An Abstract of the Thesis of

Wendy Lou Manley for the degree of Master of Science

in the Department of Biology to be taken May 1987

Title: SOME EFFECTS OF SALINITY ON THE POPULATION DYNAMICS AND REPRODUCTIVE BIOLOGY OF THE NUDIBRANCH HERMISSENDA CRASSICORNIS

Approved: _____
Dr. Paul P. Rudy

Fluctuations in the Hermissenda population were observed in lower Coos Bay. Salinity was monitored over the winter to observe the relationship between rainfall and the bottom salinity profile, and to determine if salinity could be correlated with patterns of abundance. Hermissenda were collected twice monthly and their abundance and size class distribution evaluated. Animals were generally more abundant in summer than in winter, corresponding to seasonal high and low salinity. Large animals, more numerous in summer, were essentially absent during winter. The peak in abundance of small animals occurred in the winter. Laboratory experiments were performed to determine if reduced salinity interrupted reproduction in this species. Production of abnormal nidosomes and failure to begin development were observed at salinities below 25 °/oo. Rates of developmental abnormalities were greatest at low salinities. Adult mortality doubled from 34 to 27 °/oo and were determined to be osmoconformers.

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CHAPTER I

INTRODUCTION

Hermissenda crassicornis (Eschscholtz, 1831) is an aeolid nudibranch locally common in the lower Coos Bay estuary on the southern Oregon coast. Graduate students at the Oregon Institute of Marine Biology, diving twice a month since 1983 to collect this species for neuroscience researchers in Woods Hole, have observed fluctuations in the population inhabiting the boat marina in Charleston near the mouth of the estuary. In the summer, collectors have generally found animals abundant and easily gathered in large numbers, while in the winter, collectors have had difficulty finding animals and have occasionally failed to obtain sufficient numbers for a shipment of 100 animals (D. Anderson, G. Chen, personal communication). There was some concern that collecting might be detrimental to the population over the long term. Attempts to develop laboratory culture of this species have met with limited success (Harrigan and Alkon, 1978) so wild specimens continue to be collected.

Little is known about the population dynamics of Hermissenda. Its range extends from Alaska to Baja California (Morris et al., 1980), and a separate population occurs in the northern half of the Gulf of California (Brusca, 1973). It is frequently abundant; Costello (1938) reported it as the most common of 22 species collected in Monterey Bay, California, while Jaeckle (1984) commented, "In terms

of abundance and geographic distribution, Hermissenda crassicornis is the dominant littoral opisthobranch in Humboldt County, California." Scattered reports indicate that seasonal fluctuations in abundance occur. Costello (1938) observed that numbers in Monterey Bay appeared elevated during winter months and lowered during summer months. Lance (1966) reported that population densities in Mission Bay, California were greatest in the intertidal during spring and summer months, and that "vast numbers of copulating slugs and their nidosomes" were observed during November and December. Goddard (1984) noted greater numbers of Hermissenda on the Charleston docks in spring and summer.

The apparent decline of the Charleston population in fall and winter suggested that seasonal rainfall might alter the salinity regime of the estuary enough to increase mortality and/or disrupt reproduction. Hermissenda are found largely in marine (rather than estuarine) conditions, and may not be capable of tolerating a wide range of salinity. As soft bodied animals without shells, they are likely vulnerable to osmotic stress. Their potential for acclimation or escape by mucus secretion (Potts and Parry, 1964; Kinne, 1971) would seem limited.

Nidosomes (egg masses) encountered on dives in the Charleston boat basin indicate that Hermissenda are reproductive in the bay. The salinity range in which an invertebrate is capable of reproducing is usually much less than that permitting growth (Kinne, 1971), so it is possible that low or fluctuating salinity affects the local population. Of all stages in the life cycle of invertebrates, embryonic development often exhibits the narrowest range of tolerance

(Kinne, 1971). Any of the four stages in the Hermissenda life cycle may be sensitive to salinity stress: developing embryos within the nidosome, planktonic veligers, metamorphosing juveniles and adults. Some life cycle stages are probably more sensitive to salinity fluctuations.

The life cycle of Hermissenda has been investigated in the laboratory (Harrigan and Alkon, 1978) and is illustrated in Figure 1. Opisthobranchs are typically hermaphroditic with fertilization characteristically reciprocal and internal (Costello, 1938; Beeman, 1977). Self fertilization, while known in two other species of aeolid nudibranchs (Hadfield and Switzer-Dunlap, 1983) has not been demonstrated in laboratory animals of Hermissenda (Harrigan and Alkon, 1978). Hermissenda is protandrous (McCauley, 1985). Mating in other nudibranchs may last hours (Costello, 1938), but in this species lasts only 1-3 minutes with intromission occurring in four seconds (Rutowski, 1983) or less (Longley and Longley, 1982). Rutowski (1983) observed that sperm transfer was not reciprocal in almost 50% of observed mating interactions in which both animals everted their penes, and suggested that this high rate of failure is apparently a consequence of rapid intromission. Considerable aggression, (lunging and biting at one another) terminates mating (Zack, 1975; Rutowski, 1983).

The nidosome is a strand of white to pink encapsulated eggs which loops above the substrate and coils in a tight counterclockwise spiral (Harrigan and Alkon; 1978, Rudy and Rudy, in press). The strand of eggs is encased in a jelly-like material which also serves to attach

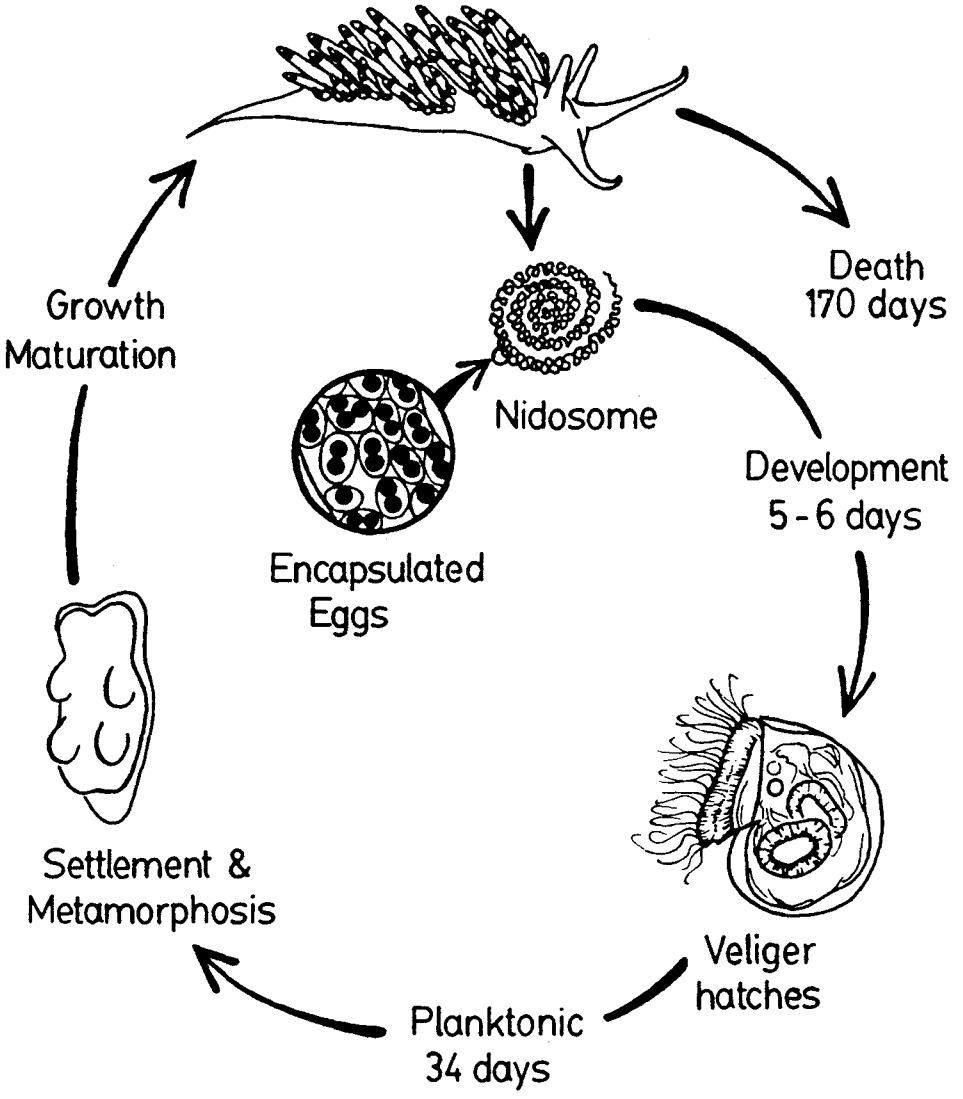

Figure 1. Life cycle of Hermissenda.

the nidosome to the substrate (Hadfield and Switzer-Dunlap, 1984). Larger animals have larger nidosomes (Harrigan and Alkon, 1978), and the number of eggs per capsule is greater (3-4 eggs and 1-2 eggs per capsule for large and small animals respectively) (Hurst, 1967). However, I have commonly observed six eggs per capsule in large nidosomes. The number of eggs per capsule can also vary with position in the egg strand (Hadfield and Switzer-Dunlap, 1984). The average egg diameter reported by Williams (1980) as 64.7 ± 1.6 microns (n=29) is in agreement with that reported by Harrigan and Alkon (1978), as 65.4 ± 1.2 microns (n=70, 7 adults).

Eggs are mixed with sperm in the reproductive tract and fertilized by the time of encapsulation (Hadfield and Switzer-Dunlap, 1984). After a single copulation, an animal can produce on average 2.6 ± 1.7 nidosomes before clear signs of infertility are evident (Rutowski, 1983).

Hermissenda egg production is prolific. The number of eggs in a nidosome typically ranges between 69,000 and 1,000,000 (Harrigan and Alkon, 1978). An animal with mating opportunities can produce a nidosome every 4.3 days on average (Rutowski, 1983). Based on these figures, maximum female productivity over a two month period could potentially be 14 million eggs. Clearly, significant mortality occurs at some stage(s) of the life cycle.

After oviposition, meiotic divisions produce two polar bodies prior to the first cleavage (Hadfield and Switzer-Dunlap, 1984). As is characteristic of the opisthobranchs, egg development occurs after the eggs are laid (Hadfield and Switzer-Dunlap, 1984). At 13 - 15°C,

a typical veliger hatches five to six days after oviposition (Harrigan and Alkon, 1978). Harrigan and Alkon (1978) reported the length and width of the 3/4 whorl shell as 105.9 ± 6.3 x 75.4 ±4.8 microns (n=25). Williams (1980) reported a length of 102.1 ± 10.3 (n=100).

Upon hatching, many opisthobranch veligers have a tendency to swim upwards. Although this tendency has been interpreted as photopositive behavior (Hurst, 1967), few species have larval eyes. In contrast, negative geotaxis has been confirmed for some species (Hadfield and Switzer-Dunlap, 1984). Veligers cultured in the laboratory get trapped in the surface film of the sea water, a problem minimized by sprinkling cetyl alcohol (hexadecanol) flakes over the surface to reduce the surface tension (Hurst, 1967; Harrigan and Alkon, 1978).

Hermissenda veligers are planktotrophic, and in laboratory cultures spend at least 34 days swimming and feeding prior to metamorphosis and settlement (Harrigan and Alkon, 1978). The natural diet of the veligers and the duration of the larval stage in the wild are not known. Harrigan and Alkon (1978) cultured a laboratory population with 5% success through to the F-2 generation using the algae Monochrysis lutheri and Isochrysis galbana and the flagellate, Chroococcus salina.

Animals which are competant to metamorphose tend to spend more time near the bottom and have eyes, a shell length greater than 300 microns, enlarged foot and developed propodium, reduced swimming activity, and a tooth at the base of the shell (Harrigan and Alkon, 1978). Metamorphosis in lab culture occurred on three species of

hydroid and was characterized by velum loss and crawling in the first 12 to 24 hours, and emergence from the shell in the next 12 to 24 hours (Harrigan and Alkon, 1978). After day 70 post metamorphosis at 13 - 15 C, animals ate less, began to shrink, and died between 45 and 70 days later at a total age of 150 - 180 days (6 months) thus confirming their subannual lifespan (Harrigan and Alkon, 1978.)

Adults can reach 9 cm (Harrigan, 1985) though animals over 6 cm are uncommon in Coos Bay. The coloration of Hermissenda is highly variable (Marcus, 1961; Burgin, 1965) and depends to a large extent upon diet. The cerata in particular exhibit marked variation. Burgin (1965) notes several color variations of the ceras, but in Coos Bay, none are as distinct as the presence or absence of a white line along the anterior surface (personal observation). West, et al. (1984) described these two morphological types.

Unlike many nudibranchs Hermissenda preys upon a variety of animals, including tunicates, hydroids, Cyanea capillata, the sea pen Ptilosarcus gurneyi (McDonald and Nybakken, 1980), ctenophores (Pleurobrachia) and hydromedusae (Aequoria) (personal observation). Jaeckle (1984) listed as prey six species each of anthomedusae and leptomedusae plus the chondrophoran Velella velella. The cannibalistic tendencies of captive Hermissenda are well known (Zack, 1975; Rutowski, 1982).

Anecdotal observations of the fluctuation in numbers of Hermissenda in the Charleston basin has led to the general hypothesis that seasonal fluctuations in salinity of the estuary may affect the population. Low or fluctuating salinities may weaken or kill adults

outright. Alternatively, some earlier stage in the life cycle may be vulnerable to salinity stress and affect adult populations indirectly. The purpose of this investigation is to study the relationship between salinity and the Charleston Hermissenda population. There are three goals to this study:

1. To document and quantify the seasonal population fluctuations of Hermissenda crassicornis;
2. To determine if the numbers of animals correlate with salinity fluctuations;
3. To determine some effects of salinity on the reproductive biology and adults.

CHAPTER II

RESEARCH SITE

Coos Bay estuary, on the southern Oregon coast 320 km south of the Columbia River is at 43° 21' North latitude and 124° 19' West longitude (Figure 2). It is a drowned river valley type estuary. Its surface area is roughly 45 km at high water (Johnson, 1972; Marriage, 1958) and it drains 1,567 square km of land, 88% of which is forested (Percy, 1973). The flow rates of the Coos River are greatest in February (311 cubic meters per second) and lowest in August or September (4.8 cubic meters per second) (Percy, 1973).

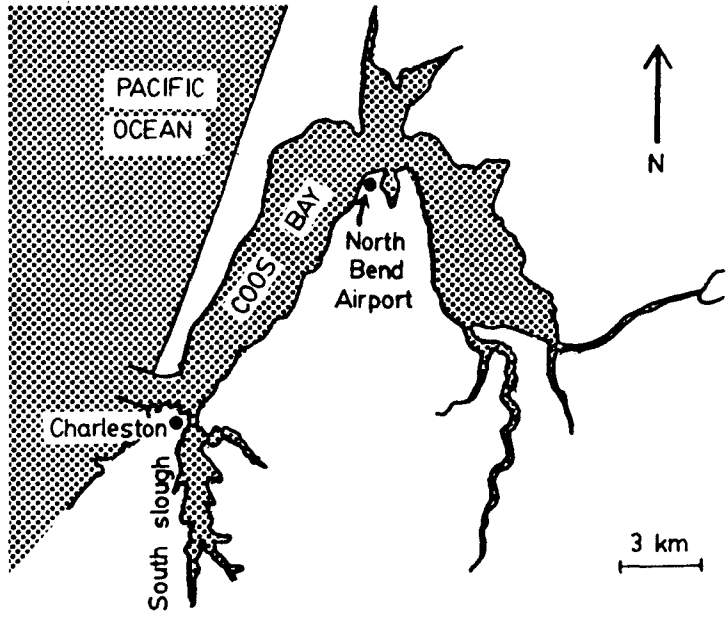

Figure 2. Coos Bay Estuary on the southern Oregon Coast.

South Slough is 8.1 km long and joins the Coos Bay estuary 1.6 km above the mouth of the bay (Figure 2). Its area is 5.3 square km and drains 75.4 square km (Department of Transportation, 1978). Near the junction of South Slough and greater Coos Bay are the Charleston boat marinas (Figure 3). Commercial and sport boats are moored here throughout the year, although in greater numbers during the summer months when fishing activities are intensified. Depths in the marina vary from five to seven meters at high water. The floating docks support well-developed fouling communities. These include tunicates, hydroids, bryozoans, the anemone Metridium senile (Linnaeus, 1767), sunflower seastar Pycnopodia helianthoides (Brandt, 1835), bay mussel Mytilus edulis (Linnaeus, 1758, and various nudibranchs including Dirona albolineata, (Cockerell & Eliot, 1905), Dendronotus frondosus (Ascanius, 1774), Dialula sandgensis (Cooper, 1862), Janolus fuscus (O'Donoghue, 1924), Aeolidia papillosa (Linnaeus, 1761) and Hermissenda crassicornis (Eschscholtz, 1831).

This fouling community exhibits seasonal variation. For example, hydroid colonies are abundant in early spring, and at that time may be relatively free of caprellid amphipod predators. As summer advances, caprellids increase and hydroids decline. In summer, tunicates are abundant but are much reduced in winter.

Near the shore where currents are not so strong, periphyton covers the muddy bottom. Ulva covers much of the bottom during the summer, but is essentially absent in winter. Crabs (Cancer magister Dana and C. productus Dana) and sea stars (Pycnopodia helianthoides (Brandt), and Pisaster ochraceus (Brandt)) are common inhabitants.

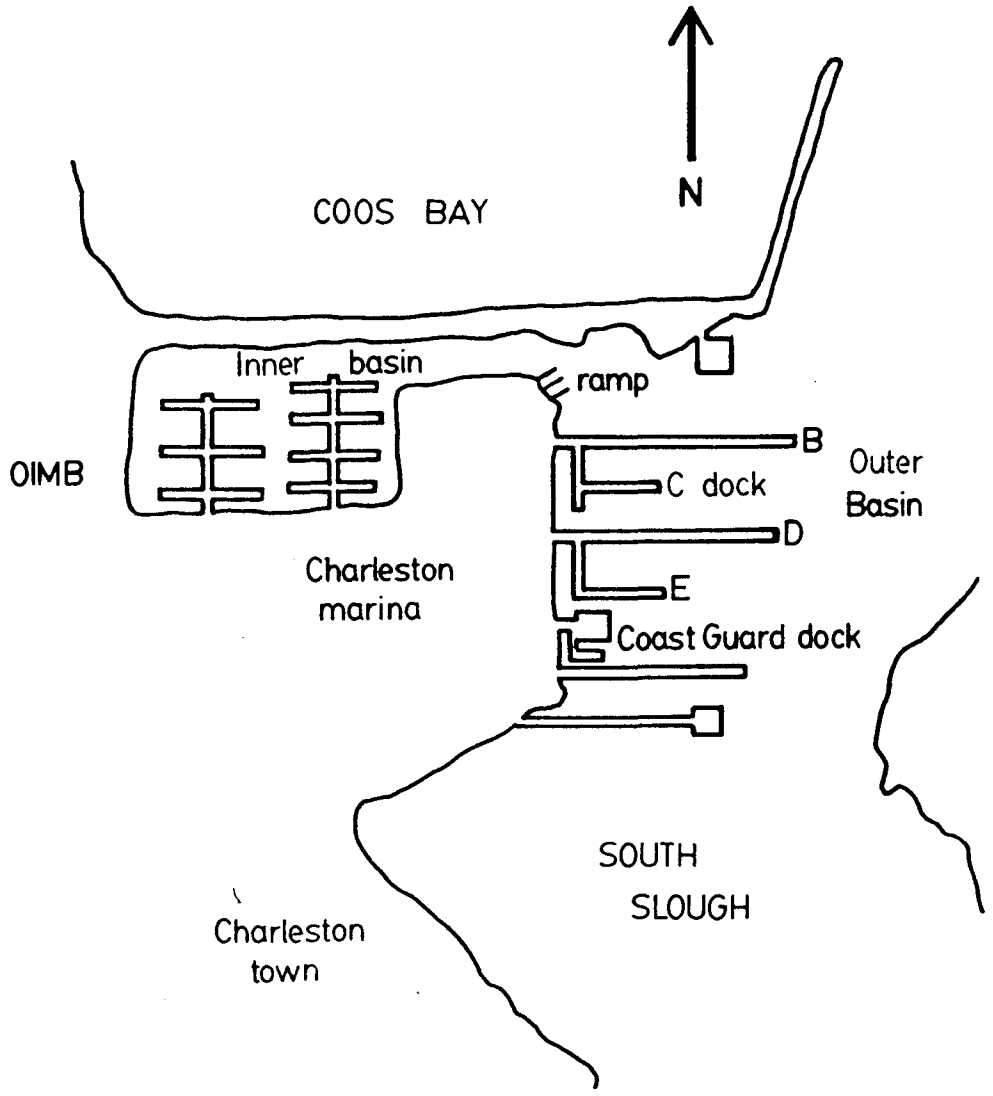

Figure 3. The Charleston boat marina.

The tides of the Oregon Coast are semi-diurnal and mixed. The mean tidal range is 1.58 meters (Johnson, 1972) and the mean diurnal range is 2.13 meters with an extreme range of 3.35 meters (Percy, 1973).

The water temperature along the Oregon coast remains fairly constant throughout the year (Figure 4). The Davidson current flows north during the winter and in the summer, strong north winds drive an upwelling system which brings cold, deep, nutrient-rich waters to the surface.

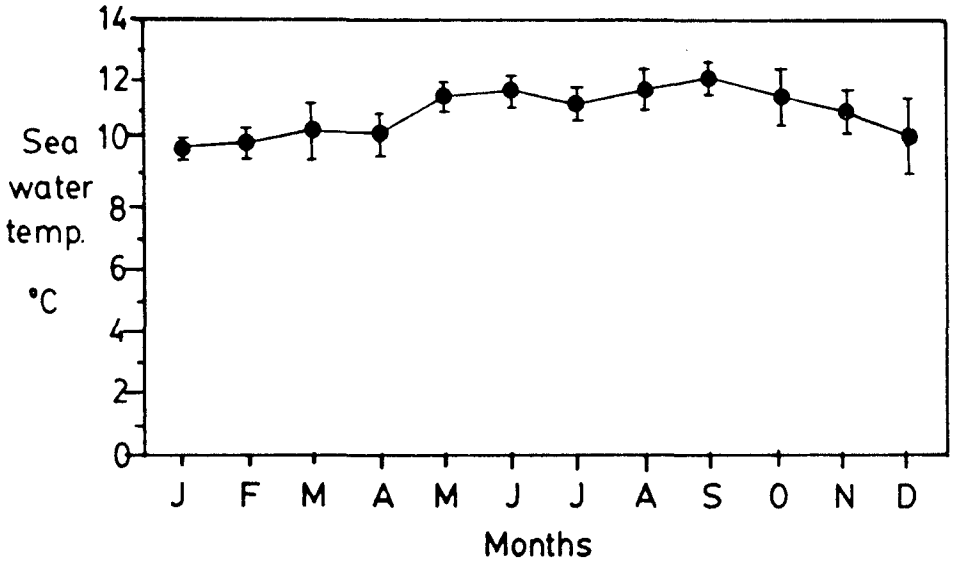

Figure 4. Annual sea water temperature at high tide at the mouth of Coos Bay by month. Averaged with standard deviations for the years 1984-1986.

The climate of the southern Oregon coast is temperate. Rainfall averages 130 cm a year along the shore and 250 cm at the headwaters of the Coos Bay drainage in the Coast Range 15-20 km to the east (Oregon State Water Resources Board, 1963). Monthly average rainfall figures calculated for the years 1964-1986 (excluding the El Nino event) are presented in Figure 5.

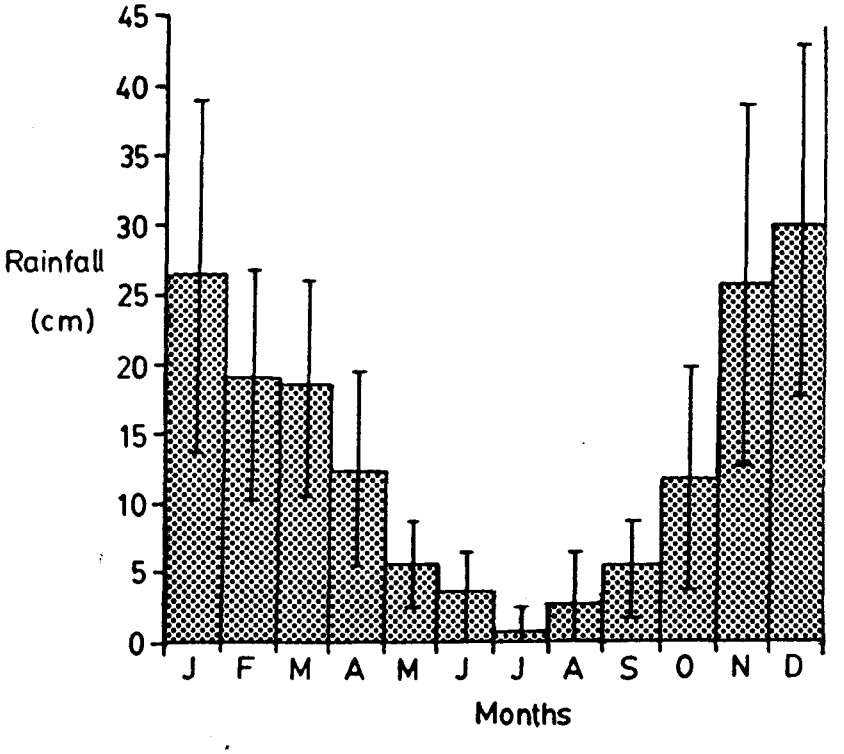

Figure 5. Annual rainfall for North Bend Airport. Averaged with standard deviations for data from 20 years excluding the two years surrounding the 1983 El Nino event.

CHAPTER III

MATERIALS AND METHODS

Hermissenda were collected approximately every two weeks by diving in the Charleston boat marina. Typically, two divers entered the water at the boat ramp and swam south in the channel which runs along the shore. Occasionally, the area out under "B" and "D" docks were explored to a maximum depth of 5 m. The length of each dive depended upon the availability of animals, varying between one and two hours. Divers attempted to collect all animals of all sizes encountered. Animals were captured with a 30 cm long fine mesh net with a 15 cm diameter ring. *Ulva* was also gathered whenever it was present to reduce contact between animals. At the surface, animals were placed directly into a bucket for transport. During periods of abundance, animals were collected from the mud bottom. When animals were difficult to find on the bottom the pilings were examined more thoroughly; D. Anderson (personal communication) discovered that during such times animals were sometimes more common on pilings. Occasionally animals were in large numbers on the native eelgrass, *Zostera marina*, along the shallows of the channel.

Collecting was not consistently synchronized with the tide cycle due to two constraints: light and turbidity. Reduced insolation in the winter limited successful diving to a few midday hours. Winter and summer differed in their respective sources of turbidity. During

winter and early spring, silt in runoff caused greatest turbidity at low tide. Diving on the flood or high tide provided for greater visibility as ocean water was much clearer. Once the summer upwelling system was underway, the marine plankton bloom made visibility consistently poor. We preferred to dive in the shallower water of low tide when lighting conditions were best.

Animals were held successfully in large tanks with either running sea water (11-12°C) or standing sea water at ambient temperature (12-14°C). Tanks were drained and cleaned about once a month. Every other day animals were fed broken Mytilus edulis which they located rapidly and ingested voraciously. Nidosomes were frequently deposited on the walls of the aquaria.

Determination of Field Population

Abundance was based on a timed exploration (Nybakken, 1978) of catch per unit effort. The total number of animals was divided by the product of the number of divers and the hours of collection to give a standardized unit of animals collected per diver per hour.

Animal Measurements and Size Class Categorization

As animals are exceptionally active for about an hour after introduction into a new tank, they were measured while moving during this time. With a ruler against the glass opposite the animal, two measurements were recorded: the total length, extending from the anterior most medial point (at the base of the oral tentacles) to the tip of the tail, and the standard length, from the same anterior point

to the most distal end of the most posterior cerata. Between 80 and 100 healthy animals were sampled on each collection date.

The total length was used to categorize animals into one of five size classes: 0-1 cm, 1-2 cm, 2-3 cm, 3-4 cm, over 4 cm. The standard length was used for animals at least 2 cm which measured 2.0, 3.0 or 4.0 cm. If the difference between the total and standard lengths was 0.5 cm or less, the animal was assumed not to be fully extended and was placed in the larger category. If the difference was greater than 0.5 cm, the animal was assumed to be fully extended and was placed in the smaller category. This system provided replicable results.

Determination of Bay Salinity Fluctuations

A Beckman Conductivity meter, model RQ, was modified for alternating current and operated continuously from October, 1986 through April, 1987. It was installed in the Coast Guard dock shelter in the outer boat basin in Charleston. The temperature compensating electrode was lowered along a wooden piling to within 0.4 m of the bottom: a depth of 2.8 m below mean low water (0.0 m tide). The meter recorded salinity continuously for one week on a 25 cm diameter circular chart. Maintenance included weekly changing of the chart, periodic inspection and cleaning of the electrode, and monthly calibration check against an AO hand held refractometer. The conductivity meter agreed with the refractometer to within 1.5 $^{o}/_{oo}$.

Surface salinity data for the study year were obtained from daily measurements taken at high tide approximately 1 km west of the Charleston boat basin near the mouth of Coos Bay. The readings for

each day were averaged by the week, but the number of days each week for which measurements were taken varied.

Rainfall

Daily rainfall is recorded at the North Bend Airport 10 km northeast of Charleston on the Coos Bay Estuary by the National Weather Service. These data were most complete and so used for this study. For comparison, Charleston rainfall values for the experimental winter were obtained from a resident within 2 km of South Slough.

Observations of Adult Behavior in a Salinity Gradient

A salinity gradient was established in a 2 liter aquarium by warming 0.5 liter of distilled water to 38°C and placing it in the tank, and then slowly siphoning 1.5 liter of chilled (6.0°C) full strength sea water (34 °/oo) onto the bottom of the tank. A control tank with full strength sea water (34 °/oo) was prepared at the same time. The tanks were left on the lab bench for four hours to permit the temperature to equilibrate to ambient temperature (12°C) before animals were introduced. To determine the vertical salinity gradient, a Pasteur pipet was used to carefully remove a few drops of water at various depths. Salinity was determined with a hand held AO refractometer.

Four medium sized (2-3 cm) animals were selected and two placed in each tank. The behavior of the animals was observed frequently over the first two hour period and their positions recorded as distance in

centimeters from the bottom of the aquarium. Less frequent observations were made over the following 21 hours. Because of the difficulty in telling the animals apart, individual positions were not obtained. After 20 hours, the salinity gradient was again sampled.

Determination of Hemolymph Osmolality

Eighteen large animals measuring more than 3.5 cm in total length were selected from a holding tank with 12 °C sea water 32.5 °/oo salinity (winter sea water). Three were bled by puncturing the pericardium with a 10 microliter capillary pipet and the osmolality of the blood determined using a Wescor Vapor Pressure Osmometer, model 5500. Twelve of the remaining fifteen animals were placed in sea water with 30 °/oo salinity. The remaining three animals were placed in sea water enhanced with Instant Ocean to a salinity of 34 °/oo. After one hour of acclimation, three animals from 30 °/oo sea water and those from 34 °/oo sea water were removed and bled. The remaining nine animals were further acclimated to reduced salinities with one hour acclimation periods, followed by the sampling of the blood of three animals. The salinities at which the animals were acclimated and tested are: 34.0, 32.5, 30.0, 27.0, 23.5, and 19.0 °/oo. Ten microliters of the sea water in which the animals were acclimated was also tested with the osmometer. The water was maintained at 9.0 to 11.0 °C throughout the experiment.

Six of the 18 animals were weighed at the beginning of the experiment on a Torbal 160 g capacity balance by placing them individually in a modified tea straining spoon from which the upper,

hinged half had been removed. Water was allowed to drain through the small holes in the strainer spoon for 10-15 seconds onto an absorbent towel before weighing, thus removing excess water from the surface of the animal. To reduce the stress on the animals, they were weighed in the spoon and then the weight of the spoon subtracted from the total weight. Animals were weighed after an hour of acclimation in each salinity and were the last six animals to be sacrificed for blood sampling.

Reproductive Responses to Salinity Stress

Experimental Conditions of Adults held in Reduced Salinity and Collection of Nidosomes

Twenty animals were selected for uniformity in size (2.5 - 3.5 cm total length) and divided into five groups of four. Each group was destined for a different salinity; those to be in reduced salinity were acclimated in a stepwise procedure by 5% sea water reduction intervals over several hours. Thus, animals to be acclimated to 70% sea water were first placed in 95% sea water for an hour, and then placed sequentially in 90%, 85%, 80% and 75% sea water for a period of at least an hour in each. Dilutions were made with distilled water in unfiltered sea water. A control group of four animals was maintained in 100% sea water.

The final salinities of the five tanks were:

100% sea water	34.0 °/oo salinity
90%	30.5 °/oo
80%	27.2 °/oo
70%	23.8 °/oo
60%	20.4 °/oo

After acclimation, animals were held for 2-3 weeks. Tanks were kept in a constant temperature box at 12.0 ± 1.0°C illuminated for 12 hours each day by a grow lamp. The water was changed every other day and animals were fed Mytilus on alternate days.

Tanks were checked at least twice daily and nidosomes were collected as soon as they were discovered. After rinsing in the appropriate dilution of filtered sea water, nidosomes were placed individually in 12 ml bowls containing filtered sea water of the same salinity as that in which they were laid and incubated in an embryological humidity chamber at 12.0 ± 1.0°C. At five days post deposition, nidosomes were examined microscopically.

This experiment was initially conducted in July and repeated twice in August. The results were combined for analysis.

Evaluation of Nidosomes

A central section of the nidosome strand was removed using tweezers and scissors and placed on a microscope slide. Using the sharp edge of a coverslip, the mass was chopped vigorously to release the capsules of live and undamaged veligers. This permitted good mixing of eggs so as to reduce the problem of patchiness of developmental stages sometimes observed in nidosomes.

Using an ocular micrometer on a microscope at 100 power the slide was scanned from side to side without overlap. Developing embryos which passed under the crosshairs of the micrometer were counted. Because all embryos in the same capsule were typically at the same stage of development, only the first embryo encountered in scanning was counted. One hundred developing embryos were counted and placed into one of four categories:

1. Underdeveloped: Arrested development in which embryos exhibit the cellular nature of early divisions.

2. Premature:Embryos which have undergone gastrulation, have active cilia, and may produce a shell, but are still very small and very opaque.

3. Normal: Veligers which have developed fully, are large and transparent (though they may contain yolk in their gut), and are ready to hatch.

4. Abnormal: Veligers which are clearly deformed. They usually lack a shell, are grossly misshapen, and are often united as "siamese twins."

The results of three replicates were averaged.

Undivided eggs were observed among developing veligers in some nidosomes. It is not known whether these undivided eggs failed to develop because they were physiologically unable to do so or because they were infertile. Infertility does not necessarily constitute a developmental response to salinity stress and so the number of undivided eggs encountered while counting 100 developing embryos was recorded but not included in the 100 embryos.

CHAPTER IV

RESULTS

Seasonal Population Fluctuations

From April, 1986 through April, 1987, collectors spent an average of 1.2 hours on each of 26 dives in the Charleston boat basin. (Notes for individual dives are located in the appendix). Data from dives which took place on consecutive days were combined (May 2 and 3, May 29 and 30, November 25 and 26). The collections on May 11 and 12 differed in location, so the data from the small basin (May 12), not part of the normal census area, were excluded. Information from 23 collections remain for consideration. To standardize the catch for comparison, the abundance for each dive was calculated as catch per diver per hour (Figure 6, page 23).

The open circles (Figure 6) indicate some uncertainty in the reliability of the data. On the May 2 dive, no animals could be located in the outer boat basin. The inner basin was then searched because animals had been discovered along its margins at low tide during the previous week. The outer basin was explored again on May 5 with poor success so dives on May 29 and 30 took place in the inner basin. The inner basin, due to its shape and separation from the bay, cannot be considered a continuation of the normal collecting area so these points should be viewed with reservation. In addition, in all

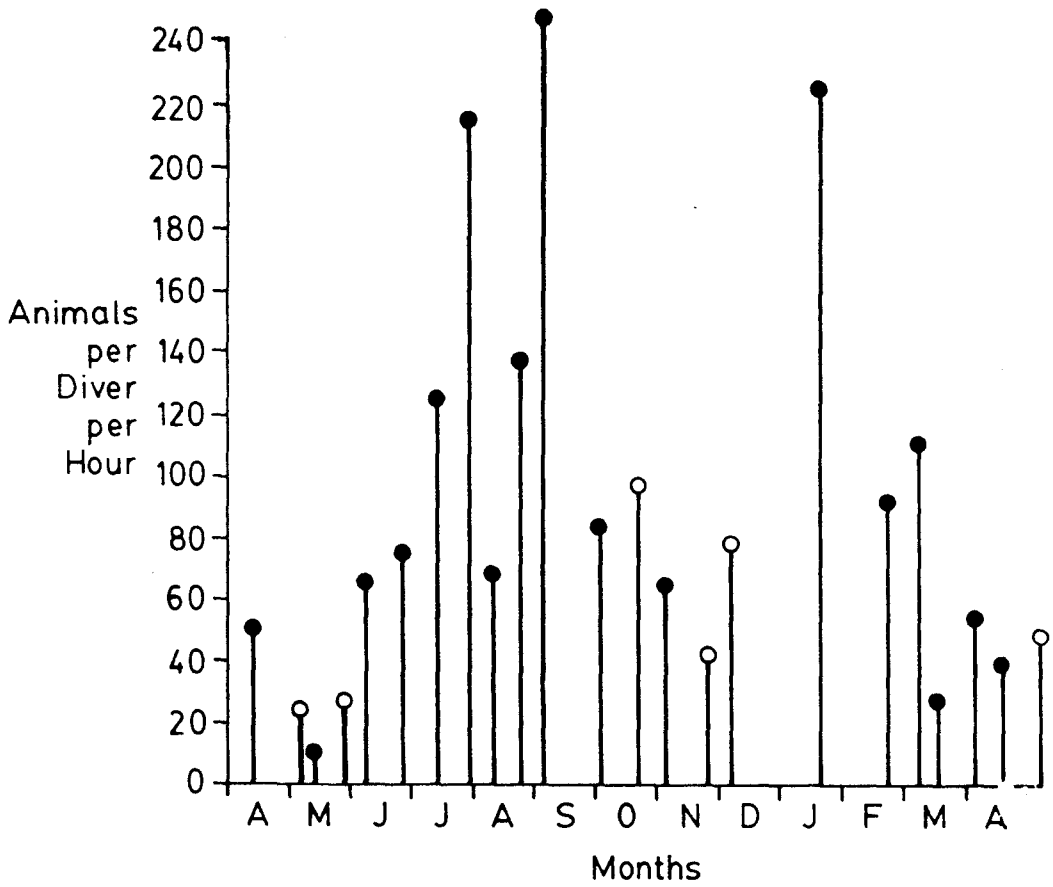

Figure 6. Animal abundance from April 1986-April 1987 reported as individuals collected per diver per hour.

May dives, animals could not be located on the bottom but were instead found on and collected from pilings. Although these data are not in conformance with the standards of the other dives, they indicate a trend in the population and are therefore included. These values likely overestimate the population normally censused.

The error of the time of the November and December dives may be as much as 15 minutes. This translates into potential error. The catch reported for the December dive as 79, for example, may be as low as 23 or as high as 105. In general, visibility limited to 3-4 m causes divers occasionally to lose track of their partner and time may be spent searching from the surface for the accompanying diver. In addition, some May dives, the October dive, and the April dive involved different divers, although the margin of error introduced by this factor is considered minimal.

Another possible source of error is the variability of underwater visibility and one might expect that turbidity might have interfered with the consistency between collections. During the August 7 dive visibility was particularly poor due to both turbidity and low light conditions (fog), and it is possible that visibility in large part accounted for the small catch. Similar conditions prevailed on the March 17 dive and low numbers were collected on that date also. Visibility played a small role in all other dives since it was rarely less than 1 meter. If the bottom can be seen at arms length, 3 meters of visibility is of little consequence to effective collecting.

The high counts in July, September, and January are real; abundance cannot be erroneously overestimated in the way that it can be erroneously underestimated, unless some episodic migration or unusual clumping occurred.

In general, the population was greatest during the summer (July - September) and lowest during the winter (November - April). There are two exceptions to this trend: a very low count in August and a very high count in January.

Size Class Distribution of Field Population

A sample of animals from each of 15 collections was measured. Three of the collections (May 11, 12) were piling animals and two (May 12 and 29) were from the small boat basin. As they deviate from the standards of the other collections, the values for these dates should be considered cautiously. The data for the May 12 and May 13 dives were lumped and averaged. On average, 90 animals were measured (standard deviation = 13) except for three samples (May 11, September 3, and March 17) where between 35 and 50 animals were measured. In Figure 7, for each collection, each size class is represented as a proportion of the population.

Animals measuring less than 1 cm were rarely collected, accounting for less than 2% of the sample in 13 of 15 collections. On only two dates did this size class constitute 5% or more of the sample measured. On May 29, 5% of the population was less than 1 cm in length and on December 8 the proportion was 6%. These figures likely underestimate the numbers of small animals present on the bottom of

the Charleston basin, in part because they were easier to overlook than larger animals. All animals of all sizes seen were collected.

For May, and October through March, animals measuring less than 3 cm constituted the majority of the population. From June to September, animals greater than 3 cm were in the majority. In June, the proportion of animals larger than 4 cm began increasing until in July they accounted for nearly 50% of the population. By September, animals larger than 4 cm had decreased to about 10% of the population, and during the winter (December through March) they were rarely collected.

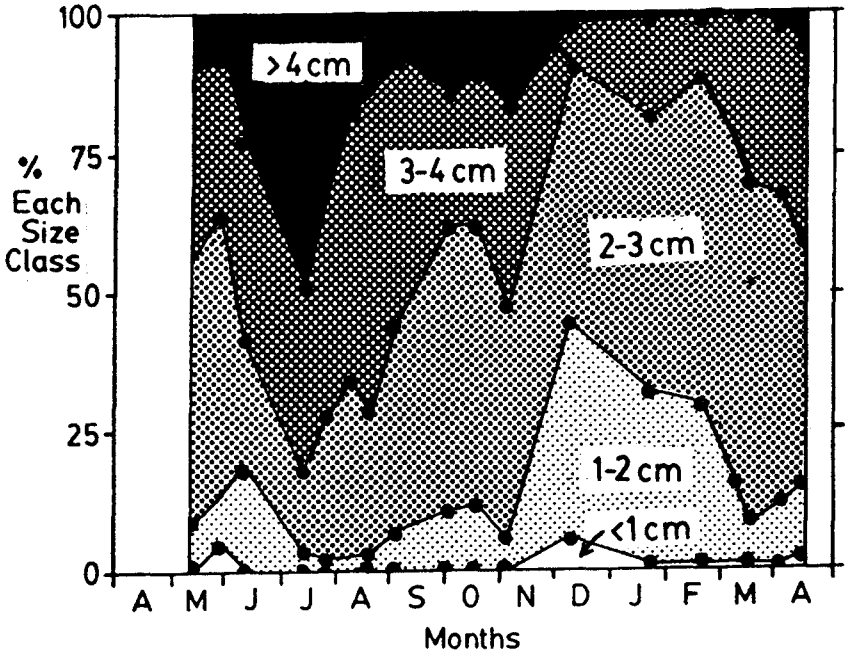

Figure 7. Cumulative proportion of the population for each size class from May 1986-April 1987.

The frequency of each size class was multiplied by the total number of animals collected per diver per hour so that the abundance of the various size classes could be compared over the course of the year (Figure 8, page 28). The Hermissenda population was elevated during the summer and contained a high proportion of large (over 4 cm) animals. During the fall numbers fell sharply. In winter a single peak of abundance tantamount to summer numbers occurs in January. Large animals are essentially absent in winter while small animals are numerous.

Rainfall Patterns

During the study year from April 1, 1986 to April 1, 1987, 177.9 cm of precipitation fell at the North Bend Airport. Less than 3% of this rainfall occurred during the summer months of June through August. Rainfall during May, July and September of 1986 exceeded one standard deviation above average while December rainfall was more than one standard deviation below average (Figure 9, page 29). Weekly totals are reported in Figure 10, (page 30) illustrating the episodic nature of coastal storms which move in from offshore. Relatively dry spells were not uncommon throughout the rainy season.

Rainfall for the 1986-87 winter was compared between South Slough and North Bend. Rainfall at South Slough was 20-30% less in November and February, 40% more in March, and within 1 cm of North Bend totals during the remaining months between September and April.

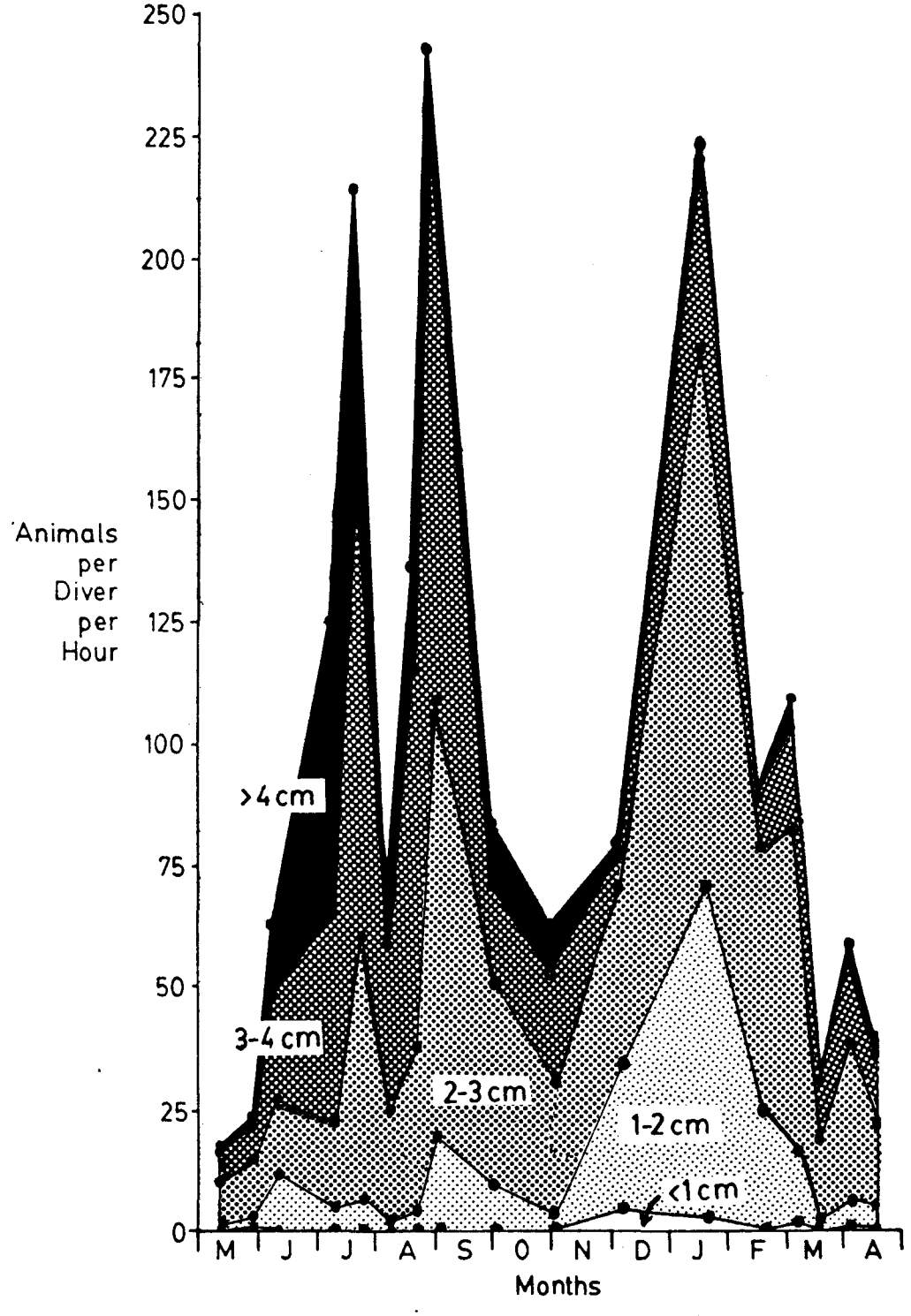

Figure 8. Abundance of each size class calculated from relative proportion of the population and catch per diver per hour. May 1986 - April, 1987.

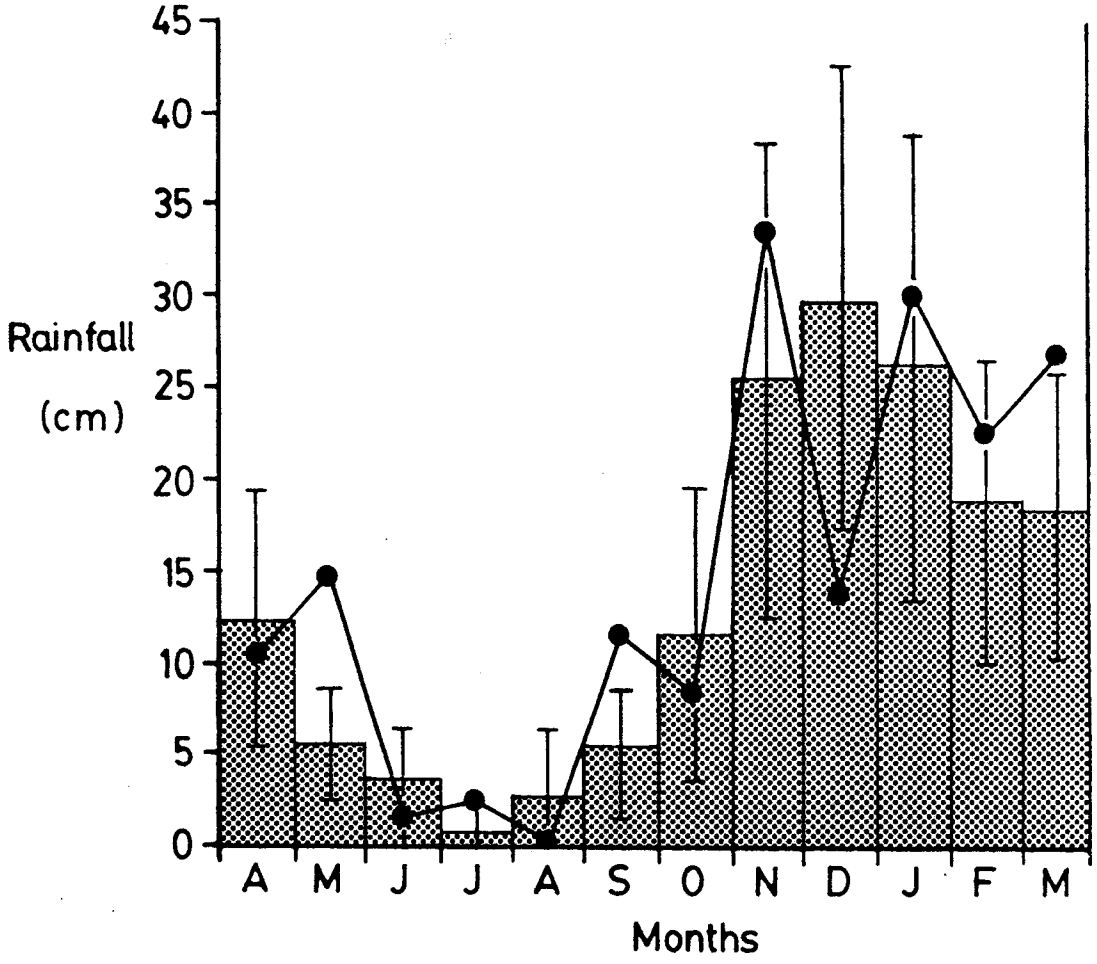

Figure 9. Monthly rainfall (dots) for the experimental year (April 1986-March 1987) against a histogram of average monthly rainfall with standard deviations calculated from 20 years data excluding the two years surrounding El Nino (July 1982-June 1984).

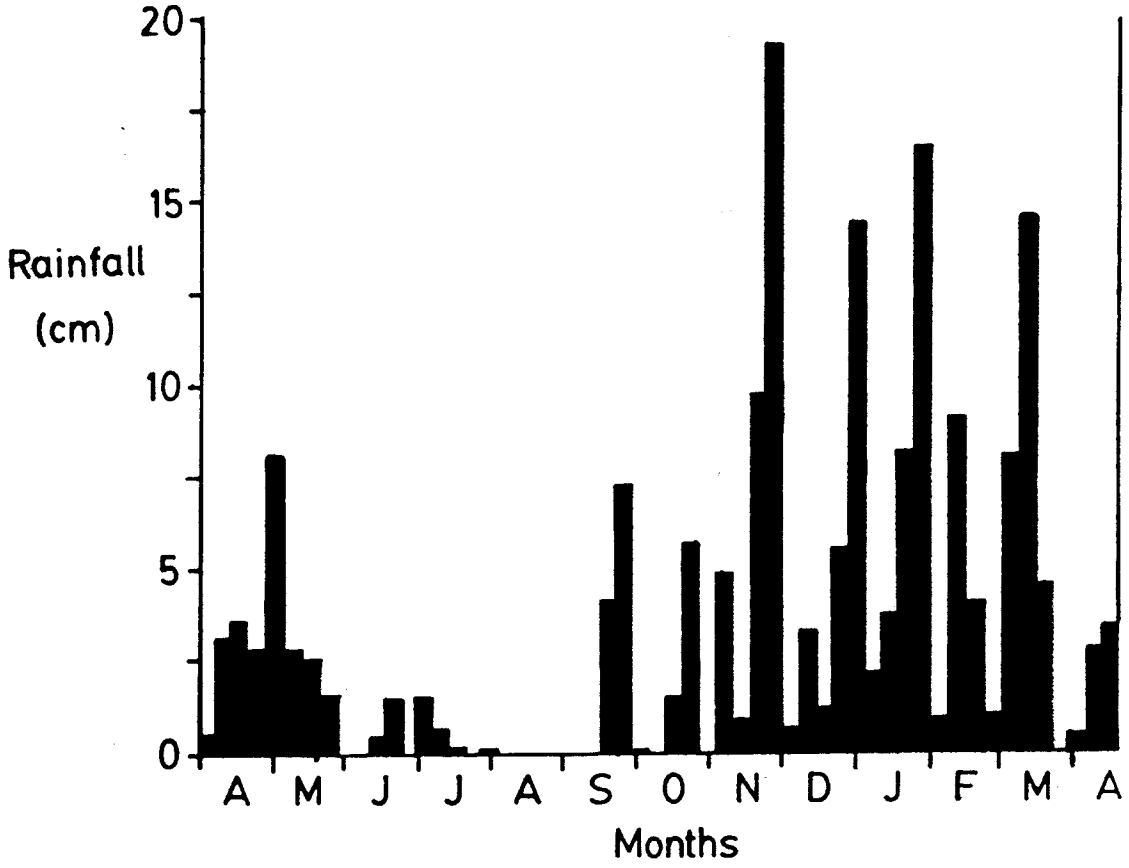

Figure 10. Weekly rainfall for April 1986-April 1987.

Bay Salinity Profile

A chart recording of the week beginning November 25, 1986 is presented in Figure 11 (page 32) as one of the more dramatic examples of salinity fluctuations in the bay following a rainstorm. Nearly 16 cm of rain fell at North Bend Airport between November 25 and 28. Salinity was found to fluctuate in the basin twice daily in rhythm with the tides. Salinity was lowest at low tide.

The salinity of the Charleston boat basin is presented over the 1986-87 winter in Figure 12 (page 33) along with daily rainfall. The minimum and maximum daily salinity are plotted to show the extremes and provide rapid assessment of the salinity range. Minimum values represent at least one hour at the indicated salinity. Over the winter, the maximum salinity mean was 29.7 °/oo with a standard deviation of 2.9 °/oo. The minimum salinity mean was 25.0 °/oo with a standard deviation of 4.6 °/oo (n=154). The maximum range was 17.5 °/oo (12.0 to 29.5 °/oo) which occurred on November 28 after a three day storm brought 15.7 cm of rain. Not unexpectedly, heavy rainfall is shortly followed by a drop in salinity in the estuary.

Surface recordings for lower Coos Bay show that salinity remains high during the summer (Figure 13, page 34). Top and bottom salinity were checked 9 times in the Charleston boat basin from May through September, demonstrating a salinity level approximating that of normal sea water: 33-34 °/oo. By contrast, and coincident with seasonal precipitation, winter recordings showed a dramatic range of salinity

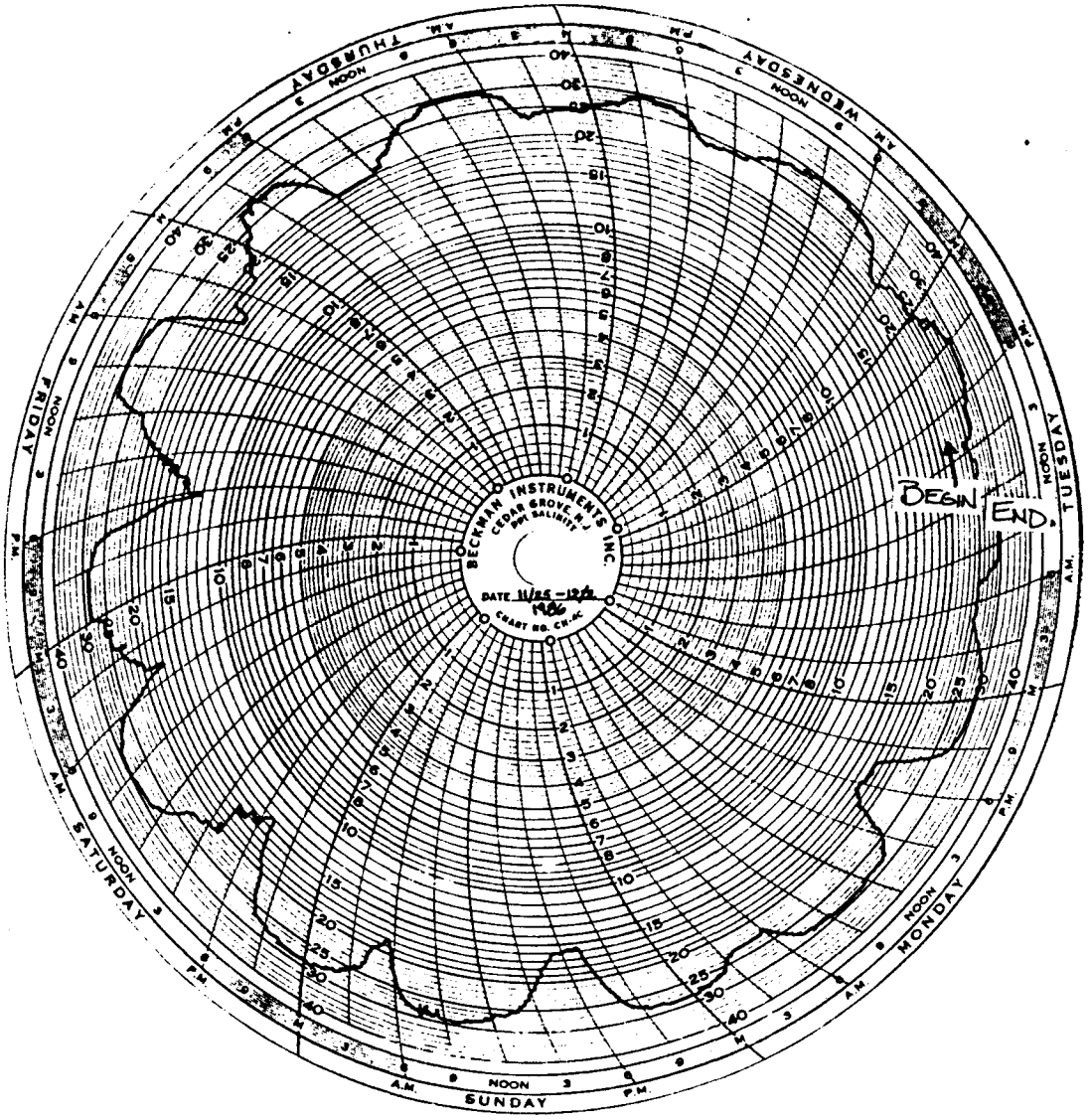

Figure 11. Example of weekly salinity recording chart.

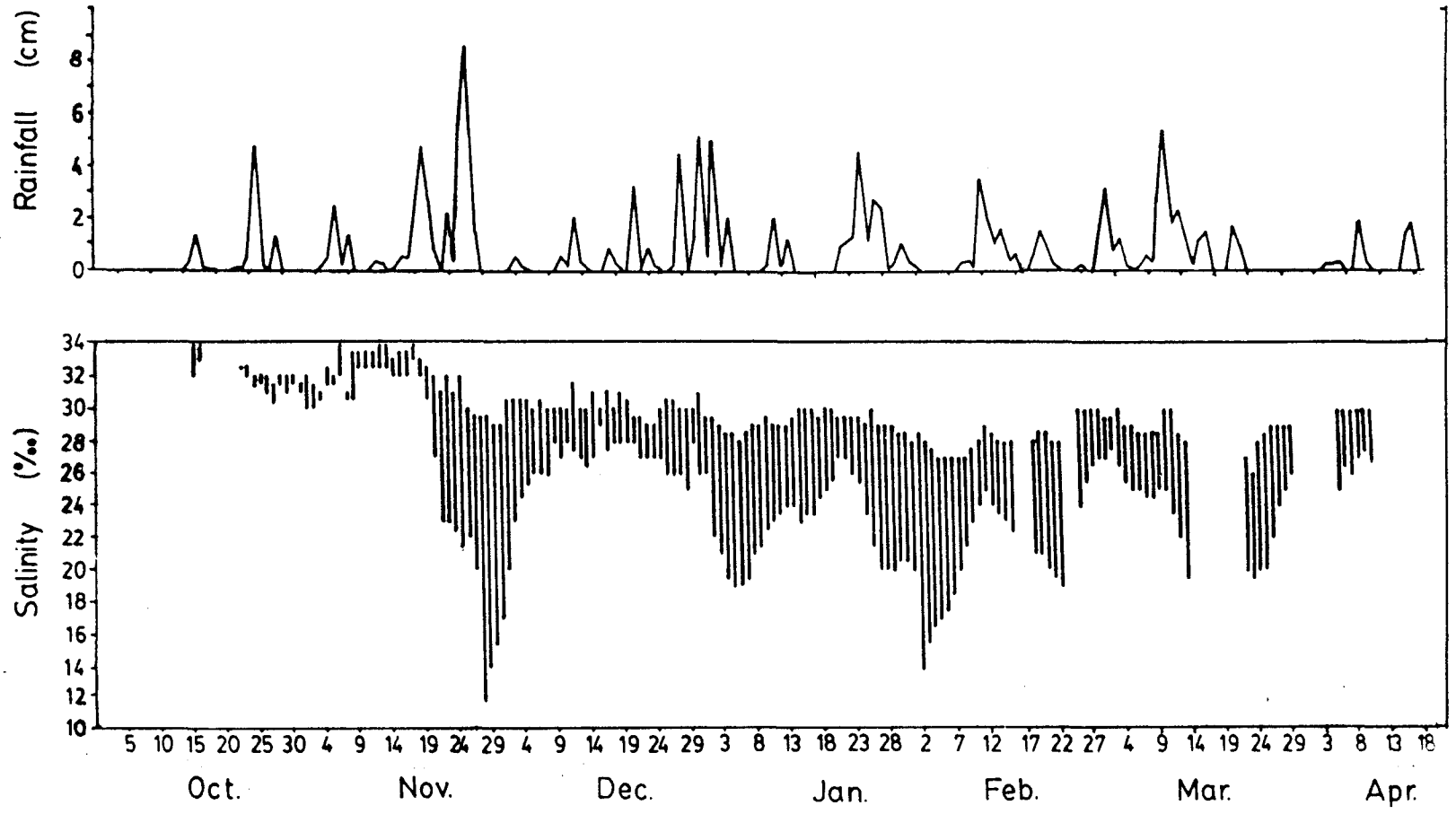

Figure 12. Daily rainfall for the winter of 1986-87 with minimum and maximum daily salinity levels recorded for the Charleston boat basin.

on a daily basis in addition to the general lowering of maximum salinity to 27 - 30 °/oo from the first half of November through March.

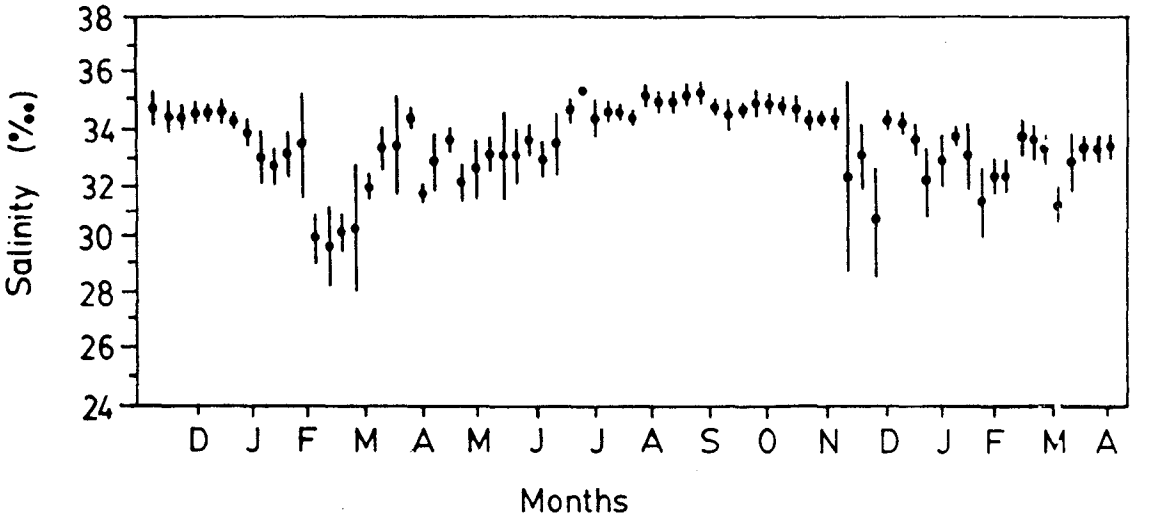

Figure 13. Average weekly surface salinity at high tide near the mouth of Coos Bay, December 1985-April 1987.

Adult Behavior in a Salinity Gradient

The salinity of the control tank after temperature equilibration was 32 °/oo throughout. The surface and bottom salinities of the experimental tank were 2 and 32 °/oo respectively.

Control animals which were dropped into the full strength sea water aquarium immediately righted themselves and began moving along the bottom. When the experimental animals were dropped into the gradient aquarium and fell through the low salinity surface water, they responded immediately with a characteristic behavior: the body

curled into an arc shape and the cerata were rigidly extended, lifted upward and away from the body, and waved about wildly. The animal twisted convulsively from side to side. After about 30 seconds the twisting ceased, and within 1 minute the cerata settled down as the animal resumed normal behavior.

When animals are first placed in an aquarium, they typically move across the bottom and up the side to the surface where they often leave the side of the tank and move along the underside of the surface film. Within 3.5 minutes one of the animals in the control tank was hanging from the surface, and the other was nearing the surface. After recovery from the salinity shock of entry, experimental animals also began moving up the sides of the aquarium. However, when an animal had ascended 7 cm up the side of the tank from the bottom (9cm total depth) it suddenly stopped forward motion. The anterior half of the body lifted off the glass, and the animal reared back and swayed slowly from side to side. After a few seconds it turned downward, recontacted the glass and moved downward for 2-4 cm. The path gradually turned again toward the surface and the animal moved upward until it stopped again at the 7 cm level and repeated the swaying behavior. This sequence was repeated several times before the animal returned to the bottom and eventually reduced the intensity of this searching behavior.

Control animals moved rapidly to the surface and with occasional exception, remained there for the first five hours of the experiment. Experimental animals made many attempts during the first hour to reach the surface but never advanced higher than 7 cm, corresponding to

20 °/oo, but thereafter remained within 1 cm of the bottom where salinity was high. The position above or below 7 cm of control and gradient tank animals was evaluated using a Chi-square calculation. The distribution of observations was significantly different between control and gradient tank animals ($\chi^2 = 24.67$, $p < 0.005$).

At 20 hours, the salinity gradient was tested and significant mixing was observed to have occurred. The maximum salinity on the bottom was only 30 °/oo and surface salinity had risen to 9 °/oo. Salinity at the 7 cm mark had dropped to 16.5 °/oo from 20 °/oo. The experimental animals were on the sides of the aquarium, ascending to 7 cm as before, but clearly tolerating lower salinities since the gradient had changed. The control animals moved down onto the sides of their aquarium.

Hemolymph Osmolality

The results of the measurements of the osmolality of the blood and seawater of adult animals at various salinities are presented in Table 1 (page 37). Failure to obtain blood from one animal at 32.5 °/oo resulted in only two data points for this salinity. The mean of the sea water concentration was graphed against the individual readings of blood in Figure 14 (page 38). In all six salinities tested from 19 to 34 °/oo blood concentration conformed closely with external concentration indicating osmoconformance in this species.

The weight changes of six animals are reported for each salinity as the percentage of the original weight in Figure 15 (page 39). In five animals some weight gain was observed although it was not

Table 1. Osmolality of External Water and Hemolymph of Animals Acclimated to 6 Dilutions of Sea Water Salinities (Salinity Measured with AO Refractometer)

SEAWATER			HEMOLYMPH	
Salinity	readings	mean	readings	mean
(°/oo)	mOsm	mOsm	mOsm	mOsm
34.0	1021 1003 1022	1013	1006 1012 1018	1012 6
32.5	885 887	886	881 896	888 10
30.0	858 861	859	859 872 909	880 26
27.0	767 774 764	768	783 772 799	785 14
23.0	661 666 662	663	673 671 682	675 6
19.0	533 530 538	534	563 556 550	556 6

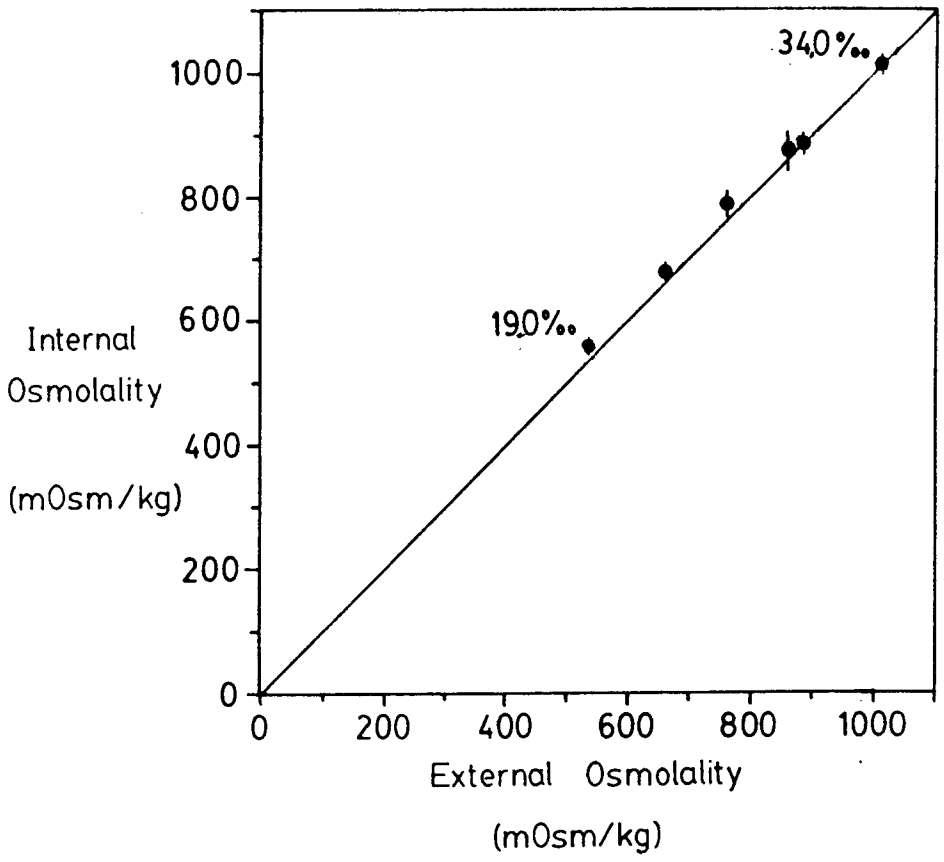

Figure 14. Osmolality of <u>Hermissenda</u> hemolymph against external osmolality.

proportionally consistent for all animals. One animal appeared to lose weight with salinity reduction until placed in 23 °/oo.

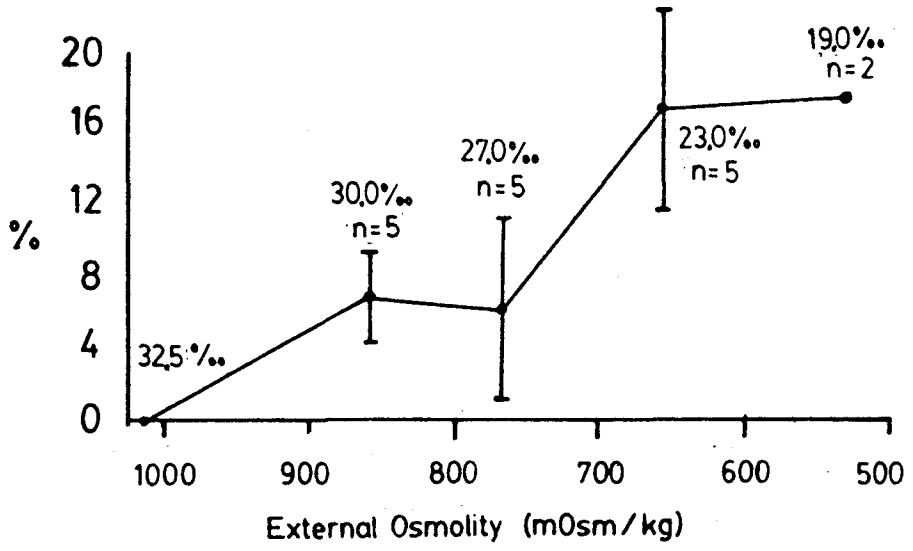

Figure 15. Average weight change with salinity reduction.

The cerata provide an enormous surface area in relation to the volume of this animal, giving it tremendous capacity to hold water on its surface. A few more seconds of drainage on an absorbent towel repeatedly results in further reduced weight. Since the animal cannot be dried off for weighing, it is reasonable to presume that inaccuracy is responsible for the variability observed.

Adult Salinity Tolerance

While there was an attempt to maintain an equal number of animals at each salinity, animals occasionally died. When possible they were replaced. To standardize the number of animals in each treatment,

"total animal-days" were calculated by multiplying the number of animals present in the tank by the number of days of the experiment. Thus, deaths per 100 animal-days can be compared between experimental salinity levels that had different numbers of animals.

The mortality of adult animals which were acclimated to and held in reduced salinity for egg production is presented in Figure 16. The values for three experiments were averaged and the standard deviations calculated. No standard deviation was calculated for 20 °/oo because this condition was not replicated. Adult mortality was highest at 20 °/oo salinity and twice that observed in full strength sea water.

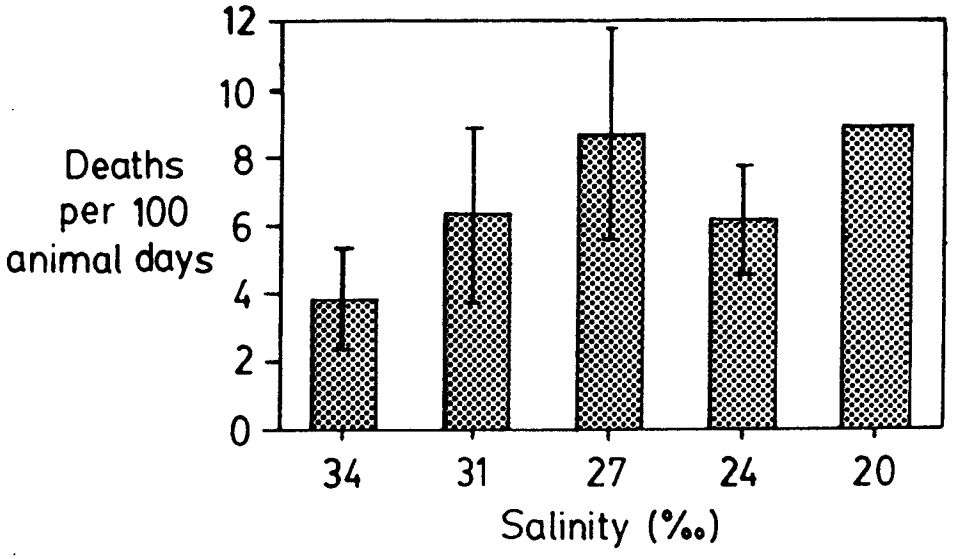

Figure 16. Mortality rates of adults held at various salinities averaged for three experiments and reported as deaths per 100 animal days.

Reproductive Responses to Salinity Stress

Nidosome Production

Nidosome production was evaluated also by using animal-days calculations. The numbers of nidosomes produced per 100 animal-days for each experiment were averaged and the standard deviations calculated. No standard deviation is presented for 20 °/oo because experimentation at this level was not replicated. The results are presented in Figure 17. Animals at 31 °/oo salinity produced 11 nidosomes per 100 animal-days, half that produced by control animals. Animals in 27 °/oo salinity produced more egg masses than control animals. Overall, there is no clear trend in nidosome production which relates to salinity.

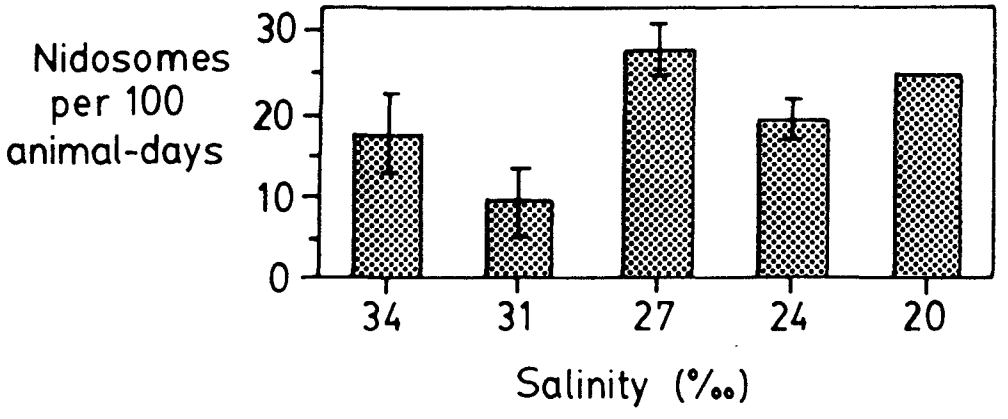

Figure 17. Nidosome production of animals held at various salinities averaged for three experiments and reported as number of nidosomes per 100 animal-days.

Abnormal Nidosomes

Unusually appearing nidosomes were noted throughout the experiment. The strands of normal nidosomes loop up above the substrate in "primary coiling." The looping strand defines the spiral of "secondary coiling." Abnormal nidosomes exhibited a lack of primary coiling corresponding with a reduced gelatinous casing. These egg strands did not loop up off the substrate but appeared as tiny squiggles in two dimensions. Abnormal primary coiling was the most common of the nidosome abnormalities but the spiral conformation of secondary coiling was sometimes misshapen and freeform as well (Figure 18).

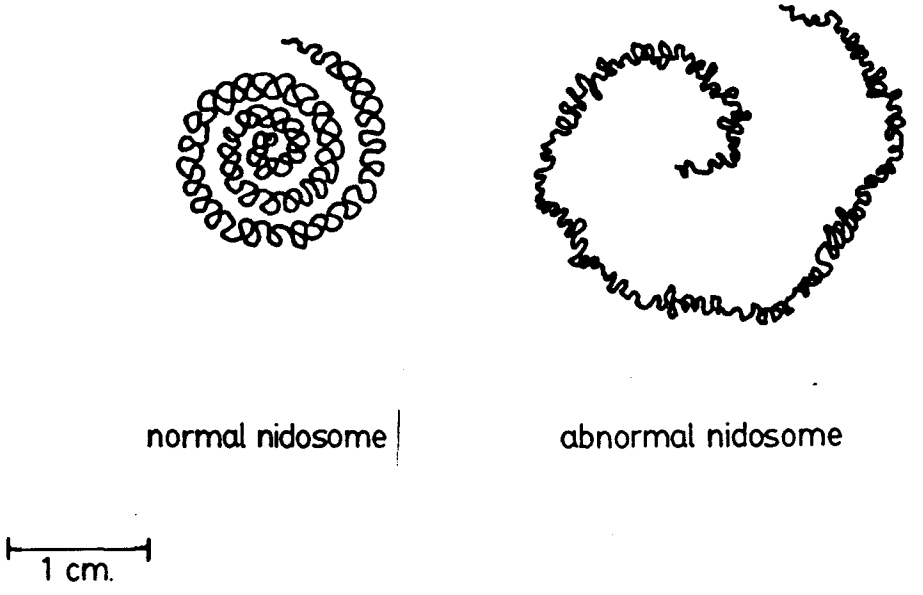

Figure 18. Normal and abnormal nidosomes.

In Table 2, the frequency of abnormal nidosomes is presented. Abnormal nidosomes were not observed at the higher salinity levels (31 and 24 °/oo), however at 20 °/oo, 91% of the egg masses were clearly abnormal.

Table 2. Incidence of Abnormal Nidosomes at Various Salinities

	SALINITY (°/oo)				
	34	30	27	24	20
Number of abnormal nidosomes	0	0	2	12	10
Total number of nidosomes	37	30	42	39	11
% of abnormal nidosomes	0	0	5	38	91

Failure to Begin Development

Some eggs did not divide. It is not known if their failure to begin development was a result of infertility or physiological inability to divide. Figure 19 (page 44) presents the fraction of undivided eggs in each nidosome for the five salinity levels. Reduced salinity does appear to affect reproduction such that at lower salinities a sizeable percentage of eggs fail to begin development; the cause is unknown. In five of eight nidosomes at 20 °/oo, all eggs failed to begin development.

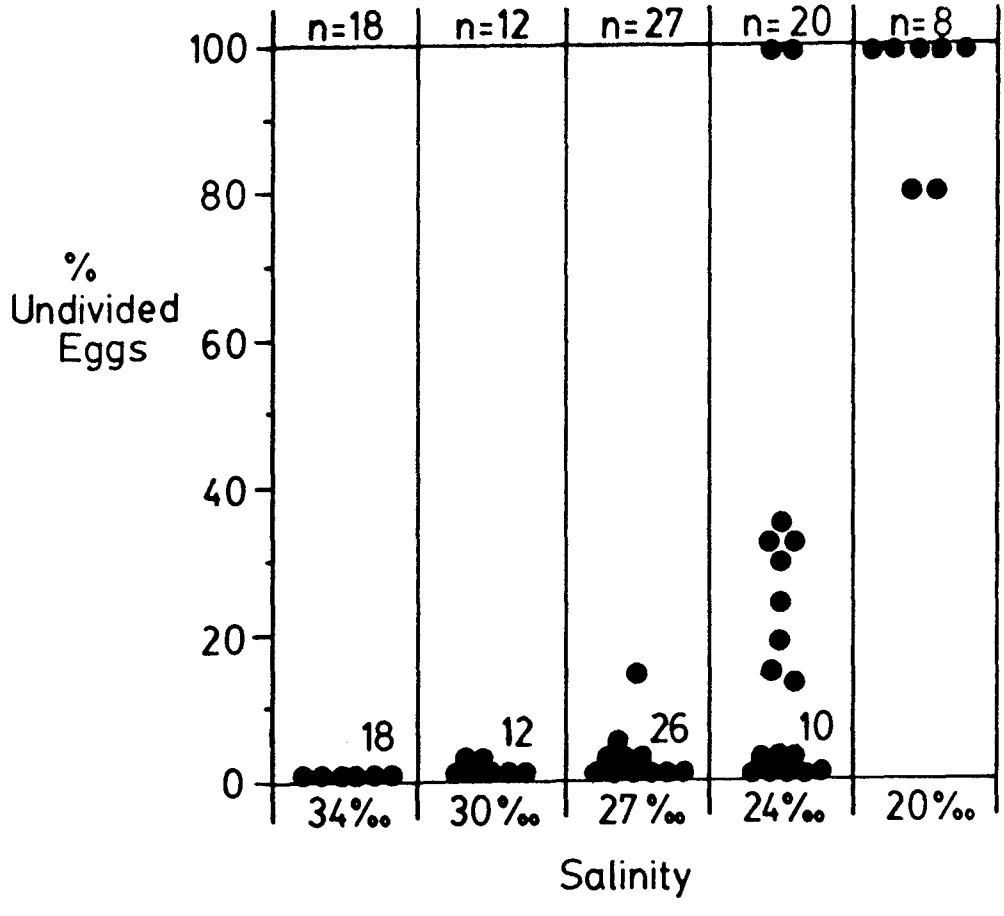

Figure 19. Failure to begin development at various salinities represented as proportion of undivided eggs in the nidosome.

Abnormal Development

Gross abnormalities were observed in developing veligers at all salinity levels. These abnormalities, examples of which are illustrated in figure 20 (page 46), include failure to develop the shell, siamese twinning, and deformity. Despite these conditions, nearly all were alive and moving when observed on the fifth day post oviposition. All had developed active cilia (although not necessarily on oral lobes), and some had even hatched and were motile. It is assumed that such bizarre morphology constitutes developmental failure.

Abnormal veligers and underdeveloped veligers which had died during early divisions were grouped as abnormally developed veligers. Of the veligers which began development, the proportion of abnormally developed veligers is presented in figure 21 (page 47). No data are presented for 20 $^{o}/oo$, as no development occurred. At higher salinities, normal development is greater than at lower salinities but developmental failure is unexpectedly high. Lower salinities show strikingly greater rates of failure.

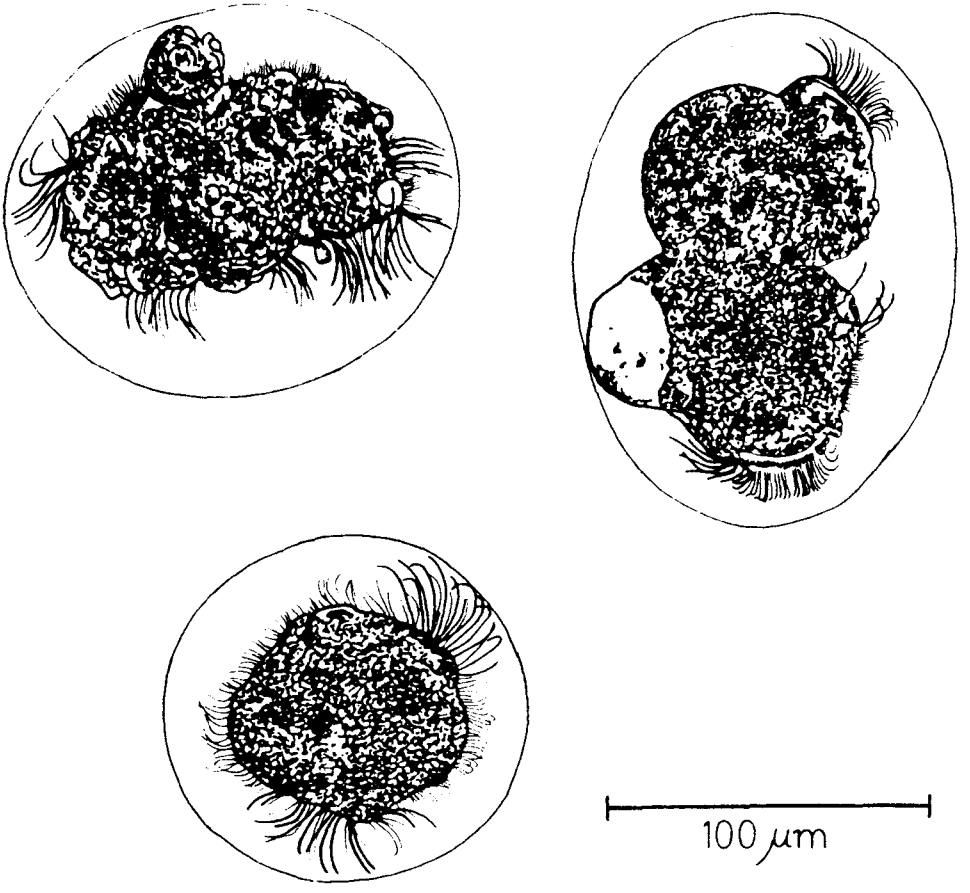

Figure 20. Abnormal veligers.

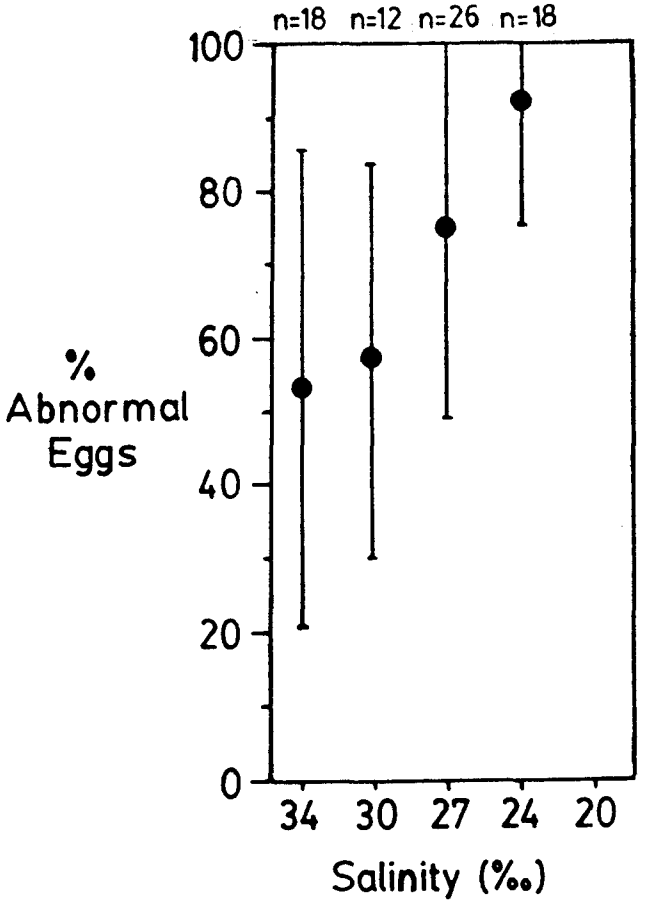

Figure 21. Proportion of abnormally developed veligers at various salinities.

CHAPTER V

DISCUSSION

Population Fluctuations

The bottom population of Hermissenda fluctuated over the experimental year from April 1986 to April 1987. The numbers gradually increased from May to July, 1986 and then declined. Another peak in abundance, was observed in January of 1987.

The relative abundance of the different size classes also fluctuated. Very small animals (1 cm or less) are easier to overlook in the field than larger animals and so are underrepresented in the collection data. Medium sized animals (2-4 cm) made up greater than 50% of the population in all collections except one in July. The greatest seasonal fluctuation was observed in small (1-2 cm) and large (4 cm or greater) animals. In summer, large animals are common and small animals rare. In the winter, the situation is reversed.

Several factors which may vary seasonally and account for the fluctuation in local Hermissenda populations are: predation, food, disease, movement (active and passive), recruitment, temperature and salinity. This research explores and considers only the effects of salinity on the population through adult mortality and reproduction.

The salinity of the bay responds quickly and markedly to heavy local rainfall. After winter rainstorms, bottom salinity frequently fell below 20 °/oo, extending over a range of 10 °/oo or greater. Reduced and fluctuating salinity characterized the winter months from November through April.

The high numbers of Hermissenda collected in January confirm that animals are present in the bay during periods of fluctuating salinity. Over 80% of the animals collected in January were under 3 cm. If low or fluctuating salinity reduces growth rates, or if food had been scarce, some of these animals could have hatched from eggs deposited as early as August and so developed in high salinities. If food had been abundant and growth not hampered by low or fluctuating salinity, it is possible that many of the January animals settled out in December when rainfall was slight and salinity fluctuations were narrow. In either case, the large number of animals collected in January probably tolerated low and fluctuating salinities unless they immigrated into the area from greater depth in mid January. Because nearly 5% of the animals collected on December 8 were smaller than 1 cm, I am inclined to consider that small animals, recently settled out on the dock fauna, were shocked by fresh surface waters following the November storm and dropped to the bottom. They confirm that recruitment occurs in autumn, although the original source of these individuals remains a mystery.

Environmental Salinity and Adult Mortality

If adult mortality increased in these salinity conditions, I would expect the population to decline after the first rains of autumn. The samples suggest a population decline of nearly 40% between the September 7 and October 3 collections. The first rain of the season (12 cm) fell the last two weeks of September. However, it is likely that this first rain had little impact on the bottom salinity of the boat basin. Much of the rain was certainly absorbed by dry hillsides, and because the 7 cm of rain in October caused only a minor drop in salinity, the salinity following the September rains probably did not drop enough to cause significant mortality. The timing of the population decline corresponds to high mortality, but because there is an extended period of time between the two collections, the population crash is not pinpointed and cannot be correlated with salinity.

Two alternative factors may account for the population decline in early fall: predation or food. A high incidence (to 30%) of oral tentacle damage in otherwise healthy animals was observed in August and September and may indicate increased levels of predation. Few predators on Hermissenda are known. Although Birkeland (1974) reported that Hermissenda were common prey to the sea star Crossaster papposus, the type of injury I observed was more likely the result of a more selective feeder such as fish. Pycnopodia helianthoides, a common basin resident, was considered a potential general predator after it was observed to consume a dorid nudibranch in the laboratory.

I collected a small specimen (under 20 cm) and starved it in the lab for 3 weeks. It failed to eat two Hermissenda released in its aquaria within 2 days, and shortly thereafter readily consumed broken Mytilus. Cannibalism does not appear to be responsible as it typically involves healthy animals attacking and selectively eating the cerata of animals in poor health.

Common Hermissenda food items (dying medusae and other carrion) which are abundant on the bottom of the basin in the summer decline noticeably in the fall (personal observation), possibly contributing to adult mortality.

Environmental Salinity and Reproduction

The reproductive cycle (egg production, development and recruitment) may be sensitive to reduced and fluctuating salinities. In the laboratory, animals held at 20 and 24 °/oo produced abnormal egg masses, the eggs of which did not, in large part, begin development. Larvae at these salinities which developed did so with debilitating, gross abnormalities at greater frequency than the control larvae. Development was frequently abnormal in controls. Whatever factor was suboptimal (perhaps Oxygen or nutrient deficiency in small containers), it was likely the same for all salinities.

These results indicate that adults are impaired in their ability to produce normal eggs, and that eggs exposed to low salinities are unable to develop normally. In the field, eggs are exposed to fluctuations in salinity as well as low levels. To determine if the field population might suffer from salinity-induced reproductive

failure, an estimated age from animal size can be used to track back to oviposition. The precision of this analysis is limited because the size of an animal cannot be reliably related to its age. Animals shrink when starved, and Harrigan and Alkon (1978) observed that growth rates decreased dramatically with advancing age (after day 70 in the 140 day adult lifespan). Their laboratory-reared animals (presumably better fed than wild specimens) grew to 8 cm in 5.3 months after hatching. They also found that faster growing animals attained greater size.

I rarely collected animals exceeding 6 cm, indicating some food deprivation or other suboptimal conditions. If, however, I assume that these largest animals are nearing senescence, I can examine population and rainfall data to determine if there is field evidence for salinity effects on egg production or development.

If the observed winter salinity levels affect the production of normal eggs or their development, I would expect to see a drop in the numbers of large animals about 5 months later. Low salinity conditions which prevail during the winter months of November through March would be followed by low numbers of large Hermissenda from April through August. The marked increase in large specimens during the summer of 1986 refutes this expectation. However, this assumes that bay animals originate within the bay, and the summer abundance of large animals suggests that veligers recruit from a source outside of the boat basin, probably the open coast or a more southern estuary where winter salinity does not fluctuate as much as in Coos Bay.

There may also be a genetic component involved in seasonal population fluctuations. During the summer, I have noticed a greater abundance of the morphs which lack the white ceras stripe. (This characteristic is distinct from food-mediated brilliance.) These animals also tend to attain greater sizes than those featuring the white ceras stripe. J.Goddard (1984, personal communication) considers the stripeless morph more common in California while the striped version dominates Coos Bay and the local outer coast. Perhaps the stripeless morph has greater growth potential or reaches Coos Bay via the north-bound Davidson current when it is strong during the winter.

Preliminary mating experiments indicate that the two types may not be reproductively isolated. I isolated and raised small animals of both types for 3 weeks, and then paired them. Normal looking veligers hatched, but were not raised through metamorphosis to the F-1 generation to determine fertility.

Environmental Salinity and Recruitment

Hermissenda spend one month as veligers in the plankton. If the large animals seen in July are nearing senescence, they settled out of the plankton no earlier than March. If the winter salinity regime interferes with recruitment, I would expect that large animals would be abundant in the period four months after the summer high salinity. High salinity from March through August would translate into an abundance of large animals between July and December. The observed decline in large animals prior to December casts suspicion on

salinity-mediated recruitment. Further doubt arises from the high number of small animals seen in December and January following the initial salinity drop in November.

The Possible Role of Other Factors

Food may play an important role in the abundance of the large size class during the summer, and qualitative field observations support this. If competent veligers seek out the rich hydroid colonies on the floating docks for metamorphosis during March, then feed extensively on the plentiful carrion on the bottom, they might grow more rapidly and result in the large size class observed during the summer. In the laboratory, young animals which were fed tunicates developed more brilliant coloration than those which were fed various cnidarians. Diet-generated color variations observed in the field are evidence that animals do in fact settle out on the docks and later move to the bottom. It is interesting, however, that Harrigan and Alkon (1978) found competent veligers spending more time near the bottom of the aquaria (perhaps where the Obelia provided for metamorphosis were located?), Virtually all animals collected from the docks from spring through late summer exhibit a brightness in color which reflects consumption of tunicates. Tunicates are proliferating and growing during this time of the year and laboratory animals seemed to prefer the tadpole larvae as they settled out. Most bottom animals were pale by comparison, though some retained bright colors, possibly as a result of recent residence time on the docks above. Winter animals are never as bright as summer specimens, and coincidentally,

tunicate colonies are much reduced in winter and probably not reproducing.

The possibility that animals are actively or passively moving between the docks and the bottom using pilings or drifting with currents has not been addressed in this research. The extremely low numbers of small animals collected suggests that in fact the sample collected here counted only a portion of the population inhabiting the Charleston boat basin. Further investigations are necessary.

Finally, non-genetic adaptation may play an interesting role in the population fluctuation. Kinne (1971) states that:

> Non-genetic adaptations to salinity acquired during very early ontogeny, for example, during embryonic development or immediately upon hatching, tend to be more stable and more complete than those acquired in older individuals.

If animals that develop in fluctuating salinity acclimated more easily to fluctuating salinity as adults, one might expect variability in adult salinity tolerance over the year. Animals that develop during the summer (June through August) and mature in October through December may not exhibit as great a tolerance to salinity changes as those which developed during the winter (in the bay).

CHAPTER VI

SUMMARY

1. The bottom population of Hermissenda crassicornis in the Charleston boat basin peaked in July and January of the April 1986 - April 1987 study year.

2. Throughout the year, nearly half the population was intermediate in size (2-4 cm). In the summer, the remainder of the population consisted of animals larger than 4 cm while in the winter, animals smaller than 2 cm dominated the balance.

3. Seasonal rain storms caused immediate fluctuation in the salinity (maximum range, 12 - 29 °/oo) and seasonal depression of the maximum salinity (to an average of 29 °/oo, down from 34.5 °/oo).

4. The first fall rains of 1986 preceded a significant decline in the Hermissenda population. The associated salinity drop was likely not great enough to account for the fall in numbers via adult mortality. Osmoconformance was demonstrated for this species.

5. In the laboratory, reproductive sensitivity to salinities below 25 °/oo was observed. Nidosomes were frequently abnormal and development rarely occurred at experimental salinities of 20 and 24 °/oo. Although abnormal development was observed at all salinities, it was more frequent in lower salinities.

6. Because Hermissenda veligers spend a full month in the plankton, they are likely to travel some distance from their origin. Consequently, local salinity effects on egg production and development cannot be correlated with adult population levels.

APPENDIX

COLLECTION DATA

Dive Information

DATE OF COLLECTION	LARGE BASIN	SMALL BASIN	MUD	PILINGS	SALINITY (SURFACE) (o/oo)	SALINITY (BOTTOM) (o/oo)	TEMP. (SURFACE) (^{o}C)
4/11/86	X		X		32.0		10.2
5/2/86		X		X			
5/3/86		X		X	26.0		14.5
5/11/86	X		X	X	21.0		12.2
5/12/86		X	X	X	17.0	28.5	13.0
5/29/86		X		X	29.0	31.0	
5/30/86		X		X			14.0
6/11/86	X		X		30.0	30.0	14.6
6/27/86	X		X	X	34.0	34.0	14.6
7/10/86	X		X		33.0		(16.0)
7/25/86	X		X		34.0		13.2
8/7/86	X		X		34.0	34.0	12.2
8/21/87	X		X		34.5	34.5	10.5
9/3/86	X		X		33.5		12.8
10/1/86	X		X		32.0	33.0	13.2
10/17/86	X		X				
11/4/86	X		X		32.0	32.0	12.0
1/25&26/86	X		X		24.0	24.0	
12/8/86	X		X		26.0		
1/22/87	X		X		26.0		
2/20/87	X		X		27.0		
3/7/87	X		X		23.0		
3/17/87	X		X		18.0		
4/5/87	X		X		24.0		
4/19/87	X		X		27.0		12.8

Animal Collection Information

DATE OF COLLECTION	TOTAL ANIMALS	NUMBER DIVERS	DIVER 1	DIVER 2	HOURS	DIVER-HOURS	ANIMALS / DIVER-HRS
4/11/86	84	2	WLM	PPR	.8	1.66	50.6
5/2/86	28	1	WLM	LMH	1.3	1.30	21.5
5/3/86	35	1	WLM	LMH	1.2	1.20	29.2
5/11/86	51	2	WLM	LMH	2.0	4.00	12.8
5/12/86	138	2	WLM	LMH	3.0	6.00	23.0
5/29/86	78	2	WLM	PPR	1.7	3.40	22.9
5/30/86	125	2	WLM	PPR	1.6	3.20	39.1
6/11/86	79	1		PPR	1.3	1.30	60.8
6/27/86	136	2	WLM	PPR	.9	1.80	75.6
7/10/86	250	2	WLM	PPR	1.0	2.00	125.0
7/25/86	286	2	WLM	PPR	.7	1.40	204.3
8/7/86	202	2	WLM	LMH	1.4	2.80	72.1
8/21/87	272	2	WLM	PPR	1.0	2.00	136.0
9/3/86	320	2	WLM	PPR	.7	1.40	228.6
10/1/86	168	2	WLM	PPR	1.0	2.00	84.0
10/17/86	225	2	WLM	PPR	1.0	2.00	112.5
11/4/86	160	2	WLM	PPR	1.3	2.50	128.0
1/25&26/86	125	1		PPR	2.5	2.50	50.0
12/8/86	159	1		PPR	2.0	2.00	79.5
1/22/87	375	2	WLM	PPR	.8	1.60	234.4
2/20/87	180	2	WLM	PPR	1.0	2.00	90.0
3/7/87	163	2	WLM	WAW	.8	1.60	101.9
3/17/87	41	2	WLM	WAW	.7	1.40	29.3
4/5/87	178	2	WLM	PPR	1.5	3.00	59.3
4/19/87	95	2	WLM	VS	1.2	2.40	39.6

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