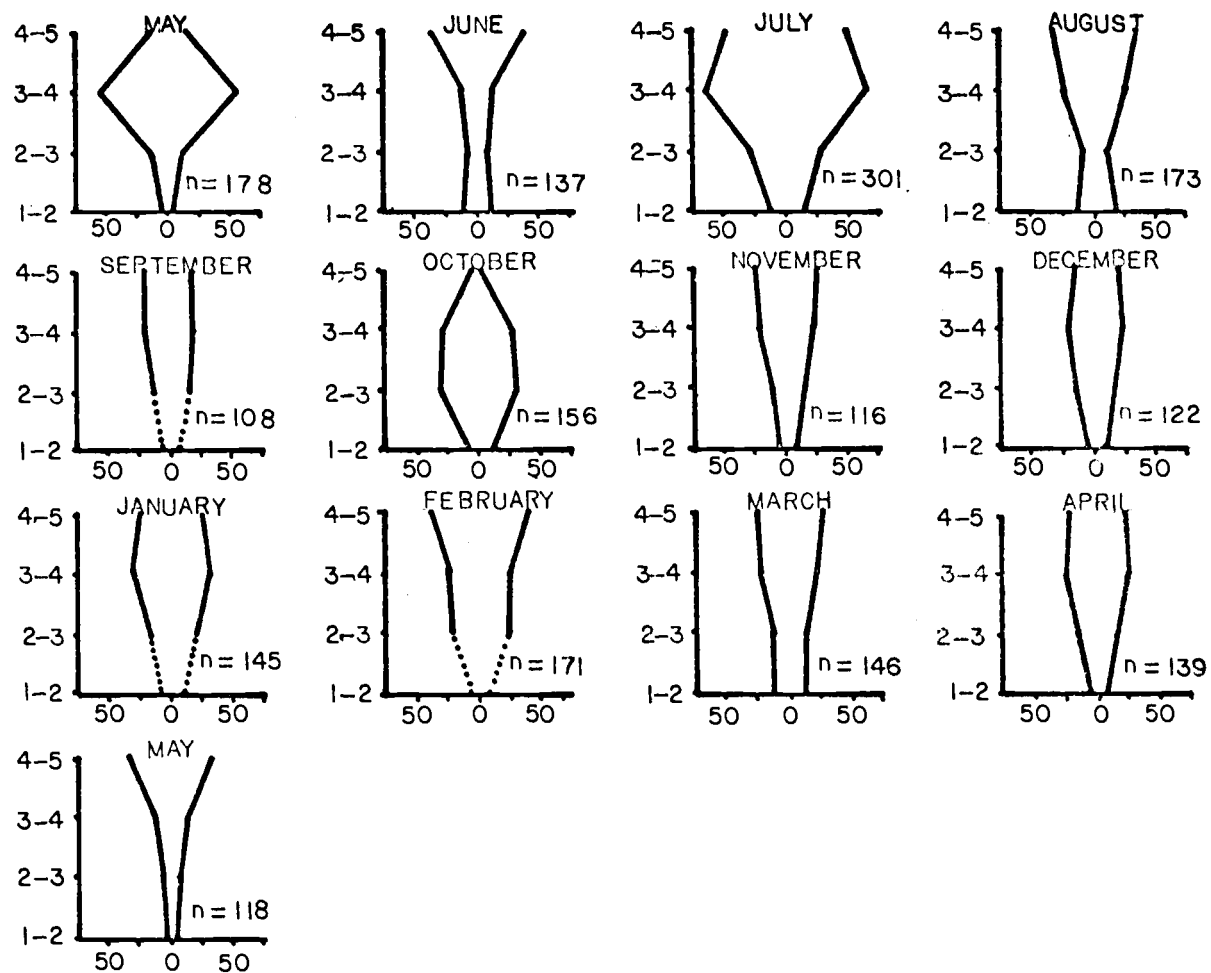


Figure 12.

movements into and out of the research area.

The mean number of crabs sampled per month at each tidal interval was compared with the mean numbers at each other tidal interval (Table 1). Monthly mean numbers of crabs at each tidal height are significantly different from monthly mean numbers from other tidal heights, except for the 3 to 4 ft interval when compared with the 4 to 5 ft interval.

Table 1. Student's t-test Between Means Applied on Monthly Mean Number (MMN) of Crabs Collected at Each Tidal Height.

Tidal level	Tidal level of comparison	D. F.	t-value	Significance level
MMN <sub>1</sub> (22)	MMN <sub>2</sub> (33)	22	3.768	**
MMN <sub>1</sub> (22)	MMN <sub>3</sub> (56)	22	4.198	**
MMN <sub>1</sub> (22)	MMN <sub>4</sub> (55)	22	5.147	**
MMN <sub>2</sub>	MMN <sub>3</sub>	22	2.375	*
MMN <sub>2</sub>	MMN <sub>4</sub>	22	2.495	*
MMN <sub>3</sub>	MMN <sub>4</sub>	22	0.452	-

\*\* = Significant at 99% level

\* = Significant at 95% level

- = Not significant at 95% level.

(Subscript denotes the lower boundary of the tidal interval; number in parentheses denotes mean number of crabs collected in that interval, e. g., MMN<sub>1</sub>(22) = mean monthly number of crabs collected in the 1 to 2 ft interval is 22; MMN<sub>2</sub>(33) = mean monthly number of crabs collected in the 2 to 3 ft interval is 33; etc.)



A population size class frequency distribution (Figure 13) indicated that the majority of the population was between 1.20 and 1.95 cm in carapace width with a mean of about 1.50 cm. There does not appear to be more than one dominant size class. Since it has been observed that a crab can increase in carapace width up to 0.26 cm per molt (1.11 cm to 1.37 cm) and since these crabs may molt up to 10 times per year, the peak in the distribution may represent the first year class. Since there is a rapid population decline at the larger carapace widths, a large population turnover each year is indicated. The frequency distribution of male and of female crabs (Figure 14) shows no size class differences between sexes. The mean carapace width of females was, however, slightly less than that for males (1.44 and 1.51 cm, respectively).

#### Reproductive Season

The Hemigrapsus oregonensis population was analyzed to determine if the sexes were segregated by tidal height. The percentage of females in monthly samples (Figure 15) indicated that the sex ratio was slightly biased in favor of females ( $p < .01$ ). There does not, however, appear to be any significant variation about the mean sex ratio, indicating that the sex ratio of the population is fairly stable throughout the year. The percentage of females at each tidal height interval (Figure 16), however, is more variable.

Figure 13. Histogram showing number of crabs in each carapace width size class during the period April, 1972 through May, 1973. Size class interval is 0.05 cm.

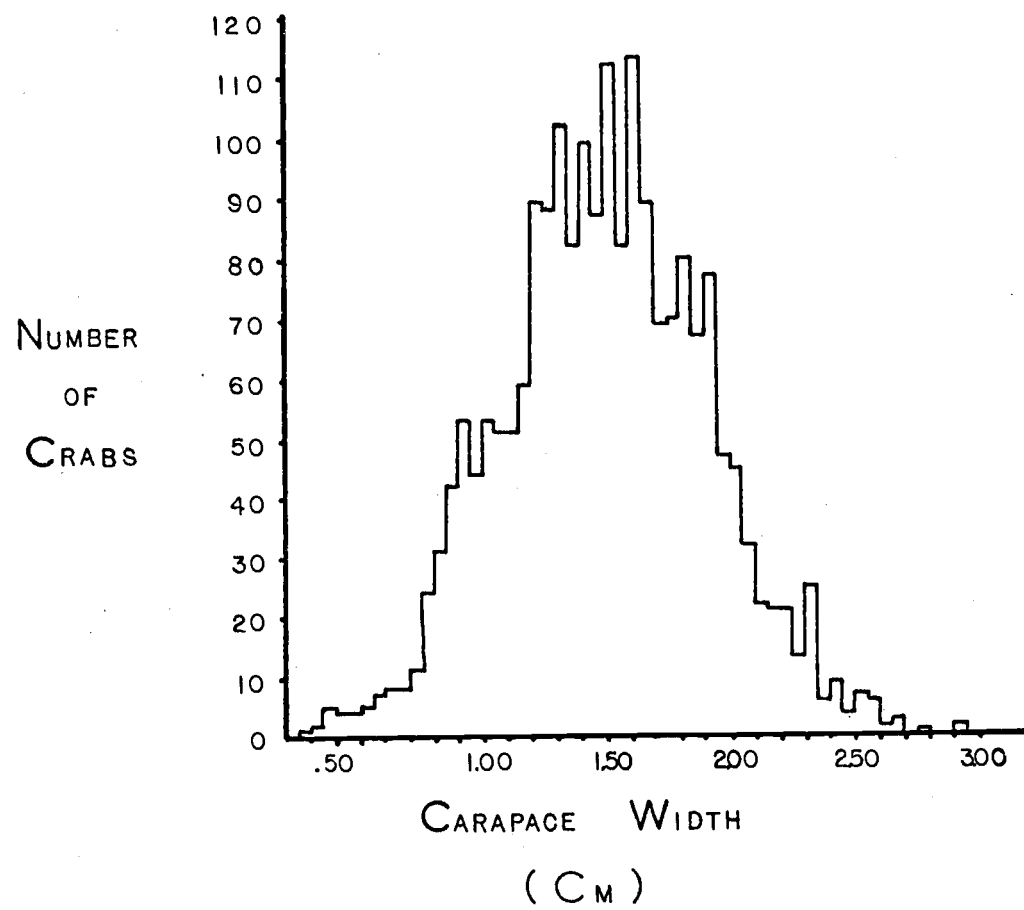


Figure 13.

Figure 14. Histogram of number of male and female crabs in each carapace width size class during the period April, 1972 through May, 1973 at Coquille Point. Size class interval is 0.05 cm.

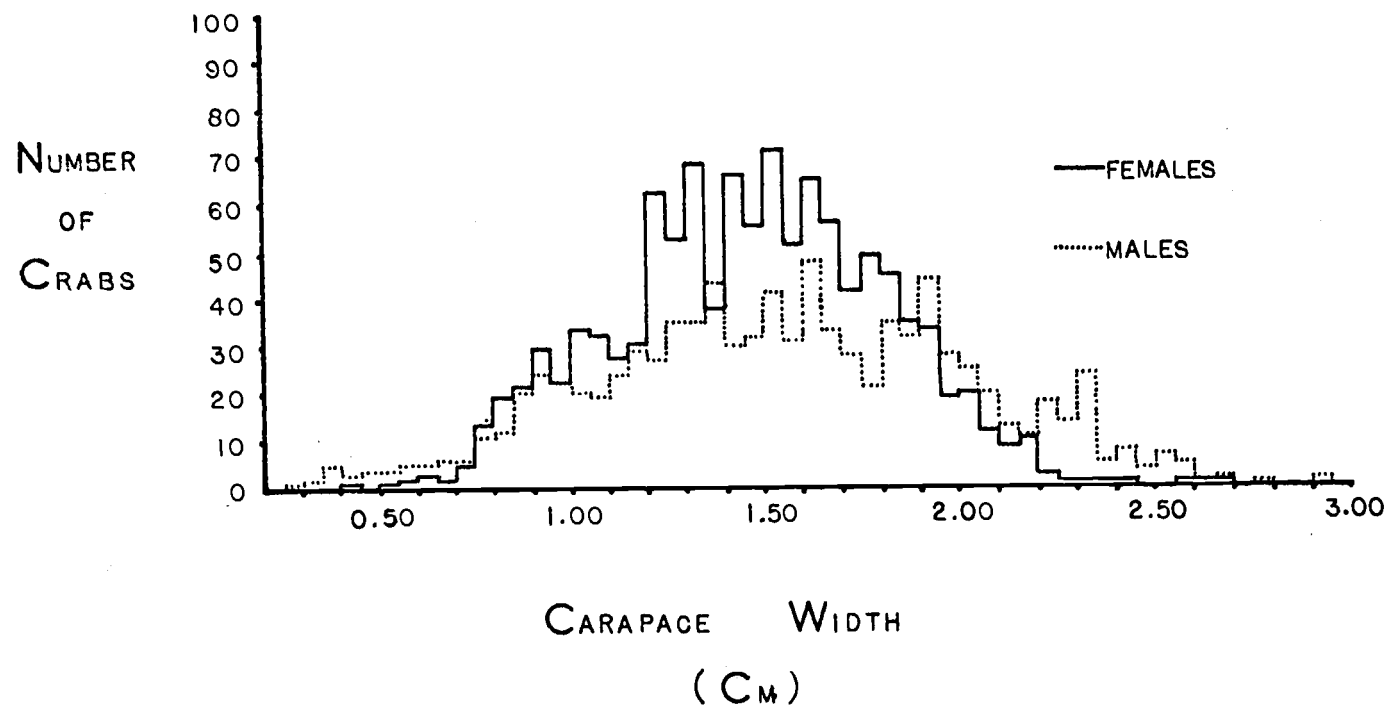


Figure 14.

Figure 15. Percentage of female Hemigrapsus oregonensis in census population for each month from April, 1972 through May, 1973. Solid line is average percentage value (53.4%) during the entire study; dashed line is hypothetical percentage value (50%).

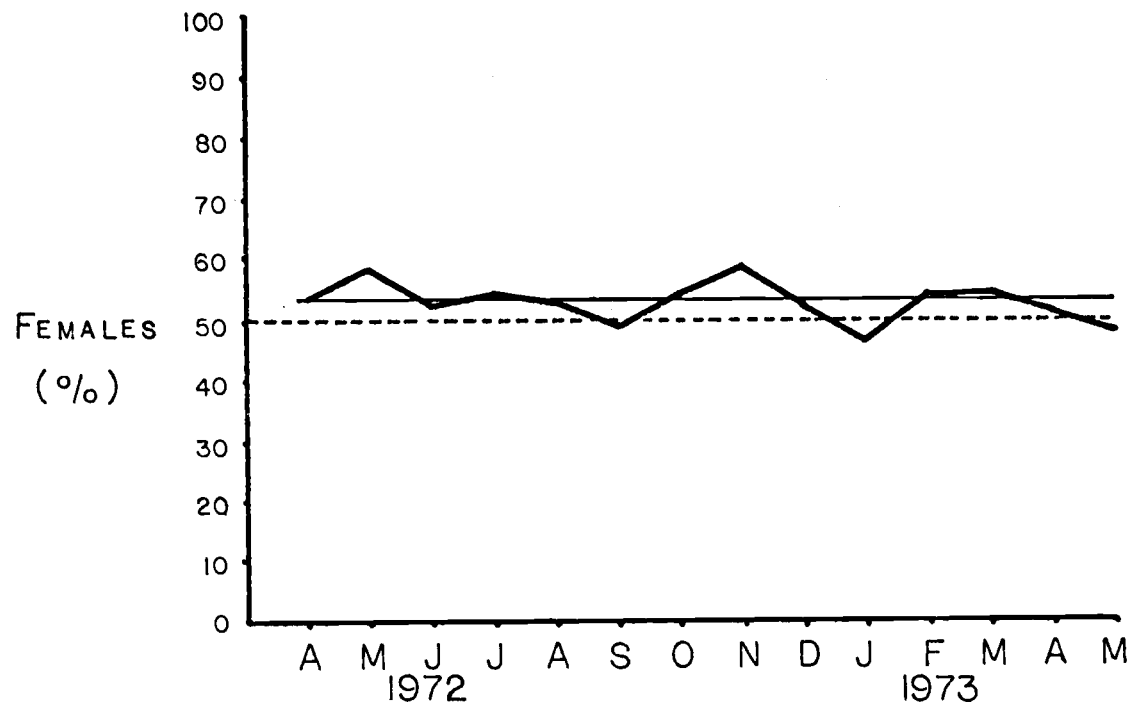


Figure 15.

Figure 16. Percentage of female Hemigrapsus oregonensis in total population sample for each month at each tidal height interval. Solid line denotes average value from April, 1972 through May, 1973. Dashed line denotes hypothetical value (50%).



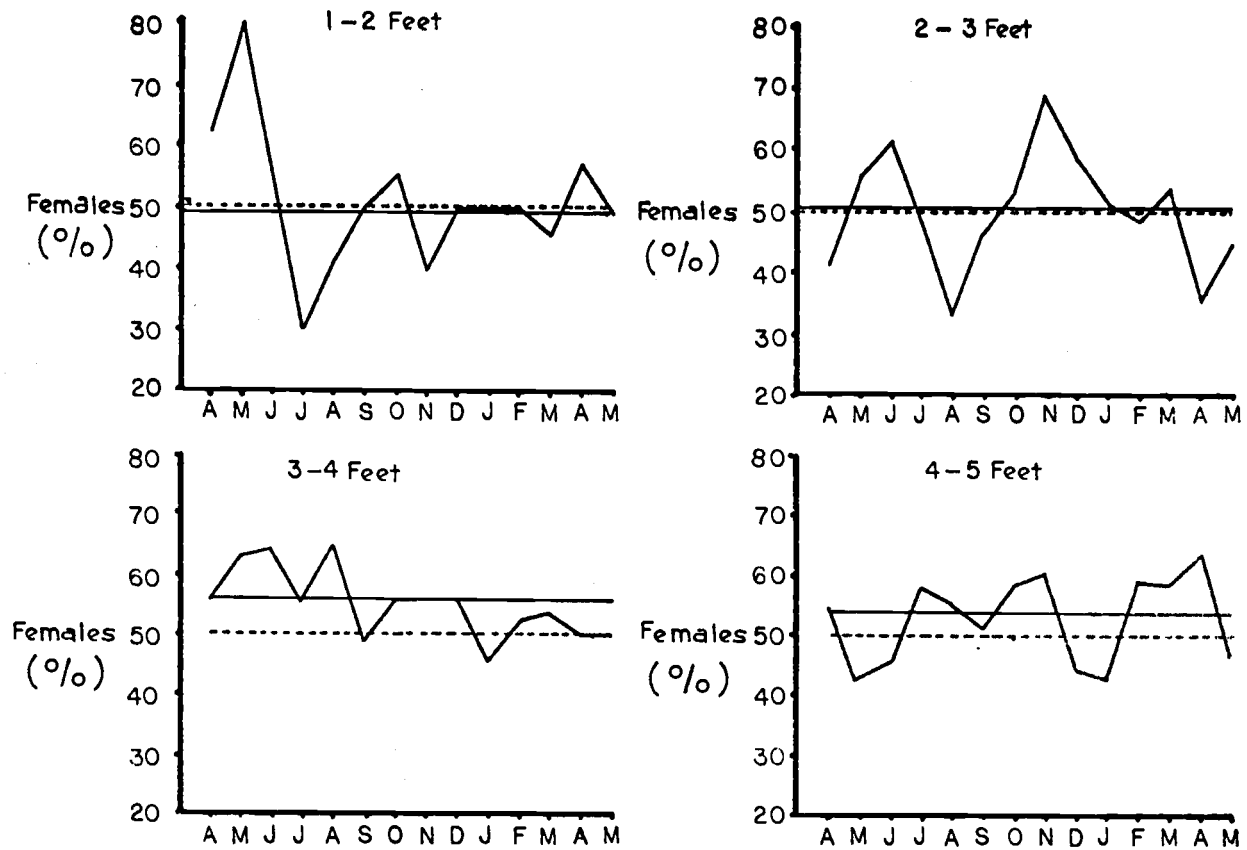


Figure 16.

The sex ratios appear slightly biased in favor of females at the higher two tidal intervals. Since the majority of the population is found in the upper areas (see Figure 11), the monthly percentage variation in the lower intervals will be greatly exaggerated due to the smaller number of crabs sampled. The sex ratio for the upper two intervals are, therefore, probably a better indication of the true population sex ratio.

The percentage berried (ovigerous) females during the year (Figure 17) showed a peak population reproductive effort during the late Winter and Spring months. The maximum percentage of berried females at any monthly interval (March, 1973), however, was only about 33% of the female population. The fewest (1.4%) was during October. There was a steady increase in the number of berried females from October, 1972 (1.4%) to March, 1973 (32.8%). The main reproductive period was in the Spring (March, April, May). The fact that some berried females were found every month indicated that the population was not synchronized for a major reproductive effort, but rather exhibited a low-level, continuous yearly production which peaked in March. The percentage berried females at each tidal height (Figure 18) reflected the population trend, indicating that there were no differences in reproductive seasons at the various tidal levels. Late Fall months (September, October, November) were periods of little or no brooding at all tidal heights.

Figure 17. Percentage of berried female Hemigrapsus oregonensis at Coquille Point from April, 1972 through May, 1973. The minimum size of egg bearing females was 0.86 cm. All female crabs smaller than this were not considered to be potentially reproductive female adults and were not included in the percentage calculations.

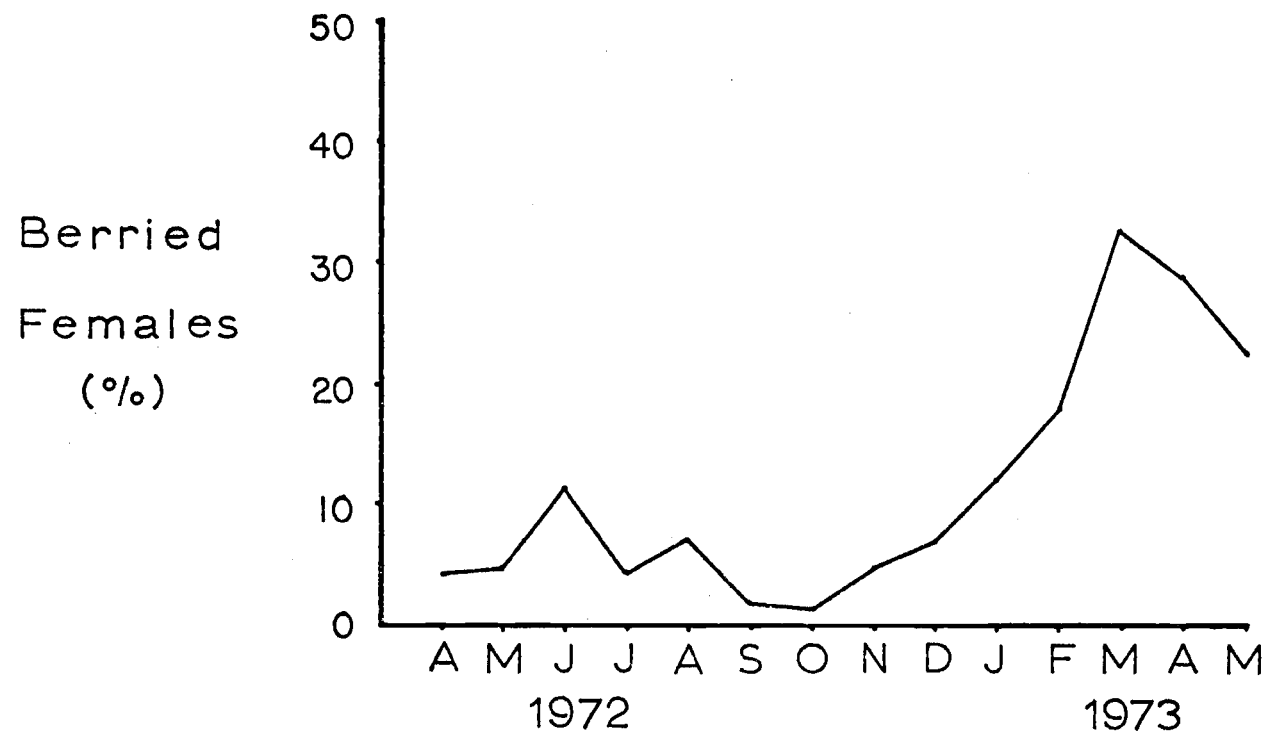


Figure 17.

Figure 18. Percentage of berried female Hemigrapsus oregonensis at Coquille Point from April, 1972 through May, 1973 at the various tidal heights. Females smaller than 0.86 cm are not included in calculations.

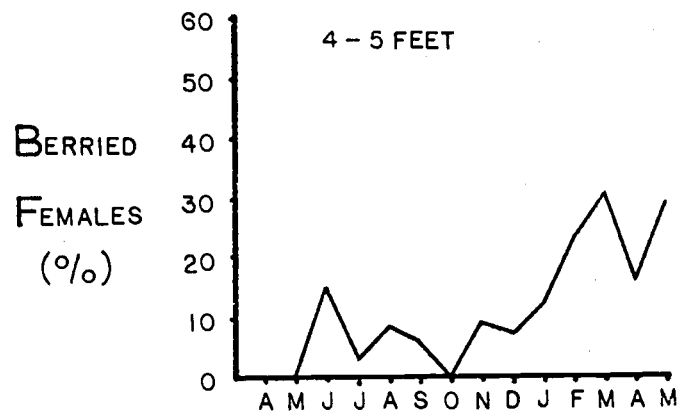
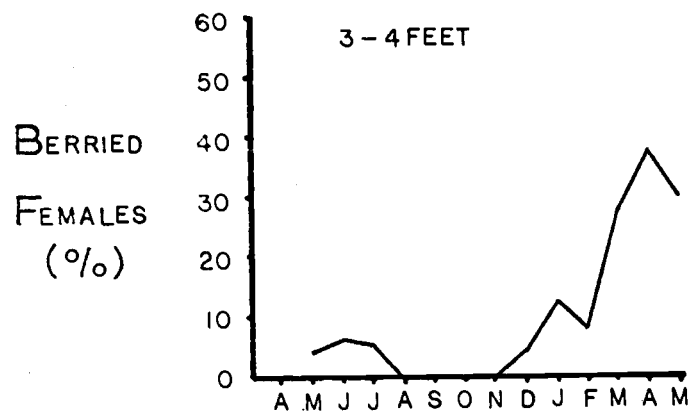
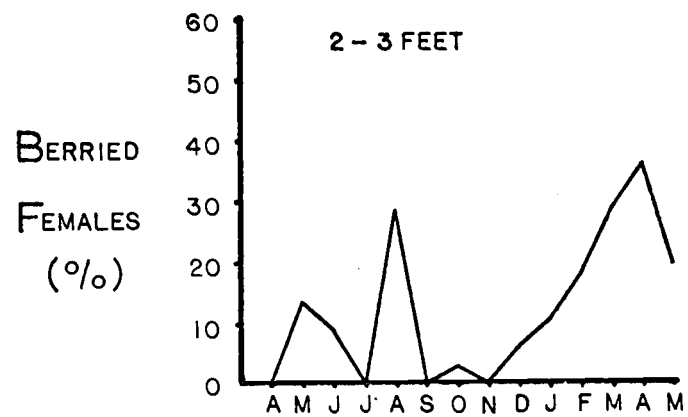
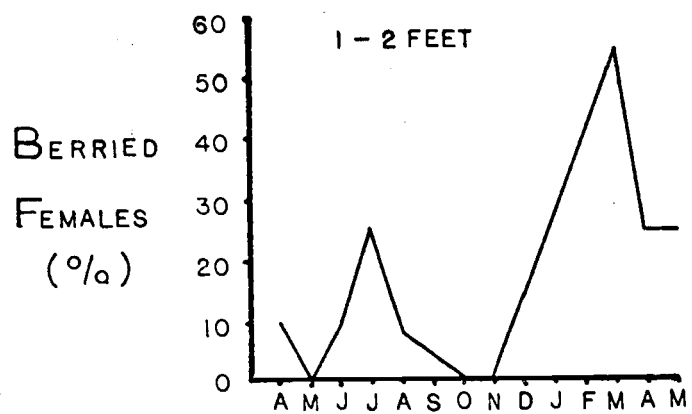


Figure 18.

A measure of female fecundity (Figure 19) was established by regressing carapace width of brooding females with the number of eggs brooded for females in various size classes. A linear relationship ( $R = 0.9018$ ) was established for females from 1.04 to 2.03 cm in carapace width. A regression model was established from which the number of brooded eggs could be estimated if a female's carapace width were known. The model is:

$$Y \text{ (number of eggs brooded)} = -1.0529 \times 10^4 + 1.3344 \times 10^4 X \text{ (carapace width in cm)}$$

$$\begin{aligned} \frac{t\text{-value}}{\text{constant}} &= -5.6813 \\ \text{variable coefficient} &= 10.4351 \end{aligned}$$

By using the model an estimate of maximum population egg production can be made. An estimate of the average egg production per female is 8,459 eggs/female per year. Thus an average annual estimate of about 67,000 eggs/m<sup>2</sup> at the collection site are produced each year. Since it appears that there is a major population turn-over each year and since there is a fairly stable adult population, it is estimated that for about every 4,500 eggs produced, 1 will survive to become an adult (99.98% mortality). The average (1.44 cm) crab would contribute about 6 adult crabs to the next year's population, 3 of which would be females. Since the population is stable, 4 of these recruits would be lost from the population through disease,

Figure 19. Relationship between carapace width of female Hemigrapsus oregonensis and the number of brooded eggs.

$$Y \text{ (egg number)} = -1.0529 \times 10^4 + 1.3344 \times 10^4 X$$

(carapace width in cm)

(t = -5.6813)      (t = 10.4351)



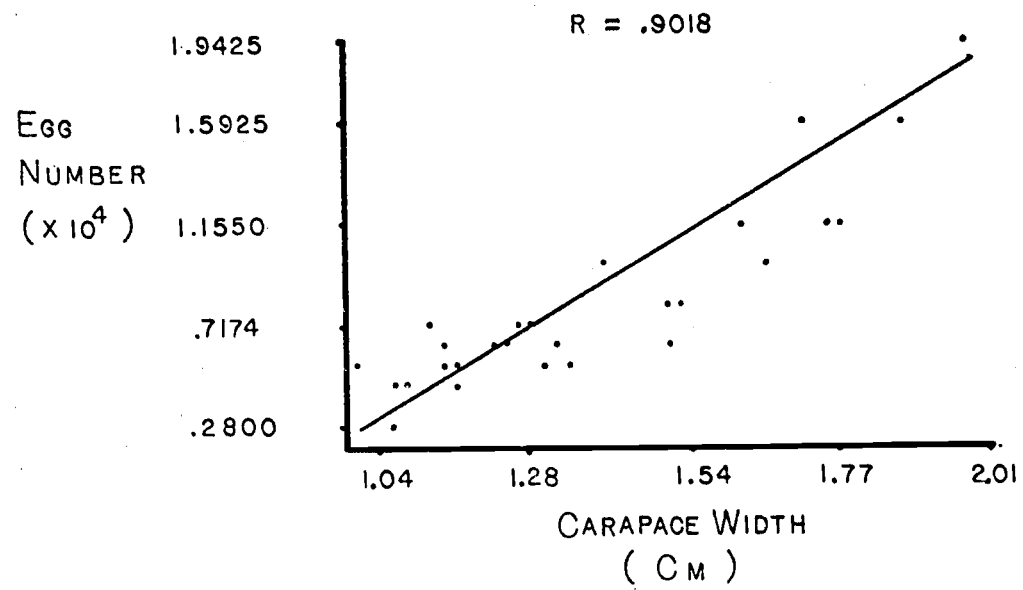


Figure 19.

predation, or emigration. Thus the true mortality rate to maintain the population in a steady state is 99.99%.

### Biomass and Production

In order to realistically estimate biomass without depleting the study population, an easily obtained field measurement of some parameter related to biomass was needed. This parameter, then, could later be converted to a biomass figure. To obtain such a parameter, crab carapace width (in centimeters) was regressed on crab dry weight (in grams). To obtain a better correlation, log transformations were made on both variables and then the regression repeated (Figure 20). A dummy variable for crab sex was included in the model to test for differences between the dry weight of male and female crabs. The completed regression model allows the prediction of any crab's dry weight, given its sex and carapace width. The model is:

Log (dry weight of male in grams) =

$$-2.007 + 3.065 \times \text{Log (carapace width in centimeters)}$$

Log (dry weight of female in grams) =

$$-2.028 + 3.065 \times \text{Log (carapace width in centimeters)}$$

#### t-value

constant = -139.7

coefficient (sex) = 13.7

coefficient (log carapace width) = 99.4

(Separate equations presented here are derived from equation of Figure 20)

Figure 20. Relationship between dry weight (g) and carapace width (cm) in Hemigrapsus oregonensis from Coquille Point in the Yaquina Bay Estuary.

Y (log dry weight in grams) =

$$-2.028 + 0.021 X_1 (\text{sex})^* + 3.065 X_2 (\log \text{carapace width in cm})$$

(t = -139.689) (t = 13.741) (t = 99.376)

\* = If crab is male, substitute 1 in (sex).  
If crab is female, substitute 0 in (sex).

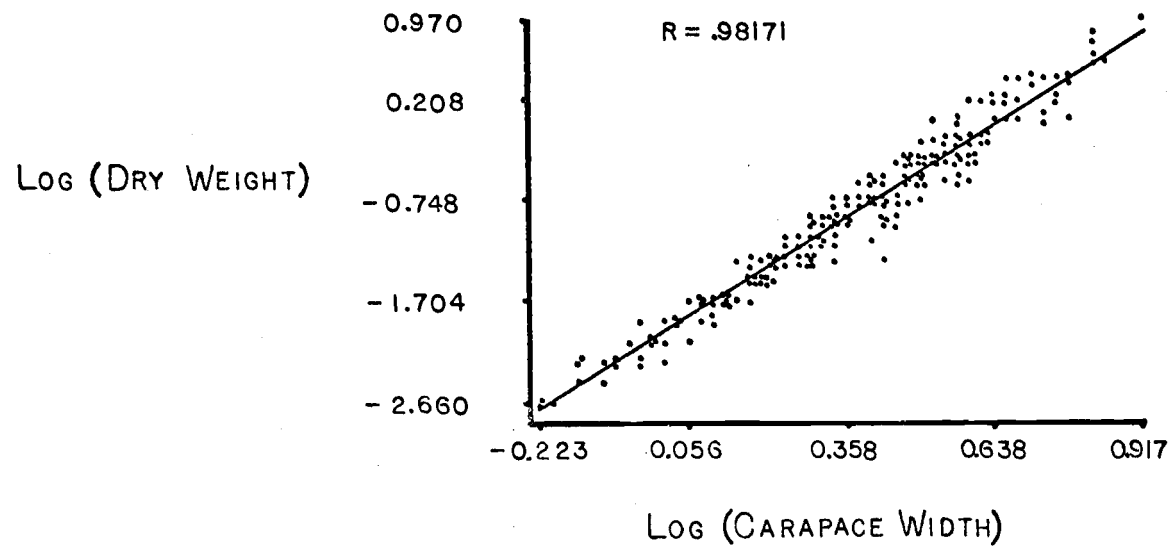


Figure 20.

Since there is such high correlation between these two parameters ( $R = 0.98171$ ), this model has excellent predictive powers for dry weight estimations.

The average dry weight per crab (Figure 21) showed a monthly average which was fairly constant throughout Spring and Summer but increased dramatically in late Fall and decreased again in January and in the Spring. The large increase in weight per crab from October, 1972 to November, 1972 suggested that few small crabs were recruited to the population at this time and that existing crabs increased in weight. Figure 17 helps to substantiate this hypothesis as October, 1972 was the period of lowest egg production. Since a lag of about 8 to 13 weeks is necessary for an egg brood to hatch, metamorphose, and be recruited into the adult population, low recruitment in November and December would be expected. Coupled with unfavorable settling conditions, few of these larvae may be recruited; hence an increase in average crab dry weight in the population would be expected. The large decrease in the average dry weight per crab in January, 1973 was a reflection of either increased larval settling success or a differential mortality on larger crabs, assuming no immigration or emigration. Figure 17, however, does not support the idea of a large January recruitment. A differential mortality rate on larger crabs was not demonstrated. Available data do not suggest an explanation.

Figure 21. Average dry weight of Hemigrapsus oregonensis at Coquille Point from April, 1972 through May, 1973.

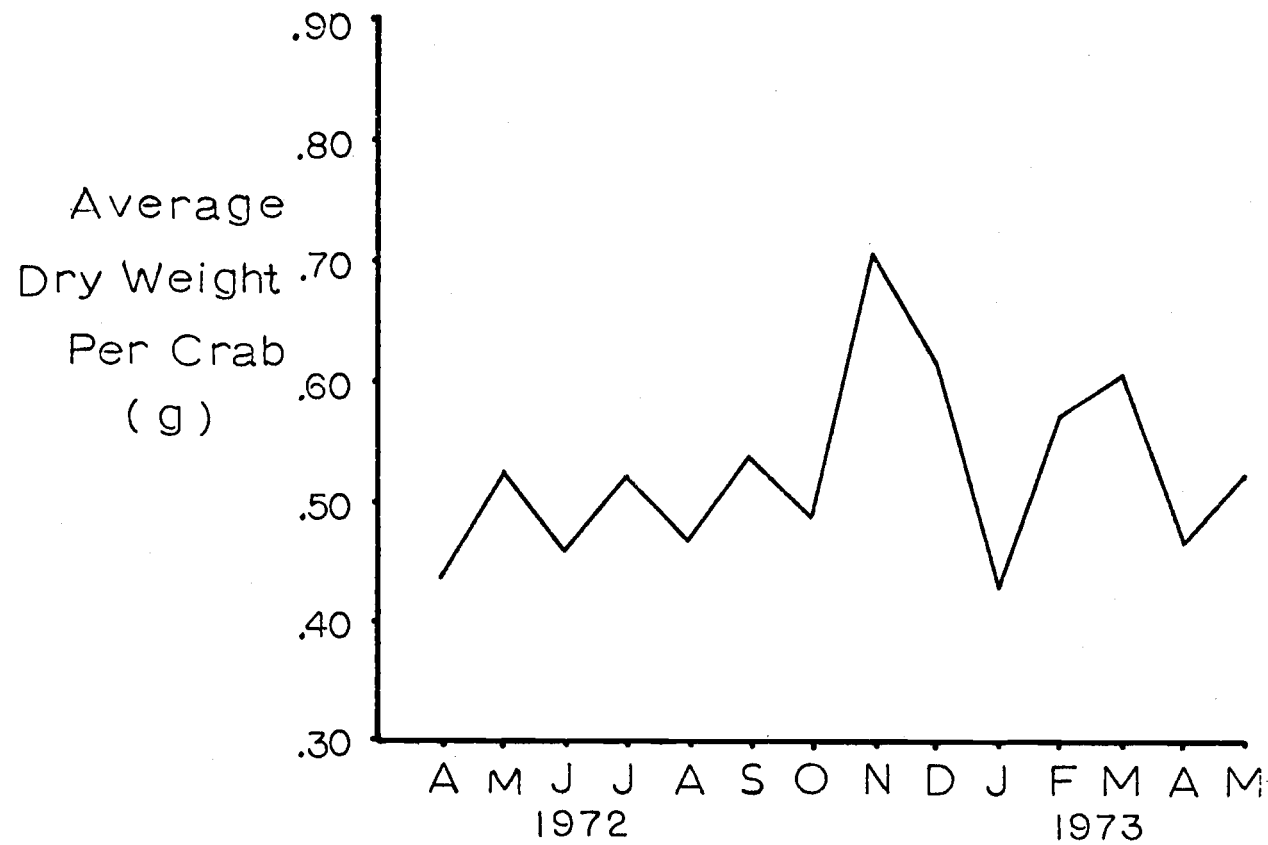


Figure 21.

The mean average dry weight per crab decreased as tidal height increased (Figure 22), suggesting a vertical segregation of crabs by size. When the average dry weight per crab was plotted for each month at each tidal height (Figure 23), it appeared as though a general increase in average dry weight per crab occurred during the study period. A regression line was fitted to the data and the slope coefficient was tested to determine if it was significantly different from zero. In each case, the slope coefficient could not be shown to be significantly different from zero ( $p < .05$ ), hence the apparent average dry weight increase can not be statistically substantiated. Since the average dry weight per crab did not increase significantly during the year, this again suggested a stable population.

It was of interest, however, to further investigate the apparent size segregation with tidal height. Table 2 summarizes the t-tests of mean monthly average dry weight per crab at each tidal height as compared to each other tidal height. The crabs in the 1 to 2 ft tidal interval were significantly heavier ( $p < .05$ ) than the crabs in levels 2-3, 3-4, or 4-5. Crabs in levels 2-3, 3-4, and 4-5, however, were not significantly different from each other. Because of the small number of crabs sampled in the 0-1 ft interval, the mean weight could not be found to be different from any other tidal level.

However, from inspection of Figure 22 and Table 2, it can be seen that smaller crabs were limited to the upper regions of the study



Figure 22. Mean average dry weight per crab in grams at various tidal heights at Coquille Point in the Yaquina Bay Estuary from April, 1972 through May, 1973. The average dry weight per crab was determined each month during the study and for each tidal height. The mean of the average dry weights per crab at each tidal height was then plotted against tidal height. Vertical bars indicate standard error about means, which are connected by solid lines.

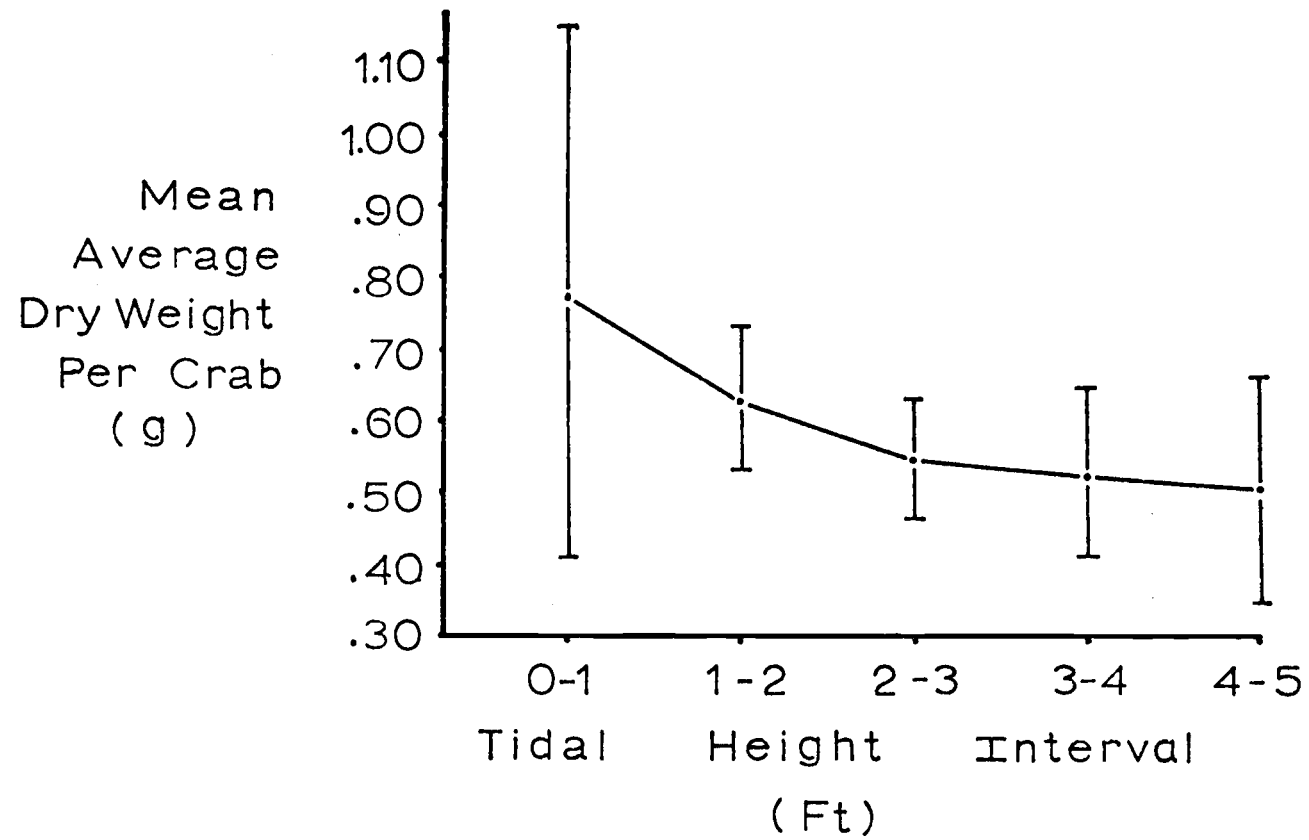


Figure 22.

Figure 23. Average dry weight per crab from April, 1972 through May, 1973 at various tidal heights. Slope coefficient represented by  $m$ ,  $t$  represents  $t$ -value for testing if slope coefficient is different from a zero value. Slope was not found to be different from zero in any of the cases ( $p > .05$ ).

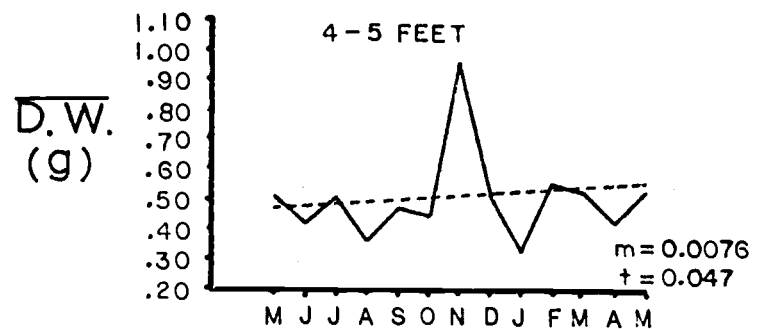
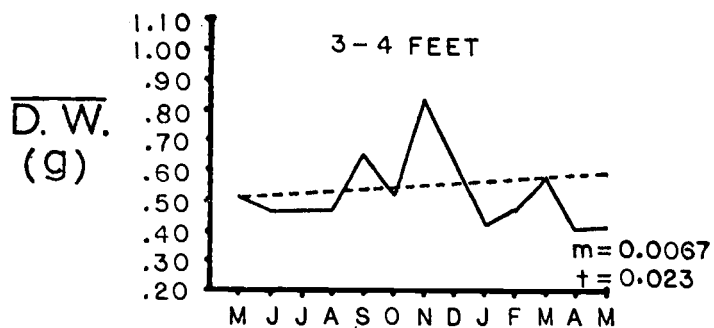
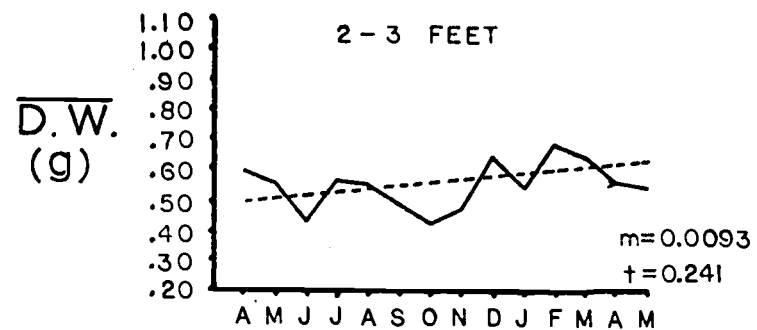
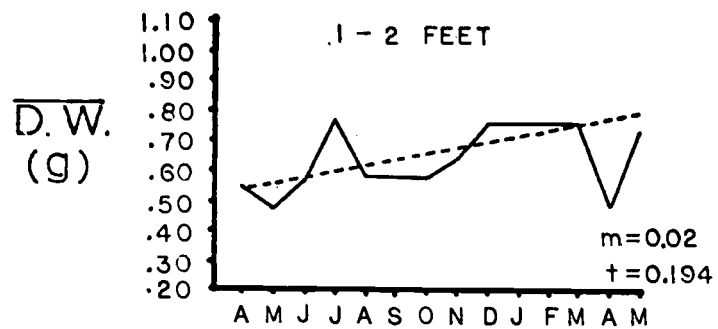


Figure 23.

Table 2. Student's t-test Between Means as Applied on the Mean Monthly Average Dry Weight Per Crab (DW) in Grams for Five Tidal Heights.

Tidal height	Tidal height of comparison	D. F.	t-value	Significance level
DW <sub>0</sub> (0.783)	DW <sub>1</sub> (0.630)	11	0.741	-
DW <sub>0</sub> (0.783)	DW <sub>2</sub> (0.555)	14	1.607	-
DW <sub>0</sub> (0.783)	DW <sub>3</sub> (0.527)	13	1.503	-
DW <sub>0</sub> (0.783)	DW <sub>4</sub> (0.510)	13	1.601	-
DW <sub>1</sub>	DW <sub>2</sub>	19	1.955	*
DW <sub>1</sub>	DW <sub>3</sub>	18	1.731	* (94.9%)
DW <sub>1</sub>	DW <sub>4</sub>	18	1.905	*
DW <sub>2</sub>	DW <sub>3</sub>	21	0.168	-
DW <sub>2</sub>	DW <sub>4</sub>	21	0.743	-
DW <sub>3</sub>	DW <sub>4</sub>	20	0.536	-

\* = Significant at 95% level

- = Not significant at 95% level.

(Subscripts as in Table 1.)

area and invaded the lower areas only as their size increased. This, then, implies that either settlement behavior of the metamorphosing larvae leads to a selection of the upper habitat areas, that some biological or physio-chemical barriers drove the small crabs from the lower regions, or that greater mortality rates existed in the lower regions for the small crabs.

The average monthly biomass in  $\text{g/m}^2$  at the various tidal levels (Figure 24) showed an increase in biomass as tidal height increased up to the 3-4 ft level and then decreased slightly at the 4-5 ft level. The biomass average ranged from  $10.18 \text{ g/m}^2$  in the 3-4 ft interval to  $1.14 \text{ g/m}^2$  in the 0-1 ft interval, a range of  $9.04 \text{ g/m}^2$ . The biomass at each tidal level during the year (Figure 25) showed less variation at the lower levels than in the upper levels. There does not appear to be any significant change in the biomass figures for any tidal height during the study period, although large fluctuations occurred. Constant biomass at the various tidal levels indicated a stable population during the study period.

Table 3 shows the results of several t-tests between mean monthly biomass values at different tidal heights. The biomass at the 0-1 ft level can be shown to be highly significantly different ( $p < .01$ ) from the biomass value at each other tidal level. Similarly, the biomass of the 1-2 ft interval is highly significantly different

Figure 24. Average monthly biomass in  $\text{g/m}^2$  for Hemigrapsus oregonensis at Coquille Point in the Yaquina Bay Estuary during the period April, 1972 through May, 1973. Vertical bars indicate standard error about means, which are connected by solid lines.

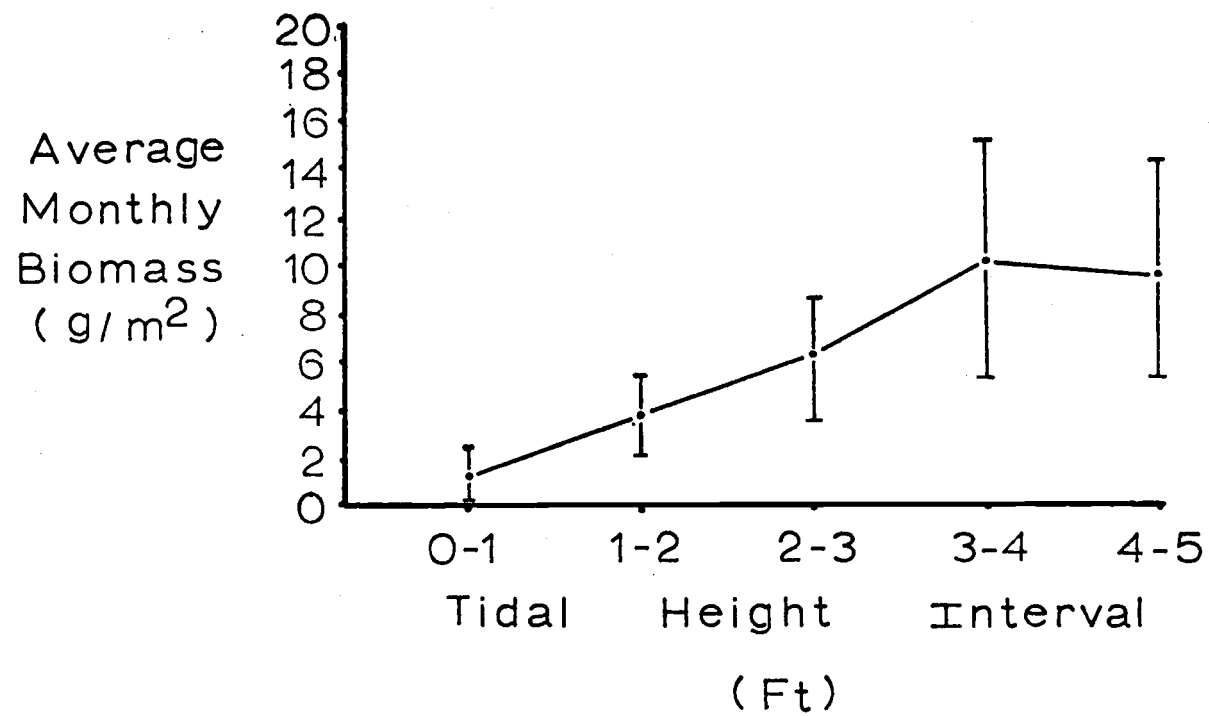


Figure 24.



Figure 25. Monthly biomass values at various tidal heights for Hemigrapsus oregonensis at Coquille Point from May, 1972 through May, 1973.

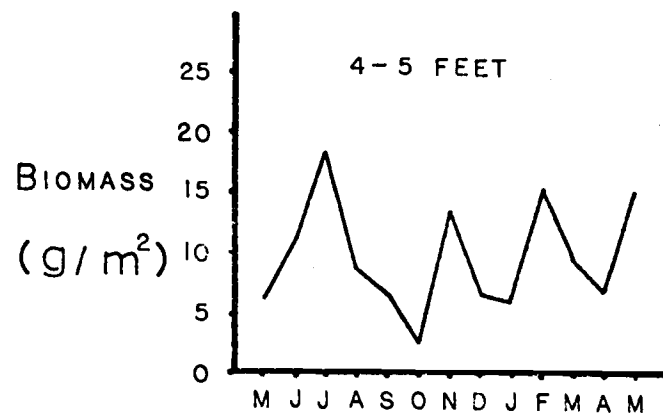
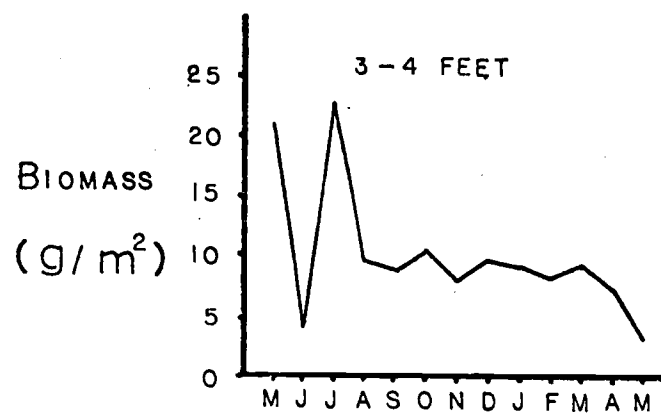
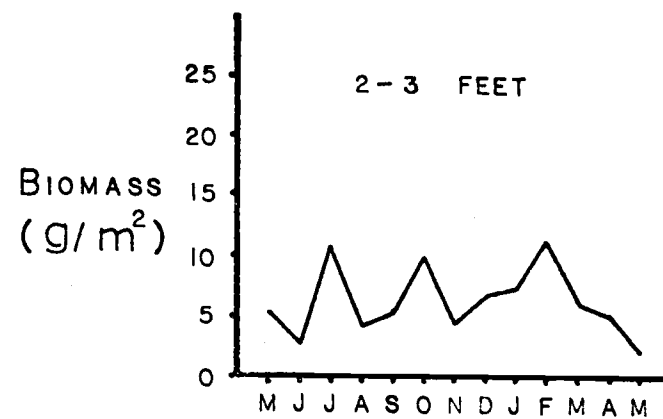
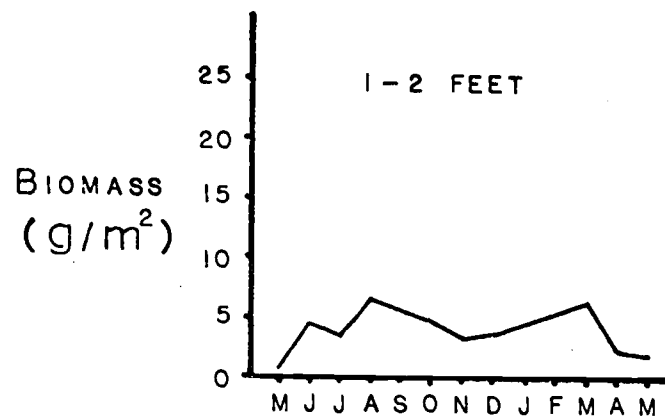


Figure 25.

Table 3. Student's t-test Between Means as Applied on the Mean Monthly Biomass of Crabs (Bio) in Grams Per Square Meter for Five Tidal Heights.

Tidal height	Tidal height of comparison	D. F.	t-value	Significance level
Bio <sub>0</sub> (1.142)	Bio <sub>1</sub> (3.807)	11	3.059	**
Bio <sub>0</sub> (1.142)	Bio <sub>2</sub> (6.229)	14	3.992	**
Bio <sub>0</sub> (1.142)	Bio <sub>3</sub> (10.182)	13	3.427	**
Bio <sub>0</sub> (1.142)	Bio <sub>4</sub> (9.782)	13	3.483	**
-----				
Bio <sub>1</sub>	Bio <sub>2</sub>	19	2.481	*
Bio <sub>1</sub>	Bio <sub>3</sub>	18	3.547	**
Bio <sub>1</sub>	Bio <sub>4</sub>	18	3.280	**
-----				
Bio <sub>2</sub>	Bio <sub>3</sub>	21	2.448	*
Bio <sub>2</sub>	Bio <sub>4</sub>	21	1.854	*
-----				
Bio <sub>3</sub>	Bio <sub>4</sub>	20	0.689	-

\*\* = Significant at 99% level

\* = Significant at 95% level

- = Not significant at 95% level

(Subscripts as in Table 1.)

( $p < .01$ ) from the values of the 3-4 and 4-5 ft levels. The mean monthly biomass value for the 3-4 ft level, however, could not be shown to be significantly different ( $p > .05$ ) from the biomass value of the 4-5 ft level. Therefore, a definite biomass segregation by tidal height has been demonstrated.

The average monthly production rate ( $\text{g/m}^2$  per month) at each tidal height is plotted in Figure 26. The 0-1 ft level and the 1-2 ft level showed an average negative production rate of about  $-0.10 \text{ g/m}^2$  per month. The 2-3 ft level showed a greater negative production value while the 3-4 ft level showed the greatest average negative production. Average monthly production was highest in the 4-5 ft interval. The negative productions in the lower regions suggested that the population was declining or that emigration was occurring from these levels. The net monthly production was about  $-1.23 \text{ g/m}^2$  per month or about equivalent to 2.3 average (carapace width 1.5 cm) crabs lost from the population per month per  $\text{m}^2$ . This low production loss indicated that in all probability a stable population still existed. Figure 27 shows the production rates for the different tidal heights. No clear production trend existed except for a constant production rate with a large fluctuation in monthly values. Although the biomass for each tidal height was significantly different from all other tidal heights (see Table 3), the mean production values for the various levels were all near a zero value.

Figure 26. Average monthly production rate in  $\text{g/m}^2$  per month for Hemigrapsus oregonensis at Coquille Point in the Yaquina Bay Estuary during the period from April, 1972 through May, 1973. Dashed line represents zero production rate of stable population. Means are connected by solid line. Vertical bars indicate standard error about means. T-tests between means and between zero production rate were not significantly different. Production, as used here, is synonymous with standing crop fluctuation and is not meant to imply the inclusion of relative growth rate data.

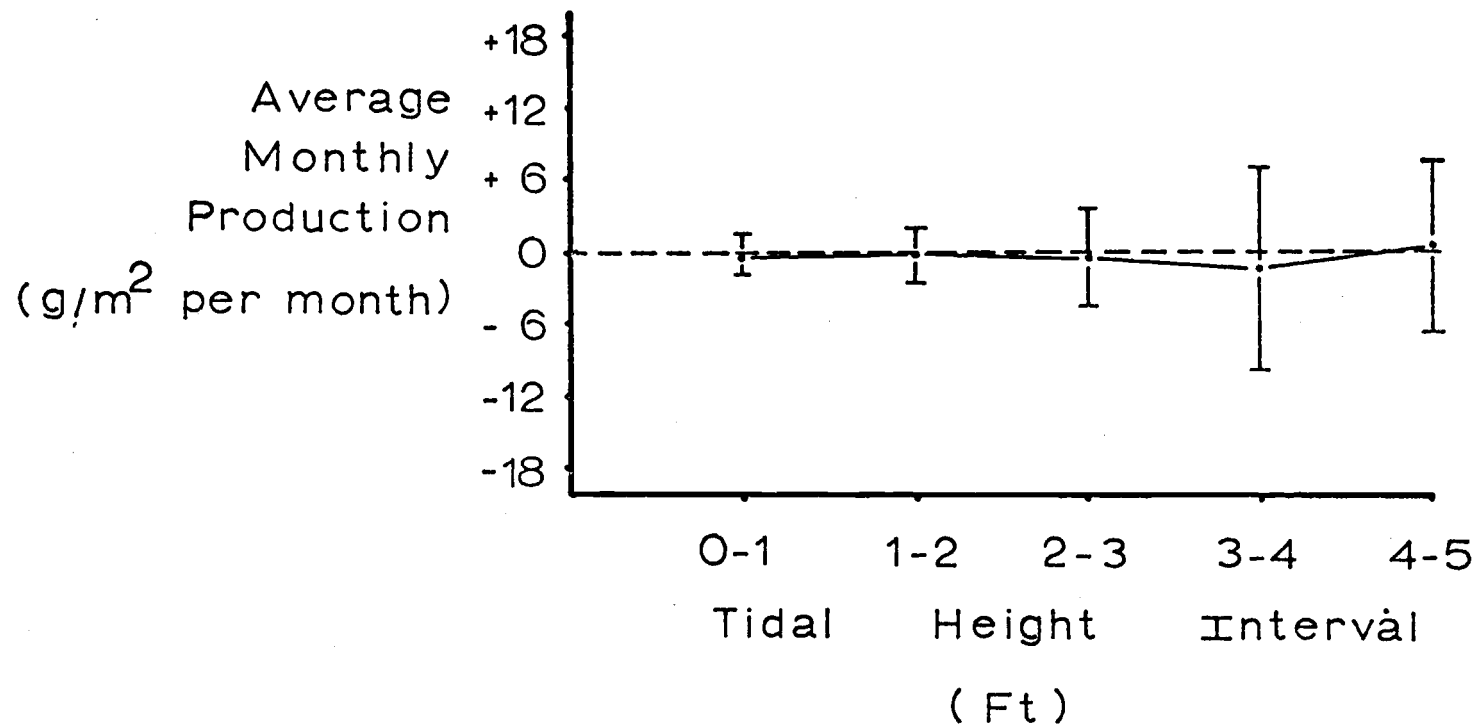


Figure 26.

Figure 27. Production rates ( $\text{g/m}^2$  per month) at various tidal heights for Hemigrapsus oregonensis at Coquille Point from April, 1972 through May, 1973. Dashed lines represent mean production rates during the study period. Mean production rates were not found to be significantly different from a zero production rate ( $p > .05$ ).

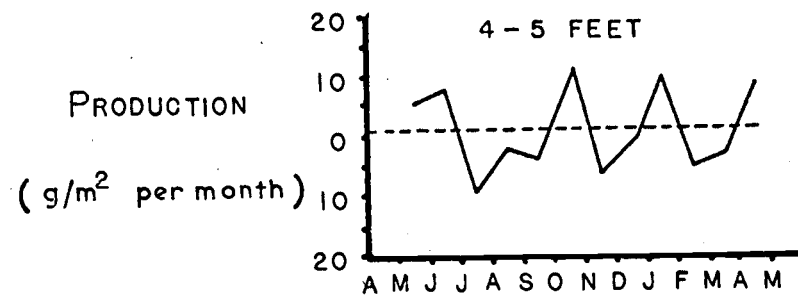
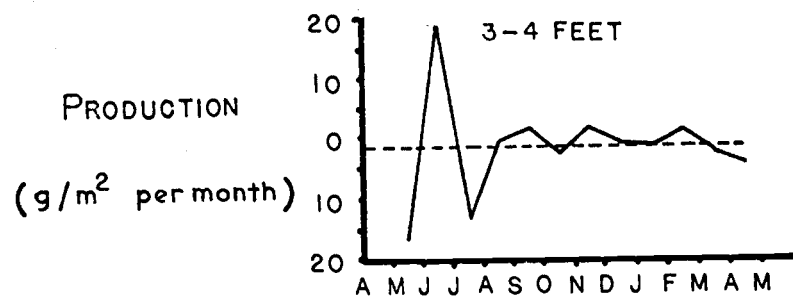
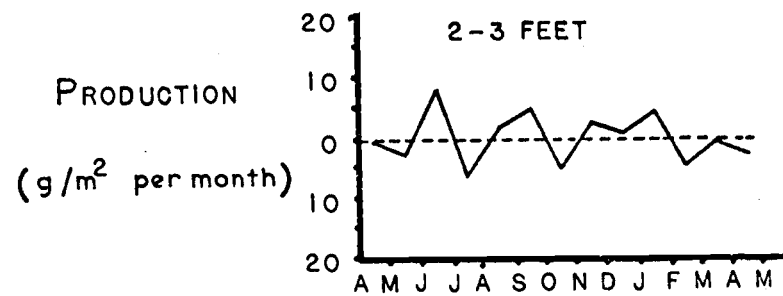
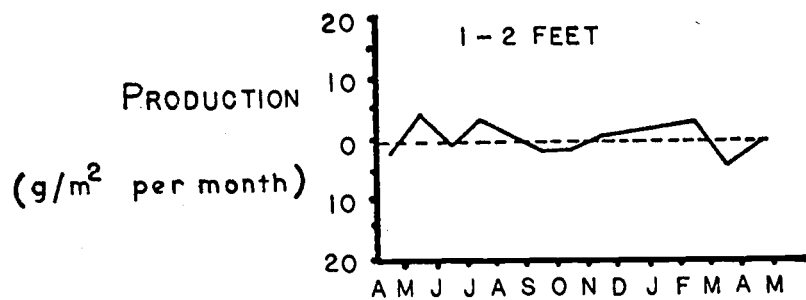


Figure 27.



A zero value of production would, of course, be indicative of a stable population. To determine if such a production rate existed, a t-test between means for each tidal height was performed (Table 4). It was found that the mean production rate for each tidal height was not significantly different ( $p > .05$ ) from any other tidal height. From a comparison of the mean production rate of the 3-4 ft interval and the 4-5 ft interval (greatest range of production) it can be determined that no production rate is significantly different from a zero production rate ( $p > .05$ ). Hence, a statistically valid argument is presented stating that, with respect to production, the population was stable during the study period.

#### Locomotory Activity Pattern

Field observations indicated nothing regarding activity at high tide. Greater activity was observed during night low tide periods than during day low tide periods. Experiments were performed to determine if this apparent night-day difference in activity existed. Additional experiments were performed to determine if activity periods were regulated by a solar day cycle (light regime), a lunar day cycle (tidal regime), or by both. Data show that subjective field observations were not valid in all cases. In about half of the experiments, lower night time than day time activity occurred. Activity seemed most dependent on the state of the tide, however. Greatest

Table 4. Student's t-test Between Means as Applied on the Mean Monthly Production of Crabs (Prod) in Grams Per Meter Squared Per Month for Five Tidal Heights.

Tidal height	Tidal height of comparison	D. F.	t-value	Significance level
Prod <sub>0</sub> (-0.0108)	Prod <sub>1</sub> (-0.3366)	11	0.0345	-
Prod <sub>0</sub> (-0.0108)	Prod <sub>2</sub> (-0.3139)	15	0.0933	-
Prod <sub>0</sub> (-0.0108)	Prod <sub>3</sub> (-1.4679)	14	0.3005	-
Prod <sub>0</sub> (-0.0108)	Prod <sub>4</sub> (+0.7688)	14	0.2413	-
-----				
Prod <sub>1</sub>	Prod <sub>2</sub>	20	0.4210	-
Prod <sub>1</sub>	Prod <sub>3</sub>	19	0.6124	-
Prod <sub>1</sub>	Prod <sub>4</sub>	19	0.1767	-
-----				
Prod <sub>2</sub>	Prod <sub>3</sub>	23	0.4325	-
Prod <sub>2</sub>	Prod <sub>4</sub>	23	0.4711	-
-----				
Prod <sub>3</sub>	Prod <sub>4</sub>	22	0.6984	-

\*\* = Significant at 99% level

\* = Significant at 95% level

- = Not significant at 95% level

(Subscripts as in Table 1.)

activity occurred during high tide periods, regardless of light regime. Both solar day (24.0 h) and lunar day (24.8 h) lengths seem to affect crab activity patterns.

Results are based on an average of 190 h monitoring time on each of 16 individual crabs, or over 3000 h of total monitoring time. Crabs were individually tested for periodicity in locomotor activity patterns in the activity chambers described in the Methods and Materials. Experiments were initiated within 3 h after removal of crabs from the 5 ft level at the shore.

Figure 28 shows the activity pattern of one Hemigrapsus oregonensis over a 5 day period under a natural light regime (L = 12 h, D = 12 h). This pattern has been superimposed on the tidal regime during the experimental period. The results indicate that this crab had activity bursts coinciding with periods of high tide. Both low tide and dark periods were periods of low activity. Since few crabs were ever seen moving about during daytime low tides, this suggested that periods when the crabs were covered with water were periods of increased activity. The mean length between activity bursts was found to be 24.6 h, corresponding quite closely to a 24.8 h periodicity between successive higher high tides (periodicity of a lunar day).

Figure 29 again shows a persistent activity rhythm over 7 tidal cycles, with activity peaks corresponding to periods of high tide.

Figure 28. Activity pattern of Hemigrapsus oregonensis under laboratory conditions. Activity pattern of an isolated crab subjected to an artificial light regime (L = 12 h, D = 12 h). The activity pattern is superimposed on the tidal regime for the experimental period (October 21-27, 1972).

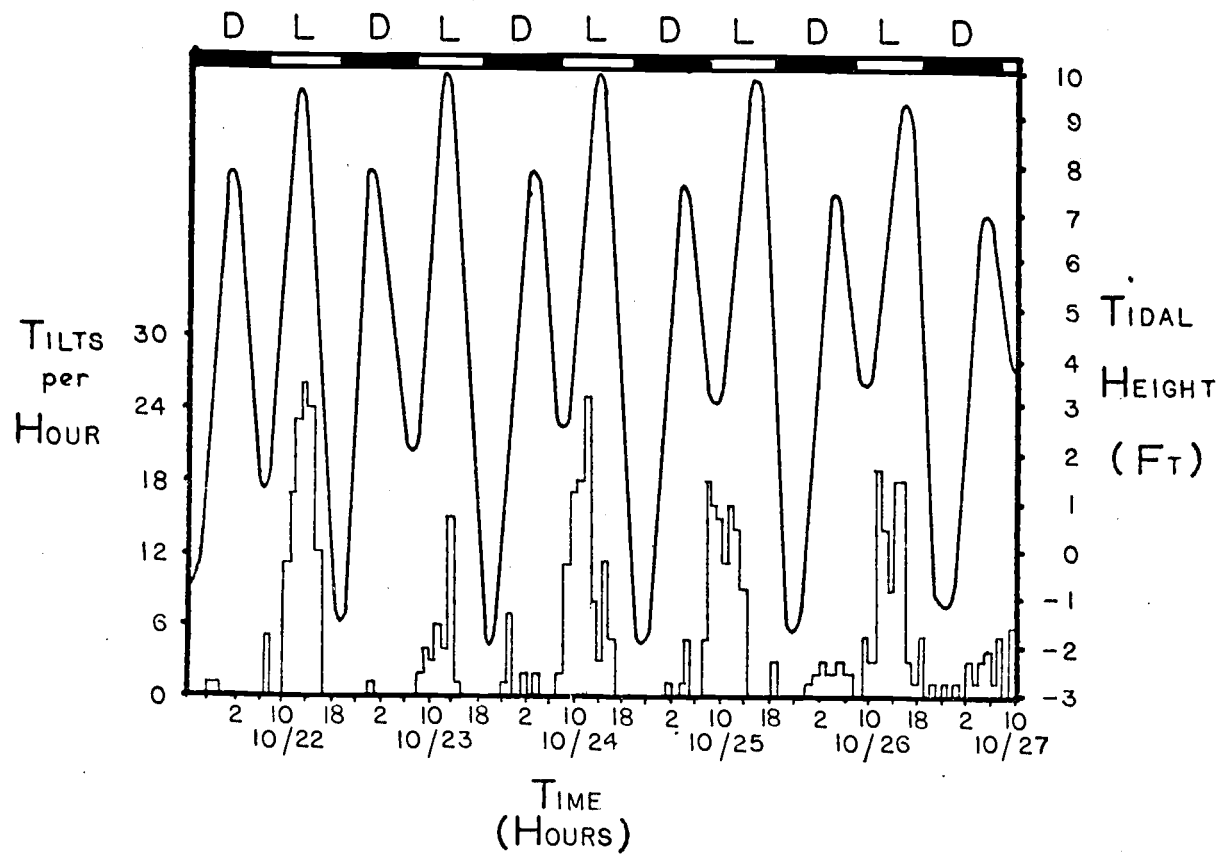


Figure 28.

Figure 29. Activity pattern of Hemigrapsus oregonensis under laboratory conditions. Activity pattern of an isolated crab subjected to an artificial light regime (L = 7 h, D = 17 h). The activity pattern is superimposed on the tidal regime for the experimental period (November 19-~~26~~, 1972).

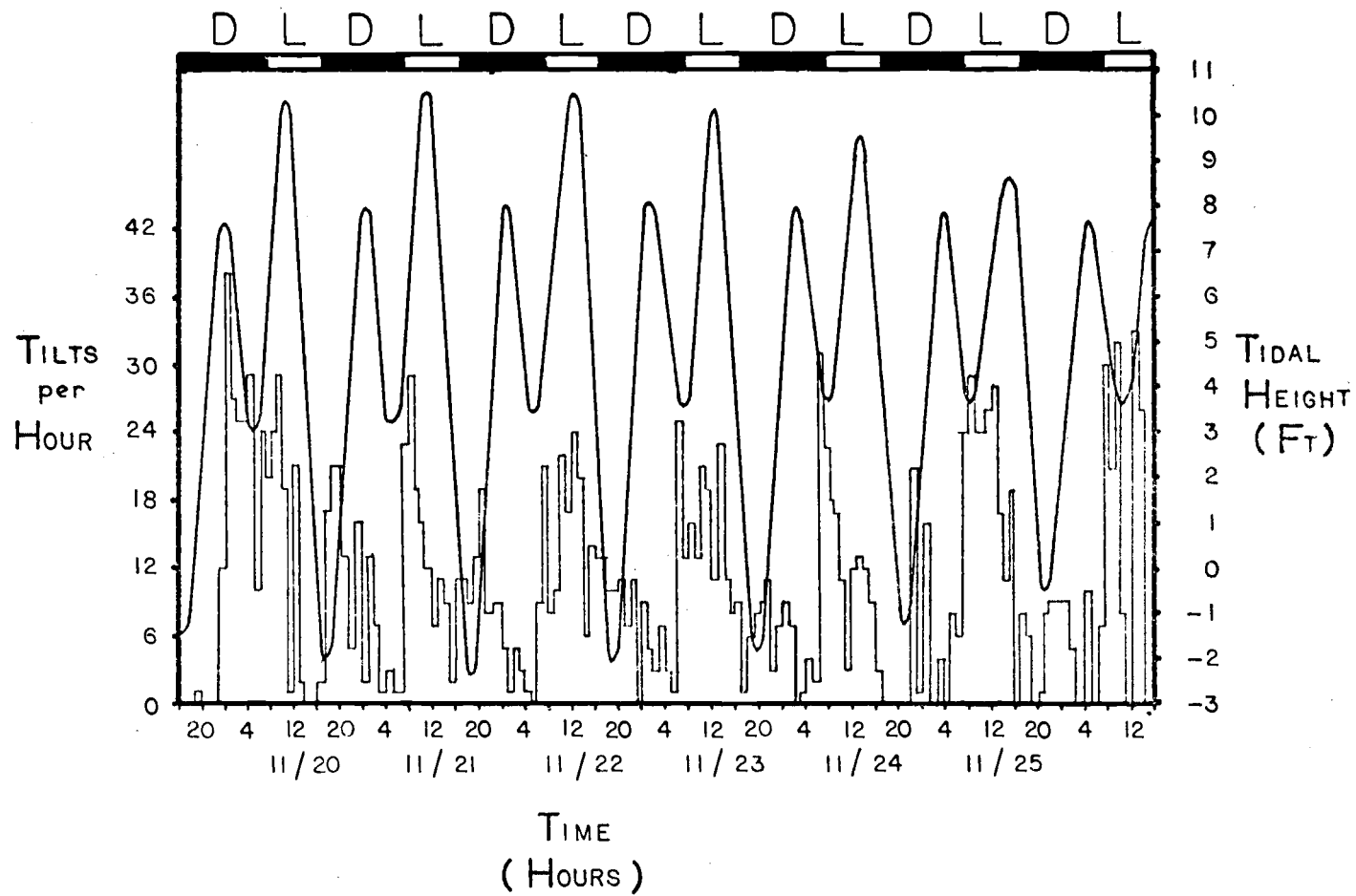


Figure 29.

However, rather than relatively low activity during darkness, great activity bursts were recorded which then trailed off, becoming large again during light or high tide periods. There was, then, an apparent cycle with a mean length between bursts of 12.2 h, almost half that of the lunar periodicity. The periods of greatest activity, however, were not precisely coincident with periods of high tide. A phase shift of about 3 h is evidenced by the crab's activity peaks preceding the predicted high tide by 3 h.

The activity peaks in the first 2 tidal cycles, as expressed in Figure 30, showed no clear rhythmicity. However, the last 5 tidal cycles indicated a clearer pattern. Again, peaks corresponded to periods of high tide. Since greatest activity occurred during periods of light, it is suggested that in the absence of re-entrainment by a tidal cycle the periodicity which emerged was dependent on the light regime. The mean duration between activity peaks was reduced to 22.2 h (L = 7 h, D = 17 h). The length of duration of the activity bursts was 15.9 h, consisting almost totally of the entire light period and the first half of the dark period.

Not all crabs in a light-dark regime showed a clear rhythmic pattern (Figure 31). After an initial activity burst, a rather constant activity pattern emerged and indicated nearly equal activity bursts during dark as well as light periods.

Not only did some crabs show no rhythmicity, some crabs



Figure 30. Activity pattern of Hemigrapsus oregonensis under laboratory conditions. Activity pattern of an isolated crab subjected to an artificial light regime (L = 7 h, D = 17 h). The activity pattern is superimposed on the tidal regime for the experimental period (November 4-11, 1972).

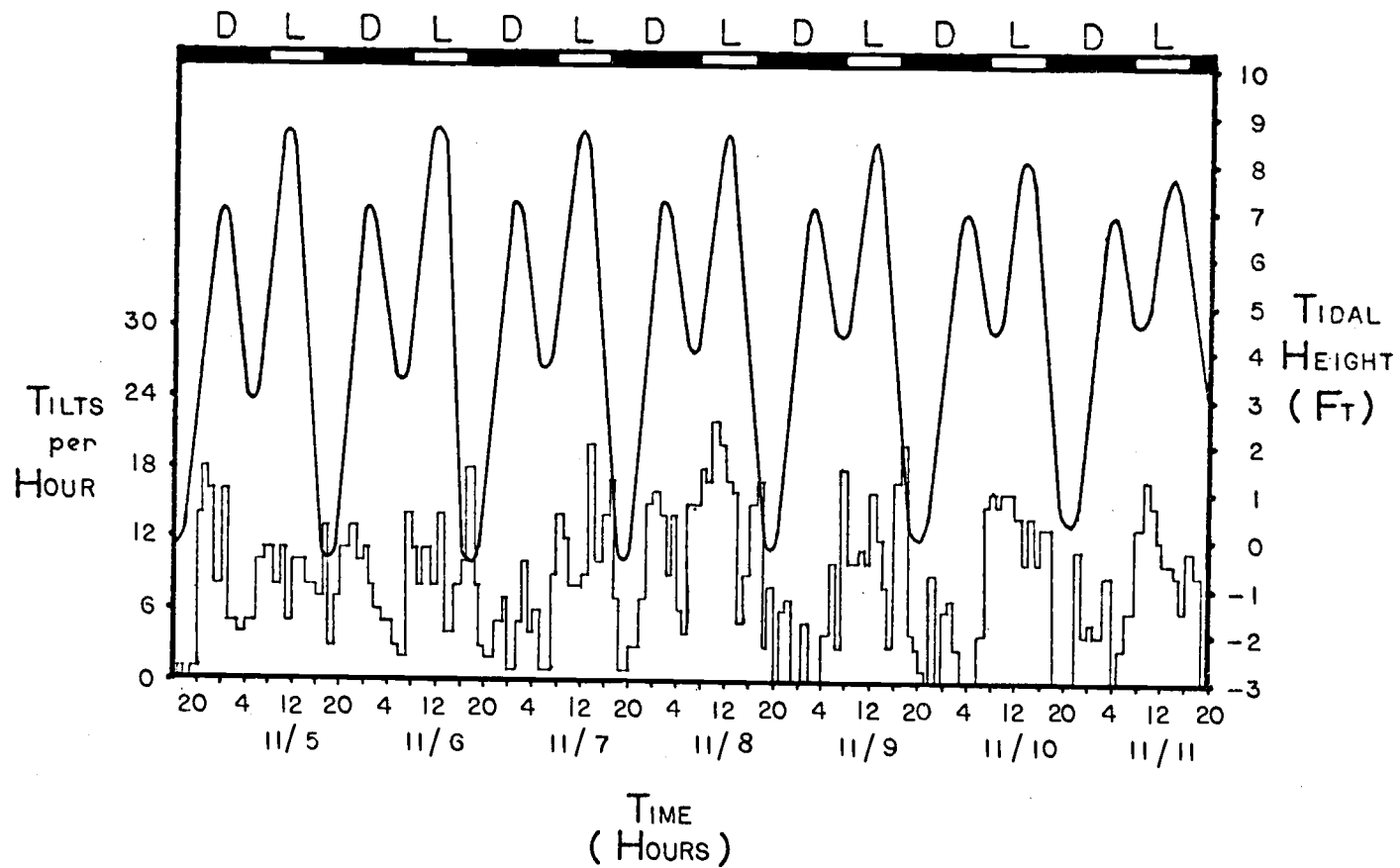


Figure 30.

Figure 31. Activity pattern of Hemigrapsus oregonensis under laboratory conditions. Activity pattern of an isolated crab subjected to an artificial light regime (L = 7 h, D = 17 h). The activity pattern is superimposed on the tidal regime for the experimental period (November 19-26, 1972).

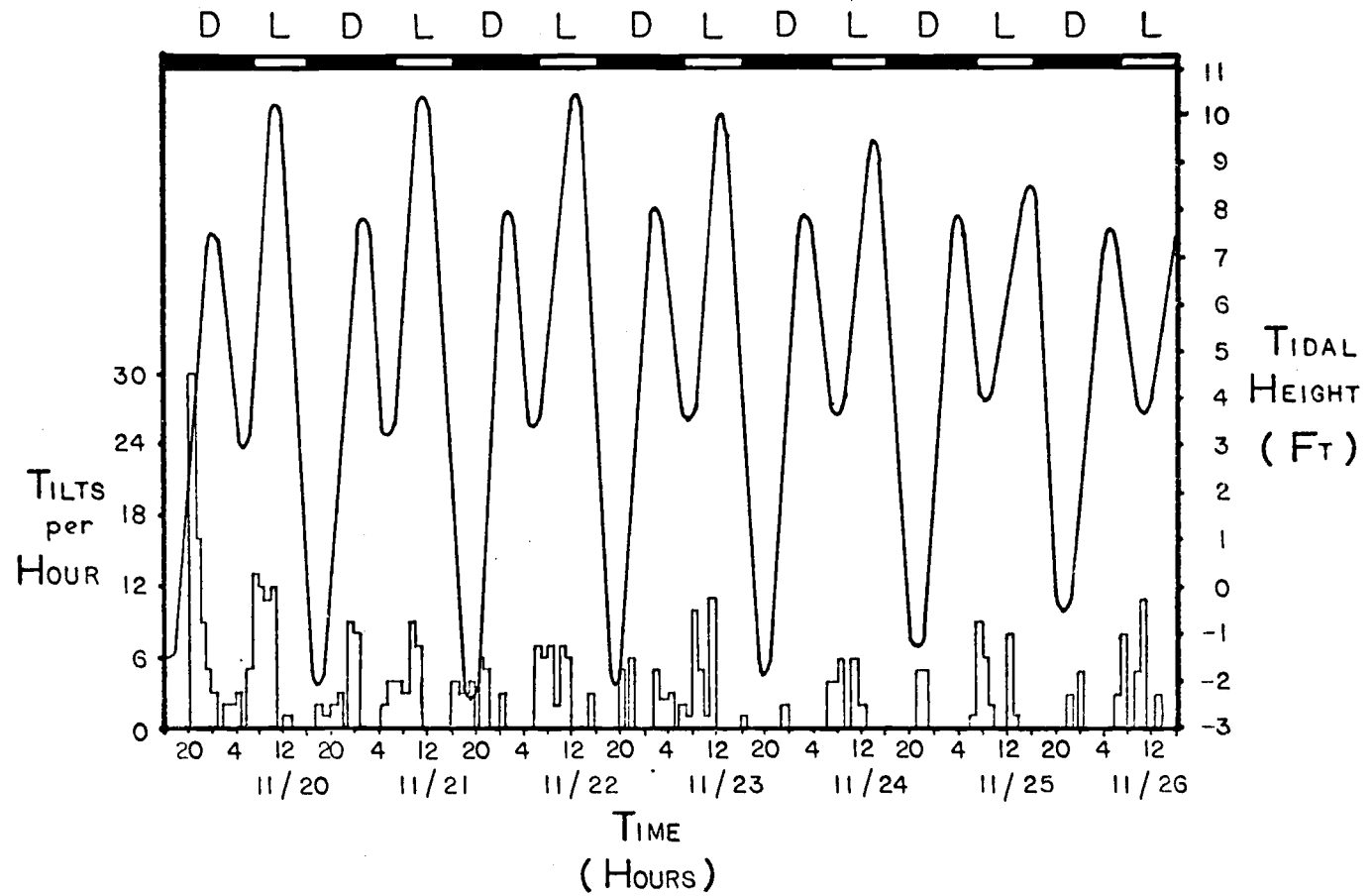


Figure 31.

showed decreasing activity during the experiment. The first 2 tidal cycles of Figure 32 showed an average activity level of 9.7 tilts per hour. The last 2 tidal cycles, however, showed an average of only 2.3 tilts per hour. The greatest hourly activity for the first 4 tidal cycles corresponded to the initiation of dark and light periods.

Figure 33 again showed an initial activity period which corresponded to high tide. The magnitude of response, however, decreased over the next 2 tidal cycles and was indistinguishable as a persistent rhythm by the fourth tidal cycle.

It is apparent, then, that not all crabs exhibit a well-defined locomotor rhythmicity. Since it was indicated that both light and high tide may be cues for initiating activity periods, an experiment was run to remove the effects of light on activating the crabs. The crabs were subjected to a natural ( $L = 7$  h,  $D = 17$  h) light-dark regime for 3 full tidal cycles and then denied any light intensity increases for the next 6 full tidal cycles. The data presented in Figure 34 show no well-defined rhythmicity during the light-dark regime; however, a clear rhythmicity emerged after the crab was subjected to a constant darkness. Since the light regime was not in effect, the rhythmicity which emerged presumably was not based on the solar day. The mean length between activity bursts was 29.0 h with an average duration of 21.6 h. It thus appears that under

Figure 32. Activity pattern of Hemigrapsus oregonensis under laboratory conditions. Activity pattern of an isolated crab subjected to an artificial light regime (L = 7 h, D = 17 h). The activity pattern is superimposed on the tidal regime for the experimental period (November 19-26, 1972).

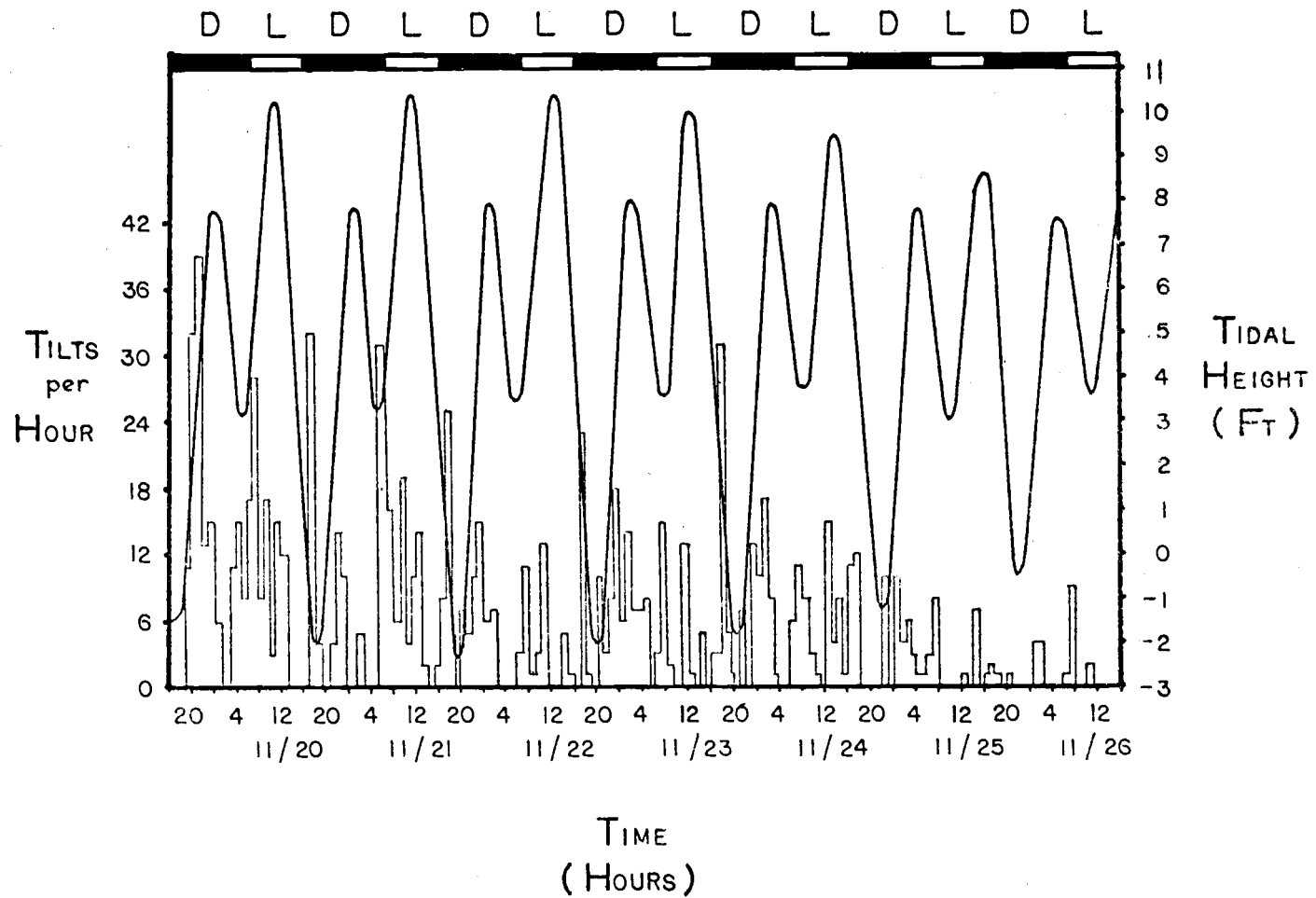


Figure 32.

Figure 33. Activity pattern of Hemigrapsus oregonensis under laboratory conditions. Activity pattern of an isolated crab subjected to an artificial light regime (L = 12 h, D = 12 h). The activity pattern is superimposed on the tidal regime for the experimental period (October 21-27, 1972). Note the apparent loss of rhythmicity (compare to Figure 30).



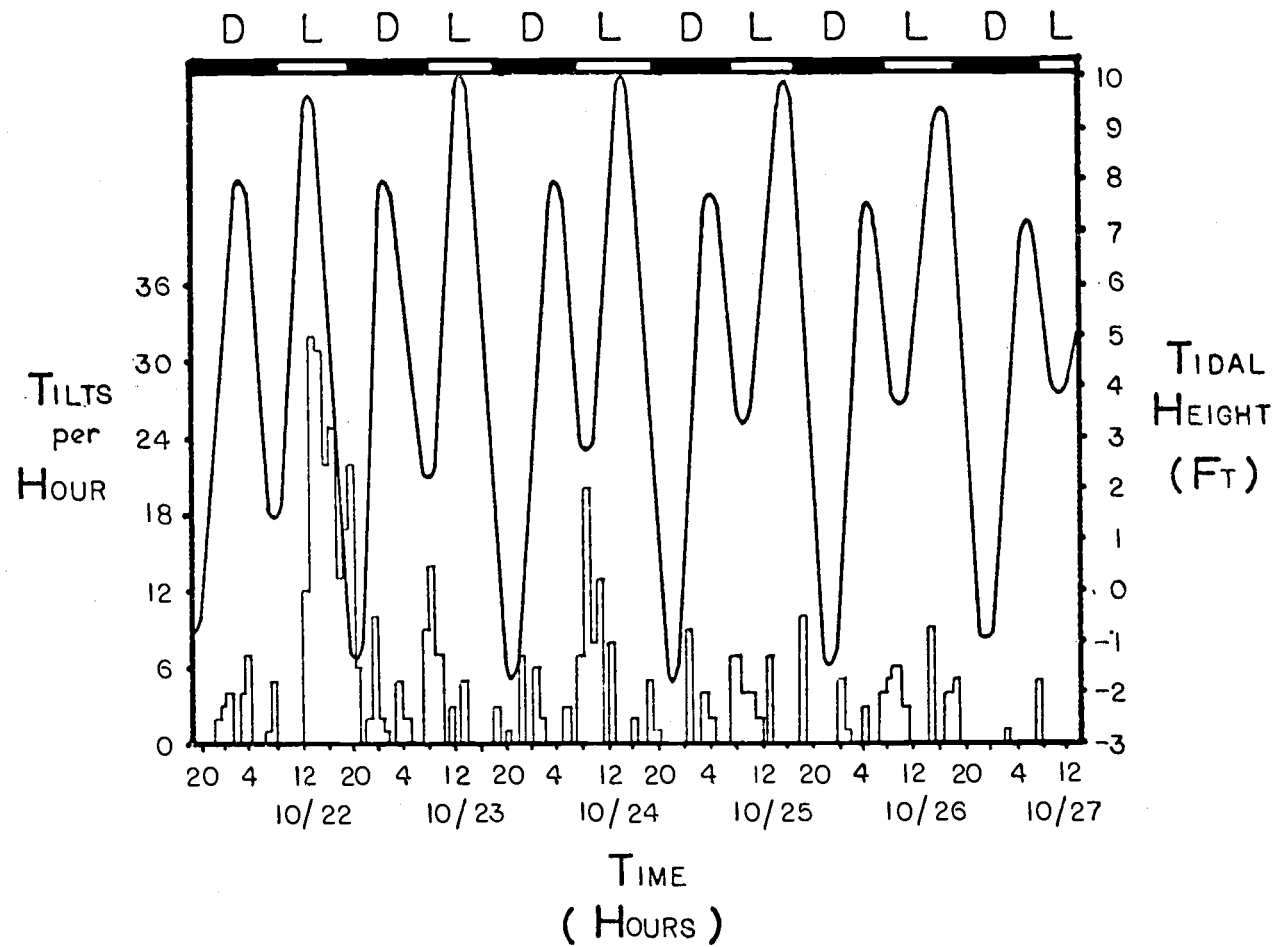


Figure 33.

Figure 34. Activity pattern of Hemigrapsus oregonensis under laboratory conditions. Activity pattern of an isolated crab subjected to an artificial light regime (L = 7 h, D = 17 h) for three consecutive photoperiods and then subjected to a constant low level light regime for the next six consecutive tidal cycles. The activity pattern is superimposed on the tidal regime for the experimental period November 26 - December 6, 1972).

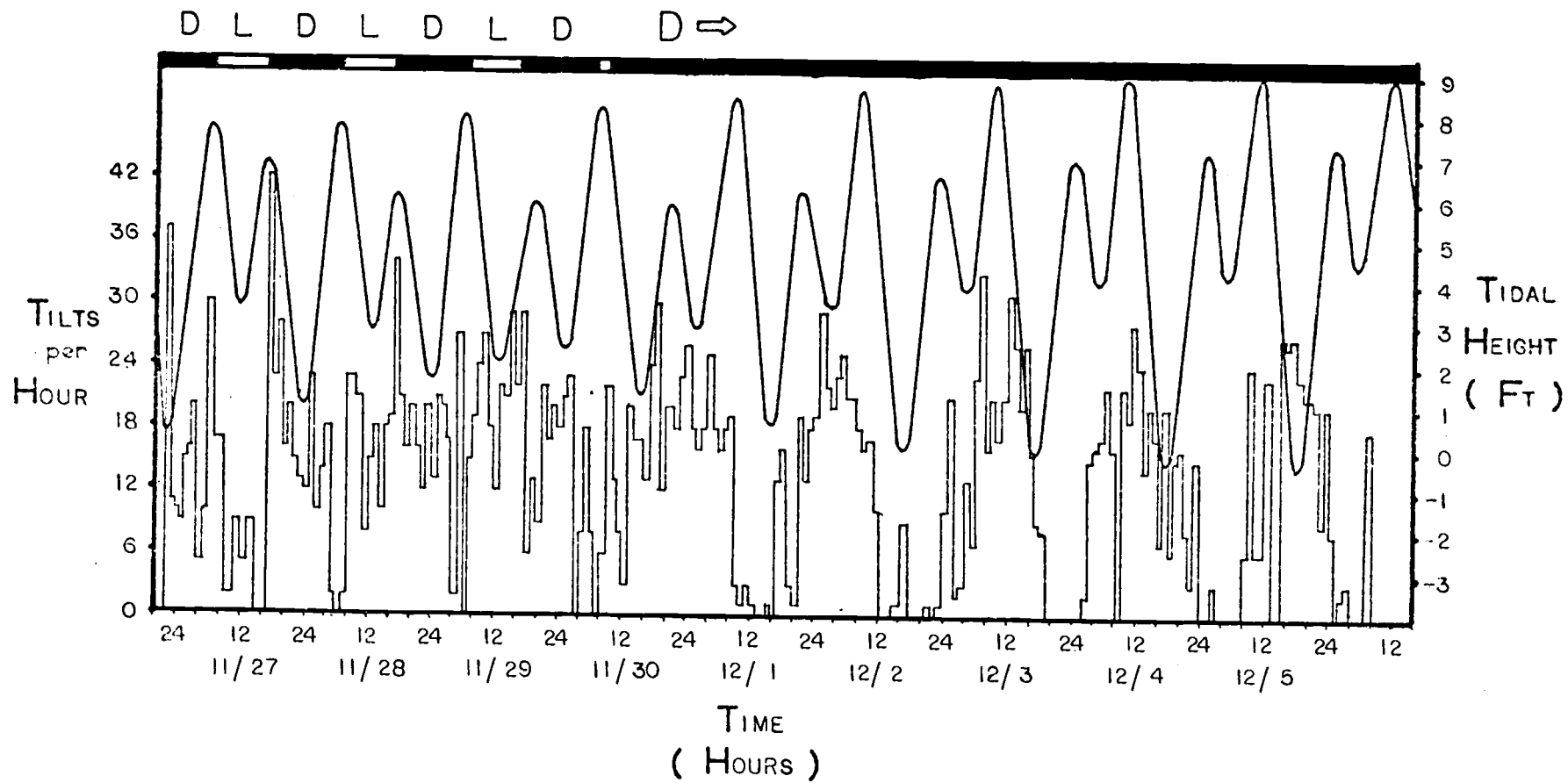


Figure 34.

constant darkness the periodicity of the locomotory response tends to expand and become out of phase with the high tide within 5 tidal cycles.

Similarly, Figure 35 showed a definite rhythmicity emerging during the constant dark portion of the experiment. The average duration between activity bursts was again 29.0 h, suggesting an endogenous rhythmicity which was greater than a lunar day cycle (24.8 h).

Additional experiments under constant darkness (Figures 36 and 37) showed initial activity peaks corresponding to high tide periods during the first 2 or 3 tidal cycles but later the activity appeared to become more random. The duration between activity peaks before disintegration of the pattern was, in both cases, considerably less (25.7 h and 23.0 h) than the 29.0 h periodicity found in those activity patterns which did not decay.

It is suspected, then, that two different entrainment factors are operative: light regime and tidal regime. The light regime seems to elicit a periodicity of about 23 h. The tidal regime, after 3 tidal cycles, elicits a periodicity of about 29 h. When both factors are operative, however, the combined effect is a rhythmicity of about 24.4 h. The 2 cycles thus seem to be antagonistic in that the emergent activity pattern is intermediate to both, being longer than the light-dark regime and shorter than the constant dark-tidal

Figure 35. Activity pattern of Hemigrapsus oregonensis under laboratory conditions. Activity of an isolated crab subjected to an artificial light regime (L = 7, D = 17 h) for three consecutive photoperiods and then subjected to a constant low level light regime for the next six consecutive tidal cycles. The activity pattern is superimposed on the tidal regime for the experimental period (November 26 - December 6).

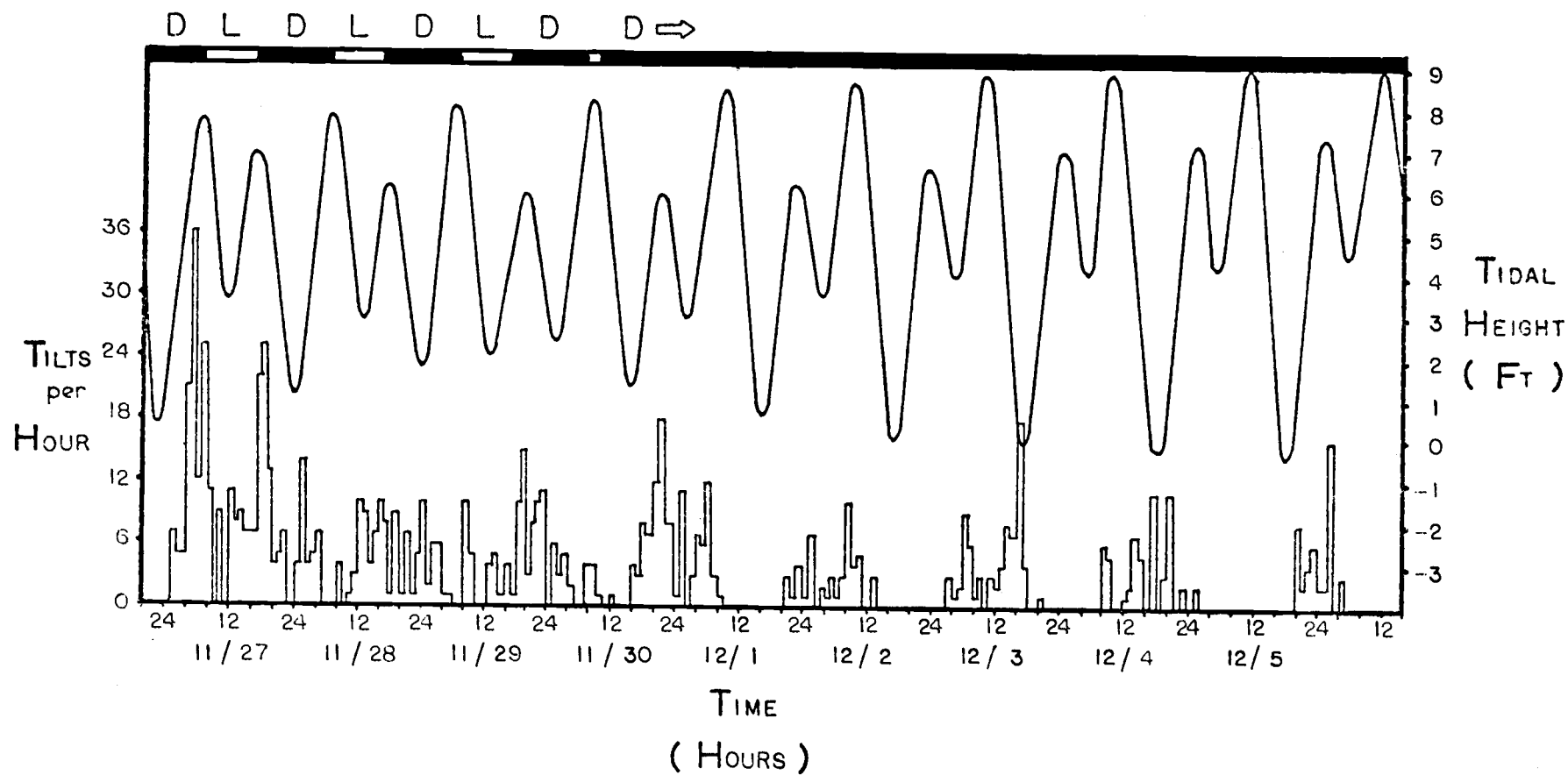


Figure 35.

Figure 36. Activity pattern of Hemigrapsus oregonensis under laboratory conditions. Activity pattern of an isolated crab subjected to a constant low level light. The activity pattern is superimposed on the tidal regime for the experimental period (December 18-27, 1972).

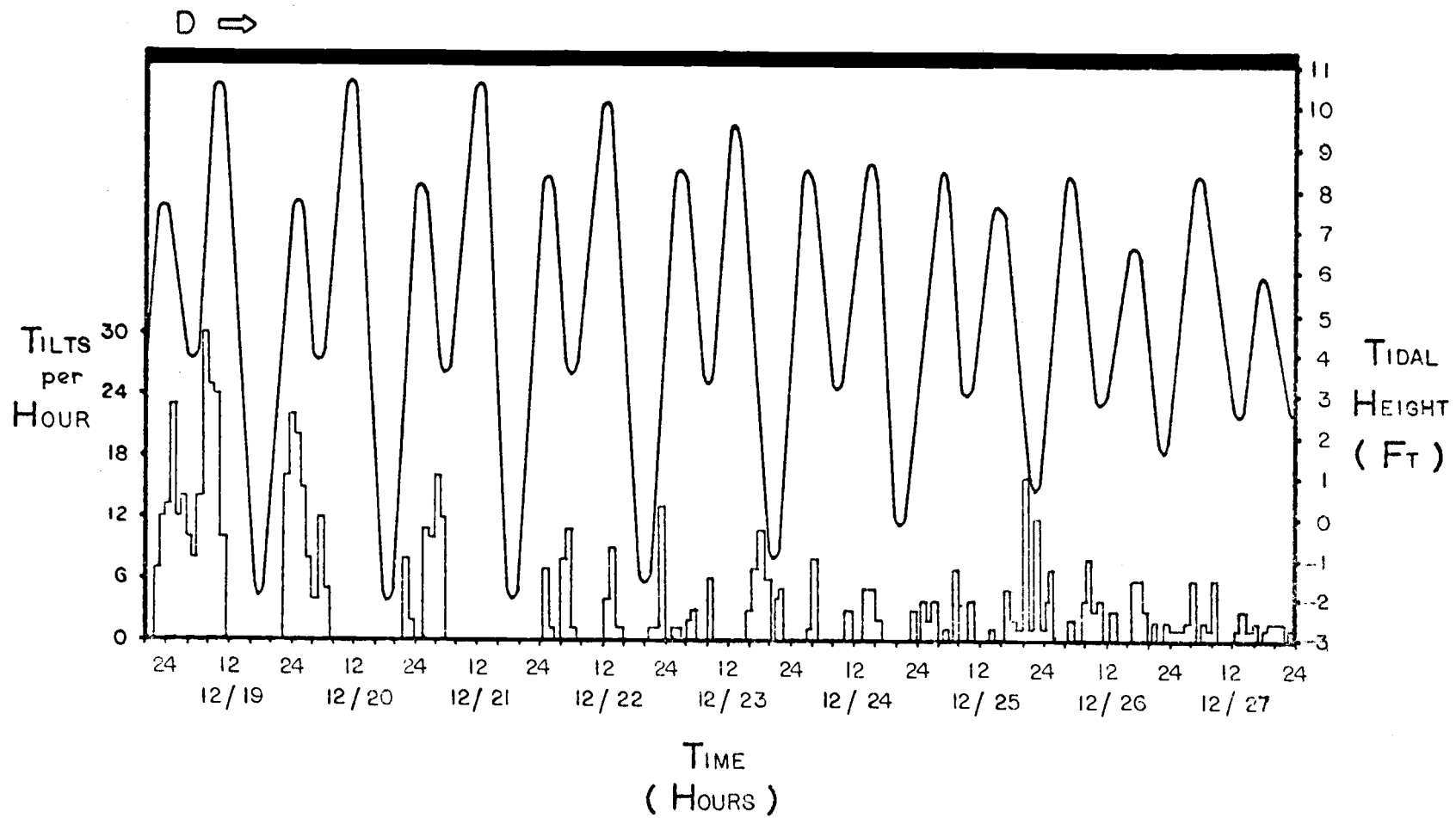


Figure 36.



Figure 37. Activity pattern of Hemigrapsus oregonensis under laboratory conditions. Activity pattern of an isolated crab subjected to a constant low level light. The activity pattern is superimposed on the tidal regime for the experimental period (December 18-27, 1972).

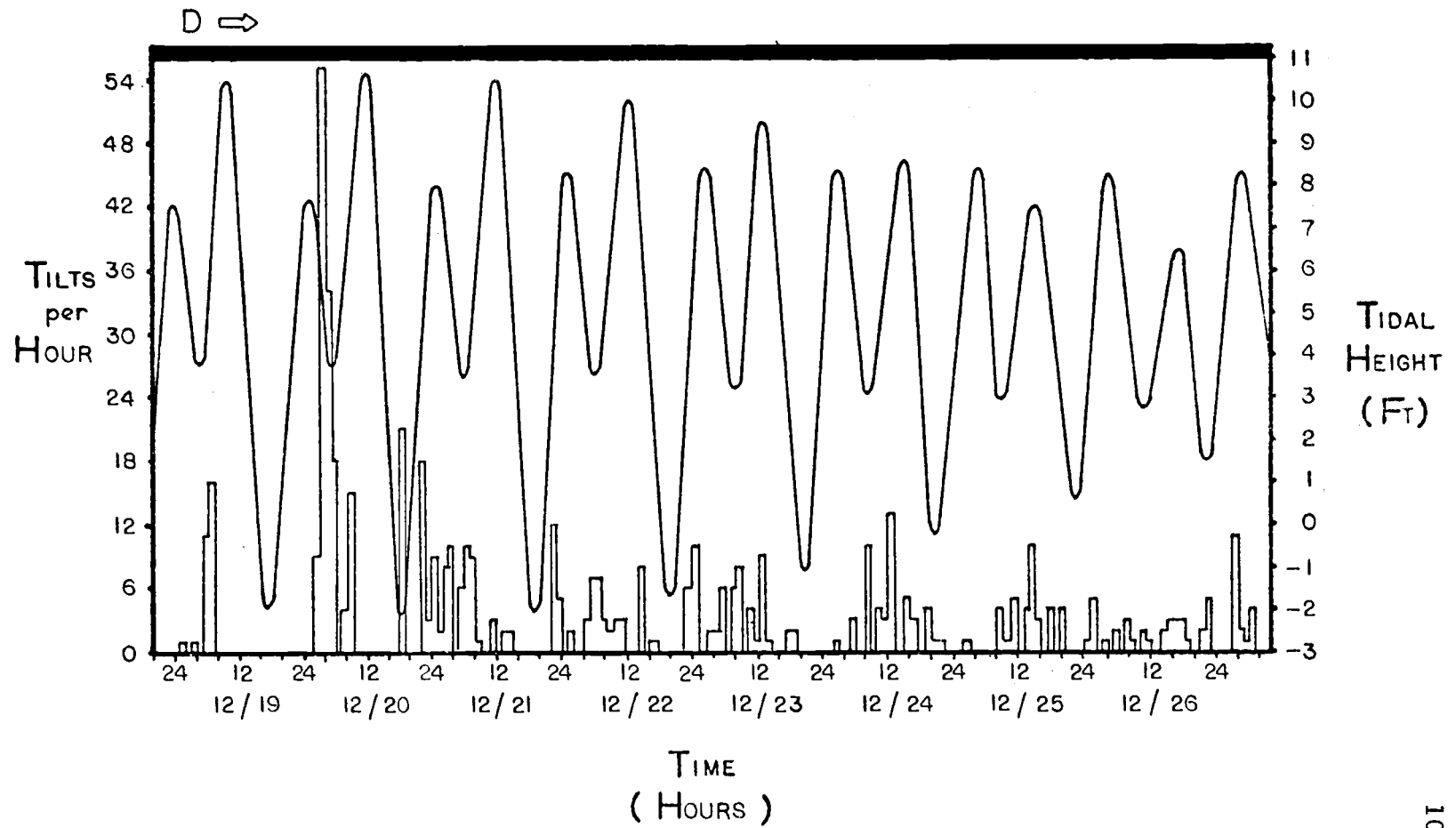


Figure 37..

regime rhythm. The resultant pattern, then, closely follows the lunar cycle of the tides.

In addition to the rhythmic behavior, the periodicity of activity relative to light, dark, and to whether the habitat was covered (high tide) or exposed (low tide) was investigated. A t-test between the mean number of tilts per hour was run for several comparisons (Table 5) under a light-dark regime. A study of experiments 1, 2, and 3 showed that the crabs were significantly more active ( $p < .05$ ) during periods of darkness (D) than during periods of light (L). These crabs were also more active during periods of high tide (C) than low tide (E). Greater activity occurred during periods of high tide (C) than during light hours (L) and greater activity occurred during darkness (D) than during low tide periods (E). It thus appeared that greatest activity in experiments 1, 2, and 3 coincided with periods of high tide (C); the next greatest period activity coincided with darkness (D) followed by low tide (E) and with least activity recorded during daylight hours (L). Activity appeared to be regulated by a tidal component (lunar rhythmicity) and a light component (solar rhythmicity).

Periods of darkness were further divided into dark-high tide (DC) and dark-low tide (DE) and light periods were similarly divided into light-high tide (LC) and light-low tide (LE) in an effort to couple the light regime and tidal regime effects. In experiment 1 of

Table 5, greater crab activity occurred during light-high tide (LC) than during light-low tide (LE), reflecting a true tidal rhythmicity. Greater activity also occurred during dark-high tide (DC) than during light-high tide (LC), suggesting a diurnal rhythmicity. In each of the first 3 experiments, greater activity was found at dark-high tide (DC) than at light-low tide (LE). Hence, the greatest activity was found to be during dark-high tide (DC), followed by dark-low tide (DE), followed by light-high tide (LC) with least activity occurring during light-low tide (LE). Greatest activity thus corresponded to dark periods and was augmented by high tides.

Experiments 4, 5, 6, and 7 (Table 5), however, presented a different activity pattern although experimental conditions were not varied. In all cases, greater activity occurred during light periods ( $p < .01$ ) than during dark periods. Greater activity also occurred during light periods than during either high tide or low tide periods. The crabs were also more active during high tide and low tide periods than they were during dark periods. This suggests that these crabs were more greatly influenced, under the artificial test conditions, by a light regime than by the endogenous tidal rhythm, which seemed to fade out and be overridden by the effects of the light regime.

A comparison of the light regime with the combined effect of

Table 5. Results of t-test Between Mean Number of Tilts Per Hour of Hemigrapsus oregonensis in an Activity Chamber Subjected to An Alternating Light-dark Cycle.

Experi- ment	L vs D	L vs C	L vs E	D vs C	D vs E	C vs E	LC vs LE	LC vs DC	LC vs DE	LE vs DC	LE vs DE	DC vs DE
1	** D>L	** C>L	- E>L	- C>D	** D>E	** C>E	** LC>LE	* DC>LC	- DE>LC	** DC>LE	** DE>LE	- DC>DE
2	** D>L	** C>L	- E>L	* C>D	* D>E	* C>E	- LC>LE	* DC>LC	* DE>LC	* DC>LE	- DE>LE	** DC>DE
3	* D>L	- C>L	- E>L	- D>C	- D>E	- C>E	- LC>LE	* DC>LC	- DE>LC	* DC>LE	- DE>LE	* DC>DE
4	** L>D	- L>C	** L>E	** C>D	** E>D	- C>E	- LC>LE	** LC>DC	** LC>DE	** LE>DC	** LE>DE	- DC>DE
5	** L>D	** L>C	- L>E	- C>D	** E>D	* E>C	* LE>LC	- LC>DC	- LC>DE	** LE>DC	** LE>DE	- DE>DC
6	** L>D	** L>C	** L>E	** C>D	- E>D	* C>E	- LE>LC	** LC>DC	** LC>DE	** LE>DC	** LE>DE	- DC>DE
7	** L>D	** L>C	** L>E	** C>D	* E>D	- C>E	- LE>LC	** LC>DC	** LC>DE	** LE>DC	** LE>DE	- DE>DC
8	- D>L	- C>L	- E>L	- D>C	- D>E	- C>E	- LE>LC	* DC>LC	- DE>LC	- LE>DC	- DE>LE	- DE>DC
9	- L>D	- L>C	- L>E	- C>D	- E>D	- E>C	- LE>LC	- LC>DC	- LC>DE	* LE>DC	- LE>DE	- DE>DC

Continued

Table 5--Continued.

Experi- ment	L vs D	L vs C	L vs E	D vs C	D vs E	C vs E	LC vs LE	LC vs DC	LC vs DE	LE vs DC	LE vs DE	DC vs DE
10	-	-	-	-	-	-	-	-	-	-	-	-
	D>L	C>L	E>L	D>C	D>E	C>E	LE>LC	DC>LC	DE>LC	DC>LE	DE>LE	DE>DC
11	-	-	-	-	-	-	-	-	-	-	-	-
	L>D	C>L	L>E	C>D	D>E	C>E	LC>LE	LC>DC	LC>DE	DC>LE	LE>DE	DC>DE

The data were analyzed for four major activity periods (L = light, D = dark, C = covered or high tide at the collection site, and E = exposed or low tide at the collection site). The data were then reorganized to compare activity periods with relation to both light and tidal cycles (LC, LE, DC, DE). An asterisk (\*) indicates that the two means were significantly different at the 95% level. Two asterisks (\*\*) indicate the two means under comparison are highly significantly different at the 99% level. A minus sign (-) indicates that the difference between the two means is not significantly different. Letter symbols under significance test indicate which mean was the larger.

the tidal regime (experiments 4, 5, 6, and 7, Table 5) indicated that greatest activity occurred during periods of light-low tide (LE) followed by light-high tide (LC) with equal activity during dark-high tide (DC) and dark-low tide (DE) (means not significantly different). These findings support the interpretation that the rhythmicity due to tidal fluctuations is absent or completely masked by the light regime rhythmicity for these 4 experimental crabs.

Experiments 8, 9, 10 and 11 showed little activity and hence true rhythmic patterns could not be detected.

It is evident, then, that not all crabs tested showed a persistent rhythmic pattern. About 25% of the crabs showed an activity pattern which was coincident with both tidal and light regimes. Of the remaining 75%, about half showed an activity pattern corresponding to only a light regime and the other half showed no apparent rhythmicity.

In order to remove the effects of a light regime, additional crabs were tested in constant low level red light (darkness). The results of t-tests between the mean number of tilts per hour for the various comparisons are given in Table 6. Experiment 1 showed that, in the absence of light or tidal stimuli, greater activity occurred during dark periods than during light periods ( $p > .01$ ) or during low tide ( $p > .05$ ). Activity was also greater during high tide than during daylight hours ( $p > .05$ ) or during low tide ( $p > .05$ ).

Table 6. Results of t-test Between Mean Number of Tilts Per Hour of Hemigrapsus oregonensis in an Activity Chamber Subjected to Constant Darkness. (Other symbols are the same as in Table 6.)

Experiment	L vs D	L vs C	L vs E	D vs C	D vs E	C vs E	LC vs LE	LC vs DC	LC vs DE	LE vs DC	LE vs DE	DC vs DE
1	** D>L	* C>L	- E>L	- D>C	* D>E	* C>E	- LC>LE	* DC>LC	- DE>LC	** DC>LE	* DE>LE	* DC>DE
2	- D>L	- C>L	- E>L	- D>C	- D>E	- C>E	- LE>LC	* DC>LC	- DE>LC	- DC>LE	- LE>DE	- DC>DE
3	- D>L	- C>L	- E>L	- D>C	- D>E	- E>C	- LC>LE	- DC>LC	- DE>LC	- DC>LE	- DE>LE	- DE>DC
4	- D>L	- C>L	- E>L	- D>C	- D>E	- C>E	- LC>LE	- DC>LC	- DE>LC	- DC>LE	- DE>LE	- DC>DE
5	- D>L	- C>L	- E>L	- D>C	- E>D	- E>C	- LC>LE	- LC>DC	- DE>LC	- LE>DC	- DE>LE	- DE>DC



During dark periods, greater activity occurred during high tide (DC) than during low tide (DE) ( $p > .05$ ). During light periods, however, no statistical differences were found between activity means at high tide (LC) and low tide (LE). During high tides, greater activity occurred during the dark hours (DC) than the light hours (LC) ( $p > .05$ ). Similarly, during the low tides greater activity was found during darkness (DE) than during light hours (LE) ( $p > .01$ ). Under a constant dark regime, then, the crabs were still capable of maintaining a rhythmicity based on both tidal cycles and light cycles. The activity progression from the greatest activity to the least was  $D > C > E > L$  and for the combined data  $DC > DE > LC > LE$ . Experiments 2, 3, 4, and 5 (Table 6) reflected the same trend in means, although they were not shown to be significantly different.

## DISCUSSION

Classically, many factors have been proposed to explain the vertical distribution of intertidal organisms (Johnson and York, 1915; Colman, 1933, Hutchins, 1947; Stephenson and Stephenson, 1949). Two of the most influential factors are substrate type and exposure time (Doty, 1946; Ricketts, Calvin, and Hedgpeth, 1968). Within the study site it was shown that the density of the crab population varied vertically. H. oregonensis was found from lower regions of heavy silt and mud loads ( $8 \text{ crabs/m}^2$ ) to higher regions of well-drained, pea-sized gravel ( $20 \text{ crabs/m}^2$ ). It appears, then, that as the substrate becomes less muddy and as the height of the shore increases up to 4-5 ft level, the population density increases. As Hiatt (1948) predicted, H. nudus is found on this beach in the uppermost areas (5 ft level) where mud loads are least. Tests by Low (1970) indicate that H. oregonensis is significantly more tolerant of mud than is H. nudus. He has also shown that H. oregonensis is equally tolerant of either clear or muddy water, suggesting some mechanism to prevent gill clogging. In addition, he has shown that H. nudus is significantly less tolerant of muddy water than clear water, suggesting that H. nudus lacks a mechanism to prevent gill clogging. The lower boundary of H. nudus in the bay would, therefore, be influenced by the abundance of mud in the water.

Since H. oregonensis extends further down into the mud-laden areas, it must have some mechanism to cope with these factors. Surrounding the branchial opening in H. oregonensis are numerous small, fine setae. These setae function in filtering particulates from the water before they enter the gill chamber. H. nudus has fewer, coarser setae than H. oregonensis and hence does not have the silt-mud particle filtering efficiency that H. oregonensis has. As a result, the branchial chambers and gills of H. nudus tend to become clogged much more rapidly than those of H. oregonensis. Thus the development of dense, fine setae appears to be of major adaptive significance in a muddy environment.

For H. nudus, the lower limit of distribution seems to be determined by the abundance of mud at the collection site. H. oregonensis, however, appears to be limited at its lower boundary by a lack of suitable habitat cover. This lower limit may also be the result of direct interspecific predation by the starry flounder (Platyichthys stellatus) and the kelp greenling (Hexagrammos decagrammus), both of which are in Yaquina Bay and are known predators of H. oregonensis (Clemens and Wilby, 1961; Beardsley and Bond, 1970; Low, 1970).

Dehnel (1960) has shown that both H. oregonensis and H. nudus are eurythermal and euryhaline. All feeding in H. oregonensis from Puget Sound ceased at 6.9 C (Knudsen, 1964-a), indicating that this

might be approaching a critical lower temperature. Within Yaquina Bay, however, temperatures did not reach this critical level. It is thus doubtful that cold water temperatures are limiting in the field.

Low (1970) has also found that both species are euryhaline (mean time to death in tap water = about 20 h). Salinities as low as 4<sup>0</sup>/oo, which may occur in surface waters during periods of heavy fresh water run-off, can be tolerated for up to 6 days with only a 50% mortality rate. Since H. oregonensis has been shown to regulate its body ionic concentrations (Gross, 1960, 1961, 1963; Dehnel and Stone, 1964; Dehnel and Carefoot, 1965) it is doubtful that a physically limiting salinity barrier exists in Yaquina Bay at the collection site which can account for the observed vertical population segregation.

Ricketts, Calvin and Hedgpeth (1968) have indicated that H. oregonensis is less resistant to desiccation than is H. nudus. Low (1970) has experimentally confirmed this. Thus H. oregonensis may be limited in its upper distribution by physical factors (desiccation) and in its lower limits by a combination of physical and biological factors (cover and predation). Competition with H. nudus is not thought to be limiting to H. oregonensis as the number of H. nudus encountered in the upper levels was never large.

Average Mean Higher Low Water was at the +2.8 ft level (yearly range: 2.2 to 3.6 ft). It appears that this level (2.8 ft) is

critical in determining the lower limit of suitable conditions for the population, since the population sharply decreased below this level. If MHLW values were a well-defined barrier, one would expect reduced numbers in the 3-4 ft interval during December, 1972 and January, 1973 when monthly MHLW values were at maxima (see Figure 9). However, the data in Figure 12 do not support the hypothesis that there would be a population shift between intervals which would follow the monthly MHLW values. It would appear, then, that vertical population distribution is influenced by other factors in addition to exposure. An exposure time of about 28% seems to be a critical value in population distributions, however. Exposures less than this (8% to 28%) tend to result in less dense populations while exposures greater than this (28% to 50%) result in more dense populations. Thus, although related, not only substrate type but also exposure time influence vertical population distributions.

An unresolved problem, however, is presented in Figures 13 and 14. Whereas the size classes of crabs revealed an approximately normal distribution about the mean, one would not expect few crabs in the smaller size classes. Large numbers of smaller crabs (.20 to 1.00 cm) would be expected to account for the large central (1.00 to 2.00 cm) portion of the population. Given so few smaller crabs and so many intermediate-sized crabs, the only possible explanations

can be either i) that the intermediate-sized crabs represent many years of recruitment from the smaller-sized crabs (implies greatly reduced growth rates), ii) that sampling efficiency on smaller-sized crabs was not as high as on large-sized crabs, or iii) that immigration of small-sized crabs was occurring from outside the study area.

The problem was not fully resolved. However, due to the large size gain per molt and frequency of molts, it is doubtful that the intermediate-sized crab peak (1.00 to 2.00 cm) is the result of many years of recruitment. Sampling efficiency may have accounted for some negative bias in the smaller-sized classes (.20 to .50 cm), but sampling efficiency above the 0.50 cm size class was not thought to be different from any other size class since crabs of this size are readily visible. The last hypothesis, settling of the young crabs outside the study area coupled with later immigration into it, can not be discounted. An high population mobility has been demonstrated earlier (Figure 12). It appears that immigration of smaller crabs into the study area balances the loss, due to emigration and higher mortality rates of larger crabs from the area. The settling site of these young crabs was not investigated. The study area was surrounded on either side, however, by extensive mud flats and subtidally by mud and Zostera beds.

The main reproductive period of H. oregonensis was from February through May (maximum in March = 32.8% of females

berried). This period is earlier than Knudsen (1964-a) found in Puget Sound for this same species. He found that oögenesis occurred during a period of decreasing temperatures (October to February). Increasing day length started December 21 and did not appear to regulate gametic production. Decreasing water temperatures seem to be a cue, then, for early gametogenesis. However, a problem not resolved by Knudsen was the cue for the initiation of gametogenesis for the second brood class (70% of females). This second period of gametogenesis corresponded to rising water temperatures. If Knudsen's assumptions are correct, then gametogenesis occurred twice yearly in the Puget Sound population, once in Fall and Winter on a decreasing temperature cycle and again in late Winter and Spring on a rising temperature cycle. H. nudus showed the same trends in Puget Sound although the second brood occurred in late June and was quite small. The peak for brooding in H. nudus was January through May and for H. oregonensis from May through August. The main period of larval hatching in these species does not overlap and thus larval competition in the plankton would be minimized.

Boolootian, et al., (1959) found that H. nudus in the Monterey Bay, California, region was a Winter brooder. Peak periods of brooding were from November through January, preceding H. nudus of Puget Sound by 1 to 2 months. If the same trend exists for H.

oregonensis in Monterey Bay as it does in Puget Sound, then the peak reproductive period would be expected to occur in March and April. This corresponds quite closely with the results found for the Yaquina Bay population. It would appear, then, that the Yaquina Bay population brooding period would more closely follow the California populations than the Puget Sound populations.

The results, however, show that only about 33% of the females of reproductive size (0.86 cm and larger) were gravid at any one time in Yaquina Bay (see Figure 17). This suggests that the bay population is either i) not well adapted to the environmental challenges of the bay or ii) not synchronized as a population for one short period of maximal reproductive effort per year. In other habitats, the female brooding percentages are virtually 100% (Booolootian, et al., 1959; Knudsen, 1964-a).

Population densities also suggest that this may be other than an optimal habitat. On the outer coast in gravelly beaches, Low (1970) has reported Hemigrapsus densities of up to 500 crabs/m<sup>2</sup>; the maximum reported in this study was about 20 crabs/m<sup>2</sup>. Although Low did not report the weight of crabs per square meter, an average carapace width of 0.92 cm was found for the females. This is considerably smaller than the 1.44 cm average found in Yaquina Bay. Extreme competition between intertidal animals for a limited food resource has been reported to result in decreased



body weights (Menge, 1972). It is possible, then, that larger densities exist on the outer coast but larger dry weights per crab exist in areas of less severe competition.

The maximum biomass values for the bay population of crabs, about  $10 \text{ g/m}^2$ , was higher than that reported for carnivorous reef crabs from Eniwetok atoll ( $5.5 \text{ g/m}^2$ ) (Odum and Odum, 1955). Since Hemigrapsus is predominantly a herbivore (Knudsen, 1964-a), comparisons between trophic levels may not be directly meaningful. Odum and Odum (1955) have, however, estimated that the conversion efficiency ratio between carnivores and herbivores is 8.3%. About  $63 \text{ g/m}^2$  of herbivores would be required to support the  $5.5 \text{ g/m}^2$  crabs. This  $63 \text{ g/m}^2$  is about 6 times the biomass value found for the herbivorous Hemigrapsus and it is suggested that the Yaquina Bay crab standing crop is considerably less than the equivalent standing crop of this tropical reef community. Additional biomass studies in Puerto Rico (Golley, Odum and Wilson, 1962) have indicated that crabs, mostly fiddler crabs (Uca), reach biomass estimates of up to  $5.1 \text{ g/m}^2$  in mangrove swamps. Teal (1962), however, has reported Uca biomass estimates of nearly  $115 \text{ g/m}^2$  in Georgian salt marshes. The Yaquina Bay biomass values for Hemigrapsus oregonensis are nearer the lower limits of the biomass range reported for other intertidal crabs. It was estimated that a population of about 850 crabs was present in the Yaquina Bay study

site, which was equivalent to a dry weight standing crop of about 460 g.

Production estimates, in  $\text{g/m}^2$  per month, revealed an over-all negative production rate which was calculated to be a loss of about 2.3 "average" crabs from the population per square meter per month. Largest production loss occurred in the 3-4 ft interval. Fluctuations of nearly  $40 \text{ g/m}^2$  per month occurred from May-June, June-July, and July-August, 1972. A negative production rate can only result if either i) a sufficiently large recruitment of young crabs is coupled with a heavy mortality of large-sized crabs or if ii) a significantly large crab migration away from the study area (emigration) occurred. Results presented (see Figure 17) do not support a large recruitment during this period nor do they support (see Figure 23) a large adult mortality (average crab dry weight did not decrease). Large fluctuations in numbers of crabs, however, (see Figure 12) does indicate a great population mobility, both vertically and horizontally.

One is left with the impression that these fluctuations are due to extensive crab foraging at periods of high tide. Moving laterally and possibly vertically at high tide, they return, as the tide ebbs, to approximately the same tidal level from which they started. If this is the case, then a crab at the 0 ft level would be able to forage 42% longer than a crab at the 5 ft level (see exposure curve,

Figure 10). By the same reasoning, however, it would be exposed to predation a greater length of time. There would seem to be an optimal feeding duration (exposure to aquatic predation) past which further foraging would be detrimental. Fewer crabs were found at the lower regions. This may be influenced by such an elevated risk to predation coupled with a scarce food supply which would create a need for long foraging trips. This would seem to indicate that the higher regions experienced considerable foraging pressures on a limited food resource and thus forced some crabs into the lower, less desirable areas. The fact that the population is not increasing corroborates the idea of a maximally exploited resource which is at, or near, its carrying capacity.

The periodicity of the tides, as expressed in varying exposure times at the different tidal levels, would be expected to exert a great influence on the foraging patterns and behavioral activities of intertidal animals. Tidally-linked behavior rhythms have been demonstrated in numerous animals: clams (Bennett, 1954), oysters (Loosanoff and Nomejko, 1951), prawns (Rodriquez and Naylor, 1972), several species of crabs (Naylor, 1958; Fingerman, 1955; Williams, 1969) and others. Periods of activity in Hemigrapsus oregonensis were found to be quite variable. Not all crabs showed a rhythmicity of locomotory patterns. Similarly, only about 50% of tested fiddler crabs (Uca crenulata) show a rhythmicity (Honegger,

1973). Hemigrapsus edwardsi from New Zealand showed a seasonal variation in activity which corresponded to vertical migrations in the intertidal (Williams, 1969). During warmer water months (December, January, February) H. edwardsi showed a persistent tidal rhythm with peak activity occurring about 1 to 2 hours preceding high tide. This tidal rhythm, however, was not as apparent during colder water months (June, July, August) when the crabs would migrate down into the lower regions of the intertidal. Under constant conditions, this crab would lose its tidal periodicity after 2 to 3 weeks but, under the same constant conditions, it would slowly re-establish its rhythmicity. The cue for initiating this re-entrainment was not established but it was thought to be endogenous in origin.

H. edwardsi seemed to lack a strong circadian component. The crabs Sesarma reticulatum and Carcinus maenas, however, display strong circadian components (Naylor, 1958; Palmer, 1967; Williams and Naylor, 1967, 1969). Naylor (1958) has shown that Carcinus displays a tidal and a diurnal rhythm for about 3 to 4 days with peak activity bursts at a periodicity of 24 h (diurnal component) and 12.4 h (tidal component). Maximum activity during the tidal component occurred at high tide periods.

About half of the tested H. oregonensis were shown to display weak tidal and diurnal rhythmicities. Greatest activity occurred

at high tide periods and this was usually intensified during dark hours. Although H. oregonensis was not shown to undergo seasonal vertical migrations as was H. edwardsi, H. oregonensis did display both tidal and diurnal components in its activity patterns.

It is speculated that H. oregonensis is most active at high tide periods when moving from cover would not result in predation from seagulls or in desiccation due to increased insolation coupled with drying winds. Activity also appears to be greatest at high tide periods that correspond with darkness. During these conditions, it is speculated that foraging would present the least chance for visual detection by fish predators.

## SUMMARY

1. The Hemigrapsus oregonensis population structure at Coquille Point in the Yaquina Bay Estuary on the Central Oregon Coast was described for the period April, 1972 through May, 1973.
2. The population was not evenly distributed from the 1 ft to the 5 ft level. The 1-2 ft interval had an average of 7.89 crabs/ $m^2$ , the 2-3 ft interval 11.84 crabs/ $m^2$ , the 3-4 ft interval 20.09 crabs/ $m^2$ , and the 4-5 ft interval 19.73 crabs/ $m^2$ .
3. Carapace width versus frequency histograms indicated no obvious size classes. Average female carapace width (1.44 cm) was slightly smaller than average male carapace width (1.51 cm).
4. The population sex ratio was slightly biased in favor of females (53.3%). No obvious segregation of sexes by tidal height occurred during the study period.
5. Egg brooding females were found each month during the study period. The main reproductive period was February through May (max. March = 32.8%). September through December was the period of fewest gravid females. The percentage berried females at each tidal height followed the same general trend: Fall minimum brooding and Spring maximum brooding.
6. The minimum size of reproducing females was found to be 0.86 cm carapace width.

7. A regression equation between carapace width and number of eggs brooded was established as a measure of fecundity.  

$$Y (\# \text{ eggs brooded}) = -1.0529 \times 10^4 + 1.3344 \times 10^4 X (\text{carapace width in cm})$$
8. A regression equation between carapace width and dry weight was established as a method of obtaining biomass and production estimates.  

$$\sigma: \text{Log [dry weight in g]} = -2.007 + 3.065 (\text{Log [carapace width in cm]})$$

$$\phi: \text{Log [dry weight in g]} = -2.028 + 3.065 (\text{Log [carapace width in cm]})$$
9. The mean monthly average dry weight per crab decreased as tidal height increased.
10. The average dry weight per crab did not increase during the study period.
11. The average monthly biomass in  $\text{g/m}^2$  significantly increased as tidal height increased up to the 3-4 ft interval. The biomass values between the 3-4 and 4-5 ft intervals were not found to be significantly different. The average biomass value was  $8.47 \text{ g/m}^2$  with a range of  $1.14 \text{ g/m}^2$  to  $10.90 \text{ g/m}^2$ .
12. Average monthly production in  $\text{g/m}^2$  per month showed an over-all negative production of  $-1.23 \text{ g/m}^2$  per month. No significant differences in production rates were found between any tidal heights. The production rate could not be shown to be

significantly different from a zero production rate, which would indicate a stable population during the study period.

13. About half of the tested crabs showed a rhythmicity in locomotory activity patterns. Greatest activity coincided with periods of high tide. Some crabs showed peak activity bursts during daylight high tide periods and other during dark high tide periods.
14. Crabs which showed no entrainment to a tidal regime and which were under a light-dark regime ( $L = 7$  h,  $D = 17$  h) showed a periodicity of 22.2 h. Crabs subjected to a constant low level light regime showed a periodicity of 29 h. Crabs in a light-dark regime which showed a tidal rhythm influence showed a periodicity of 24.4 h. It is suggested that those crabs which show a locomotory rhythmicity are influenced by two exogenous entrainment factors: the solar day (light regime) and the lunar day (tidal regime). Upon removal of these entrainment factors, weak endogenous rhythms persist but tend to decay after 3 to 9 tidal cycles.



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