

AN ABSTRACT OF THE THESIS OF

Weldon S. Bosworth, Jr. for the degree of Doctor of Philosophy
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Title: Biology of the Genus Eohaustorius

(Amphipoda: Haustoriidae) on ~~the~~ Oregon Coast

Abstract approved:

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Jefferson J. Gonor, Ph.D.

This study has identified several ecological and physiological differences between four species of the genus Eohaustorius inhabiting the sandy beaches on the central Oregon coast. This study has also documented several population characteristics which not only contribute to the successful maintenance of populations in a rigorous environment but also may act in concert with the ecological and physiological differences to reduce competition between them. In addition, this study has identified several adaptations that serve to separate the niches of Eohaustorius spp. from the other abundant malacostracans.

The four species, Eohaustorius washingtonianus, E. brevicuspis, E. sawyeri and E. estuarius, although found in close proximity throughout most of their geographic range have their maximum abundances in different portions of the sandy beach habitat. E. estuarius is most abundant in brackish water habitats; E. brevicuspis in the high and mid intertidal regions on exposed beaches; E. washingtonianus in the low intertidal and shallow subtidal in both exposed and sheltered habitat and E. sawyeri in the shallow subtidal on exposed coasts.

The principal differences between the four species included adult size; brood size and total fecundity; timing of the reproductive cycle; density; intraspecific dispersion; salinity and temperature tolerance; and, predators.

It was also determined that subtle distributional characteristics within E. brevicuspis probably act to both increase reproductive potential by decreasing the probability of interspecific matings, and to also maximize the protection of brooding females. Results of this study also suggest that the peak reproductive period of these species coincides with the time of greatest habitat instability when potential for dispersal to new habitats is greatest. During this time productivity is also at its highest and newly released juveniles would have the advantage of having a readily available and abundant food supply.

Lastly, this study has verified that these four congeners warrant species rank not only because of their morphological differences but also because of their reproductive isolation.

Biology of the Genus Eohaustorius
(Amphipoda: Haustoriidae)
on the Oregon Coast

by

Weldon S. Bosworth, Jr.

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BIOLOGY OF THE GENUS EOHAUSTORIUS
(AMPHIPODA: HAUSTORIIDAE)
ON THE OREGON COAST

INTRODUCTION

The ecological relationships of groups of species of gammarid amphipod inhabiting sandy beaches have recently been the subject of several studies by marine biologists. The objectives of these studies have been to discover adaptations by closely related species living sympatrically. These studies have purported to test the validity of the "competitive exclusion principle" (Gause, 1934) by identifying adaptations that have evolved in these species which serve to decrease competition between them by diversifying their ecological requirements, or niche as defined by Hutchinson (1957). Although investigations of this sort can lead to circular arguments (Hardin, 1960; Cole, 1960), in the majority of instances workers have been able to identify several niche differences which they have concluded contribute to a reduction of competition between the species (Croker, 1966; Dexter, 1967; Sameoto, 1966). Amphipods are desirable subjects for studies of this kind since they have a short generation time, are easily collected in large numbers, can be sexed, aged and measured with little difficulty, are easily maintained in the laboratory, and since they brood their young, one can readily determine their fecundity.

The dominance of amphipod species on temperate sandy beaches is well recognized (Dahl, 1953; Hedgpeth, 1957; Vader, 1965; Croker, 1966; Bousfield, 1970). On exposed beaches members of this order may

compose as much as 91% of the number of macrofaunal invertebrates (Dexter, 1967). On sheltered beaches the proportion of amphipods may decrease, but they still represent a substantial contribution to the biomass (Croker, 1975).

The rigors of the sandy beach environment have led to convergence of body form in these amphipods, and while there is subtle variation in morphology within different taxonomic groups, the fossorial body form that has evolved in these groups is apparently necessary for survival in this environment (Bousfield, 1970). An equally important selective pressure, competition for available resources has, in turn, led to ecological specialization within these groups which has resulted in closely related and morphologically similar species being capable of living sympatrically on sandy beaches with overlapping but nonetheless distinctive niches.

Of the gammaridean families inhabiting sandy beaches the family Haustoriidae probably best illustrates the results of this adaptive radiation. This relatively ancient and morphologically primitive group of gammaridean Amphipoda are primarily distributed in shallow marine and estuarine waters of the northern hemisphere (Bousfield, 1965). Haustoriid diversity is highest in the Atlantic where the family is represented by at least 26 species in seven genera of the subfamily Haustoriinae and 22 species in three genera of the subfamily, Pontoporeiinae (Bousfield, 1970). Two genera of the subfamily Pontoporeiinae range into the Pacific: the panarctic genus, Pontoporeia and the broadly distributed genus, Urothoe (Bousfield, 1970). The only

Pacific representatives of the subfamily Haustoriinae are the species of the endemic genus Eohaustorius, of which seven have been described (Bousfield, 1970; Bosworth, 1973), at least two other species are also present.

The distribution and biology of members of this family in the Atlantic were initially studied by Elmhirst (1931); Watkin (1939, 1940, 1941); Jones (1948); Holme (1949); Stephen (1953) and Dahl (1953). Recently there have been several more comprehensive studies of this family on both the northeastern and northwestern Atlantic coasts (Vader, 1965; Bousfield, 1965, 1970; Croker, 1966, 1975; Dexter, 1967a, b; Sameoto, 1967, 1969a, b, c; Preece, 1971; Fincham, 1970, 1971; Fish and Preece, 1970; Ladle, 1975; McGrorty, personal communication). These workers have investigated several aspects of the biology of haustoriids but have focused generally on elucidating mechanisms of niche diversity of several species occurring sympatrically by identifying the ecological differences between them.

In a study of Haustoriidae on Georgia beaches, Croker (1966) investigated the biology of seven species inhabiting the intertidal area on both exposed and sheltered beaches. The seven species he examined: Parahaustorius longimerus Bousfield, Neohaustorius schmitzi Bousfield, Lepidactylus dytiscus Say, Haustorius sp., Acanthohaustorius sp., Pseudohaustorius carolinensis Bousfield, and Protohaustorius deichmannae Bousfield. They were found to have several ecological differences including differences in intertidal zonation, timing of reproductive activity, habitat locations (i.e., on exposed and sheltered beaches),

physiological tolerances to temperature and dessication, and in some types of behavior. Although there was also considerable overlap in the species' niches in some instances, Croker (1967) concluded that:

Differences between [these] haustoriid species are considered as secondary isolating mechanisms, contributing to optimal adaptation to respective niches and reinforcing separation of species. Overlapping niche characteristics including horizontal and vertical zonations, reproductive cycles, fecundity, size ratios, food and general behavior are considered to indicate variable responses of species to environmental conditions existing over the range of their fundamental niches.

Dexter (1967a) studied similar ecological characteristics of seven haustoriid species on North Carolina barrier island and lagoonal sandy beaches. At least five of the seven species she worked with, Haustorius sp., L. dytiscus, N. schmitzi, P. longimerus and P. deichmannae, were among those Croker (1966) studied. The other two species were Acanthohaustorius intermedius Bousfield and A. millsii Bousfield. One of the Acanthohaustorius sp. she worked with was probably the same species that Croker studied. Pseudohaustorius carolinensis was not present on the North Carolina beaches she sampled. Dexter (1967) arrived at the same conclusions as Croker: that the coexistence of these species was explained by niche diversification. Although she found overlap of some of the ecological characteristics she measured, she found that the primary differences in their ecological niches were related to intertidal zonation patterns, seasons of reproductive activity, size differences, and habitats. She concluded (1967a) that the two major factors in separating the niches or in reducing competition between these species on North Carolina beaches were habitat isolation and

temporal reproductive isolation.

Sameoto (1967, 1969a, b, c) investigated the comparative ecology, life histories, physiological tolerances and behavior of five species of Haustoriids living in sandy beaches on Cape Cod, Massachusetts. These were: Haustorius canadensis Bousfield, Neohaustorius biarticulatus Bousfield [Included in this group were some N. schmitzi (Michael, 1976)], Acanthohaustorius millsii Bousfield, Parahaustorius longiremus Bousfield, and Protohaustorius deichmannae Bousfield. The ecological requirements of the species differed in several of the characteristics that both Croker (1966) and Dexter (1967) had described for the species they worked with. N. biarticulatus and H. canadensis are intertidal. The remaining three species are subtidal. Haustorius canadensis and N. biarticulatus were generally separated both vertically and horizontally in the sand, and A. millsii was separated horizontally from the former two species. Parahaustorius longiremus and Protohaustorius deichmannae were never found in the same type of habitat as the intertidal species. Tolerances to several environmental factors also differed among the five species (Sameoto, 1969c). Differences in other population characteristics were also noted. Sameoto (1967, 1969a) suggested that the limiting factor in their habitat may have been available food and concluded that spatial separation, size differences in the zones of species overlap, and timing of the release of the brood all contributed to reduction in competition for food between these species.

The work of Vader (1965), Fish and Preece (1970), Preece (1971), Fincham (1971) and McGrorty (1971, personal communication) has

identified several ecological characteristics which contribute to niche diversification in the haustoriids inhabiting the British Isles and western European coast. These species are: Bathyporeia guilliamsoniana Bate, B. pelagica Bate, B. pilosa Lindstrom, B. elegans Watkin, B. nana Toulmond, B. sarsi Watkin, Haustorius arenarius Slabber and Urothoe brevicornis Bate. They occur sympatrically in several combinations on both exposed and sheltered beaches in this region. Vader (1965) found that the horizontal distribution of B. pelagica, B. sarsi, B. pilosa and H. arenarius on beaches in the Atlantic region of the Netherlands was governed primarily by salinity although sediment characteristics appeared to play a secondary role. Fish and Preece (1970) noted differences in life history and timing of the reproductive cycle in two species, B. pilosa and B. pelagica living on beaches in Wales (Fincham, 1971). Preece (1971) studied the physiological tolerances of these species and found that B. pilosa, normally inhabiting the higher intertidal position, was the more tolerant in all experiments conducted. The experiments included temperature, dessication and starvation tolerance. Fincham (1971) discussed the influence of substrate as well as temperature and competition on the distribution of these western Europe haustoriids on beaches at Port Erin, Isle of Man. He observed that most amphipods had substrate preferences, most species being found in the finer sand. He also observed that breeding behavior was influenced by location on the beach, the deeper water (8m) populations of Bathyporeia breeding with the spring rise in temperature and the shallower water (0-3m) showing an almost continuous breeding cycle phased by the tides.

McGrorty (1971, personal communication) in a study of B. sarsi, B. pelagica, B. guilliamsoniana and B. nana in Robin Hood Bay, Yorkshire, England found that each species occurred in a recognizable zone, although there was much overlapping. Only B. pelagica was found at all levels, but the zone of maximum densities varied with season. There also appeared to be minimal spatial overlap of these species during the reproductive season. In salinity and temperature tolerance experiments those species inhabiting the highest levels on the beaches were more resistant to the greatest fluctuations. Water content of the sand may also have been important. Although there was seasonal migration up the beach of the primarily subtidal species, B. guilliamsoniana, it was never found above the zone of saturated sand.

In general these studies of haustoriids living on North Atlantic beaches have identified several of the characteristics cited by Mayr (1963) that reflect niche differences and presumably contribute to a reduction of competition between the species investigated.

According to Mayr (1963),

There are two properties which make possible the coexistence of closely related species. These are (1) mechanisms guaranteeing reproductive isolation such as geographical, habitat isolation or highest density in different habitats, temporal isolation of potentially competing life stages by staggering of the reproductive periods, maintenance of size ratios and sterility barriers, and; (2) ability to resist competition from other species utilizing the same or similar resources of the environment through subtle factors including all differences in utilization of the habitat, that is, all niche differences. Examples of the latter may be differences in horizontal and vertical zonation, behavioral stereotyping, physiological tolerances, substratum preferences, fecundity [or] sex ratio differences acting to increase biotic

potential, characteristics of food or seasonal abundance.

Aside from the taxonomic studies (Thorsteinson, 1941; Barnard, 1957; 1962; Bulycheva, 1952; Guranova, 1951; 1953; Bosworth, 1973) and a review of their zoogeography by Bousfield (1970) which describe general aspects of the distribution of Eohaustorius, there has been no published work on the biology of haustoriids along the Pacific coasts. Greenley (1969), in an unpublished intertidal survey, described the presence of three apparently different "forms" of the genus Eohaustorius living sympatrically on three central Oregon beaches. One of these "forms" resembled the species E. washingtonianus (Thorsteinson, 1941; Barnard, 1957). The other two "forms" while very similar in appearance to E. washingtonianus and to each other, appeared to have sufficient morphological and distributional differences to warrant specific rank. After reviewing Greenley's work and conducting preliminary distributional studies of my own, I described these two, E. brevicuspis and E. sawyeri, and a third which was found only in estuarine habitats, E. estuarius (Bosworth, 1973). I noted their rather subtle morphological differences and discussed preliminary evidence for differences in intertidal zonation on beaches where they co-occurred.

The sympatric Haustoriinae species studied in the North Atlantic, with a few exceptions, were of different genera. The presence of generic differences suggests that evolution in the Atlantic Haustoriinae probably occurred more rapidly or over a longer period of time than with the Pacific coast Haustoriinae which consists only of the endemic genus, Eohaustorius. Bousfield (1970) notes that unlike other genera of

Haustoriinae,

Eohaustorius, ... seems not to have undergone the physiological and reproductive modifications and adaptations vital to permanent colonization of intertidal sand beach habitats, especially in estuaries. The historical lack of extensive and stable interconnected estuarine environments in the North American-Pacific region apparently has not provided a stimulus for evolutionary radiation.

Bousfield recognized, however, that there were several species of

Eohaustorius, of which some were undescribed, and also suggested that,

the fog, high humidity and relatively mild winters of west coast beaches have permitted some eurytopic species of Eohaustorius to inhabit the upper parts of open coast beaches and to penetrate into brackish sandy beaches at the mouth of the Columbia and other large regional estuaries.

He also stated that further studies on the physiological limits of

Eohaustorius were necessary to clarify his general observations.

The sympatry of these congeneric species raises the question of whether these haustoriids are, in fact, true species in the biological sense, i.e., whether they are groups of interbreeding natural populations that are reproductively isolated from other such groups (Mayr, 1963). Mayr (1963) termed sympatric populations that are morphologically similar, if not identical, but are reproductively isolated, sibling species. He stated (Mayr, 1970) that, sibling species are of importance in biology because, "they permit us to test the validity of the biological versus the morphological species concept."

The purpose of this study is to:

- 1) determine whether these sympatric populations of Eohaustorius are reproductively isolated;

- 2) determine what ecological and physiological characteristics contribute to a differentiation of their niches;
- 3) present an explanation for the observed widespread but discontinuous distribution of these intertidal species which brood their young.

II. DESCRIPTION OF THE STUDY AREA AND METHODOLOGY

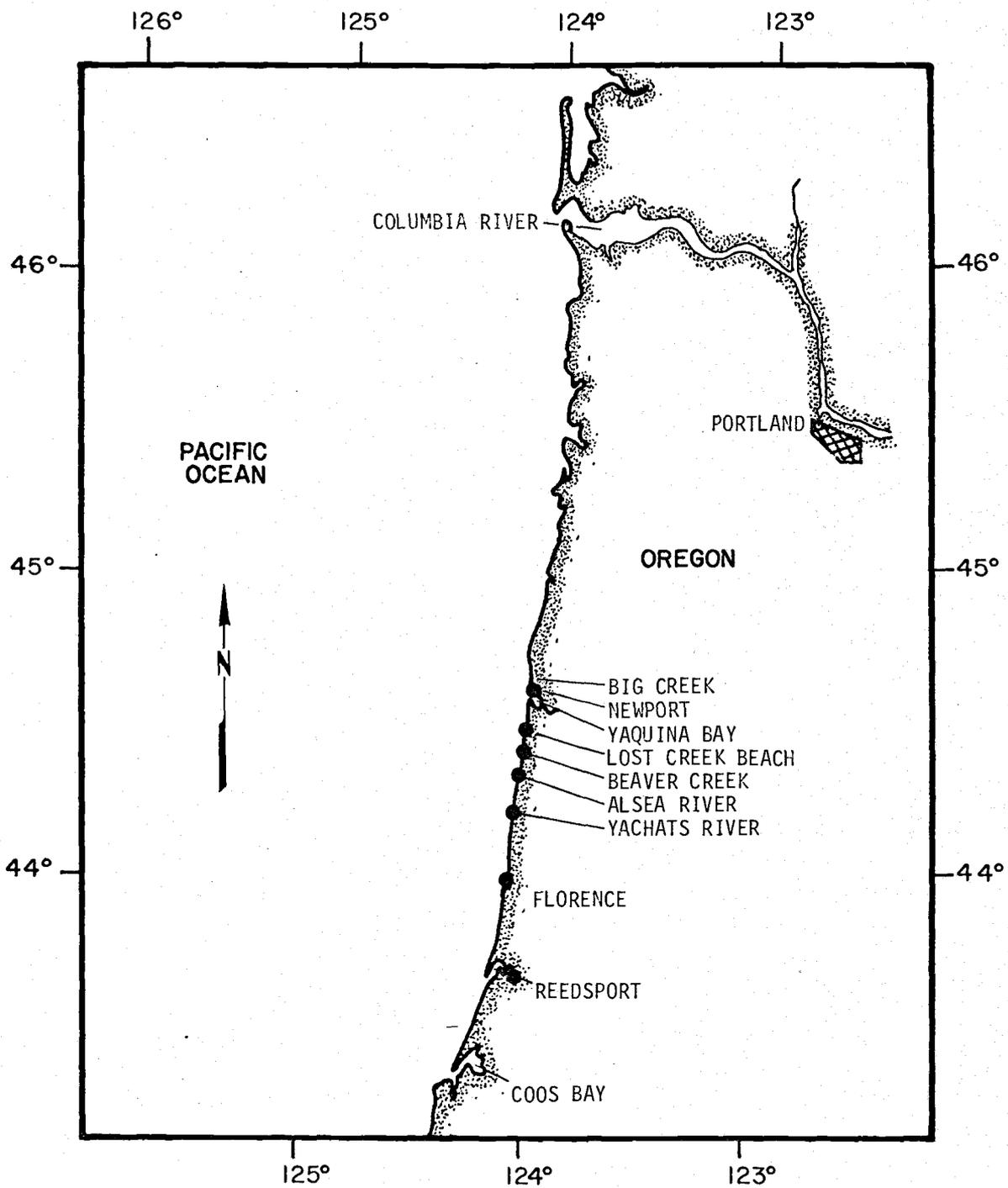
A. Description of the Study Area

1. Central Oregon Coast

The areas chosen for study are located on the central Oregon coast in the vicinity of Newport, Oregon (Figure 1). This area is characterized by a climate typical for the coastal Pacific Northwest with marked wet and dry seasons, mild and relatively uniform air temperatures and seasonal wind direction (Holbrook, 1970). The mean annual rainfall at Newport is 68.18 inches with about 70% falling from November to March. Maximum precipitation occurs during December and January and the minimum during July and August (Holbrook, 1970). The mean air temperature of the region is 50.8°F (10.4°C) and monthly means range from 43.5°F (6.4°C) in January to 57.6°F (14.2°C) in August. The annual mean daily maxima are 57.8°F (14.3°C) and 43.8°F (6.6°C) respectively and range from 49.5°F (9.7°C) to 37.5°F (3.1°C) during January and from 64.8°F (18.2°C) to 50.3°F (10.2°C) during August (Holbrook, 1970).

The coastal region of Oregon may be generally described as erosional tectonic with uplifted submarine banks and coastal terraces (Bourke, et al., 1971). The coast is characterized by mudstone and sandstone cliffs interspersed between sandy beaches (Bourke, et al., 1971; Baldwin, 1964). Besides the discontinuities in the sand habitat caused by the presence of rocky outcrops, these sandy areas are further separated by numerous rivers.

Figure 1. Map of Oregon coast showing location of study areas.



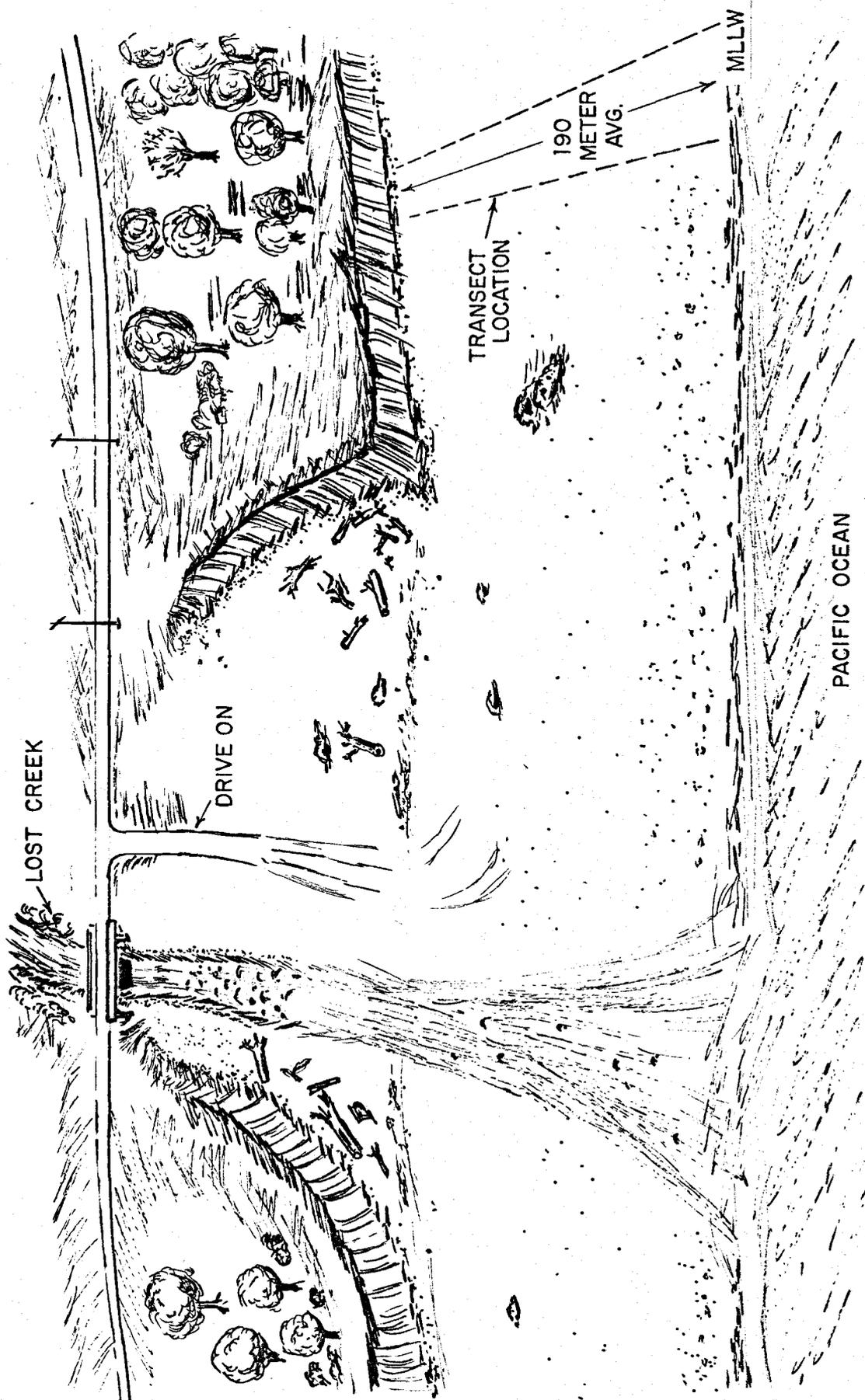
Surface sediments of the nearshore zone are primarily quartz and feldspar sands. This sand zone extends from the shoreline out to a water depth of approximately 50 fathoms (90 meters) off the central Oregon coast (Kulm, et al., 1967). The onshore-offshore transport of sand is greatest during the winter months when waves are highest (Bourke, et al., 1971). Exposed beaches may lose from 5 to 15 feet (1.5 - 4.5 m) of sediment thickness during the winter months (Kulm, 1967). The annual longshore transport is to the north but may vary with location (Kulm, 1967).

Bourke, et al. (1971) report that lowest surface water temperatures (8-9°C) and highest salinities (around 33 ‰) are observed in July when upwelling is dominant. Maximum surface water temperatures (13-15°C) occur in September and October after upwelling ceases. Temperatures range between 9.5 and 11.5°C throughout the other months. Salinities are generally from 31 to 33 ‰.

2. Lost Creek Beach

One of the two major Oregon sampling sites studied was Lost Creek Beach in Lincoln County, Oregon (Figure 2). Located approximately eight kilometers south of Newport, Oregon, at 44°32'35"N 124°04'23"W, Lost Creek Beach is an exposed beach of approximately 185 meters width from mean lower low water (MLLW) to the base of a sandstone cliff, approximately 13 feet (4m) above MLLW in the area of the transect. Lost Creek drains onto the beach approximately 200 meters to the north of the transect location. The extent of the drainage of Lost Creek across the

Figure 2. Lost Creek Beach, Lincoln County, Oregon showing location of sampling area.

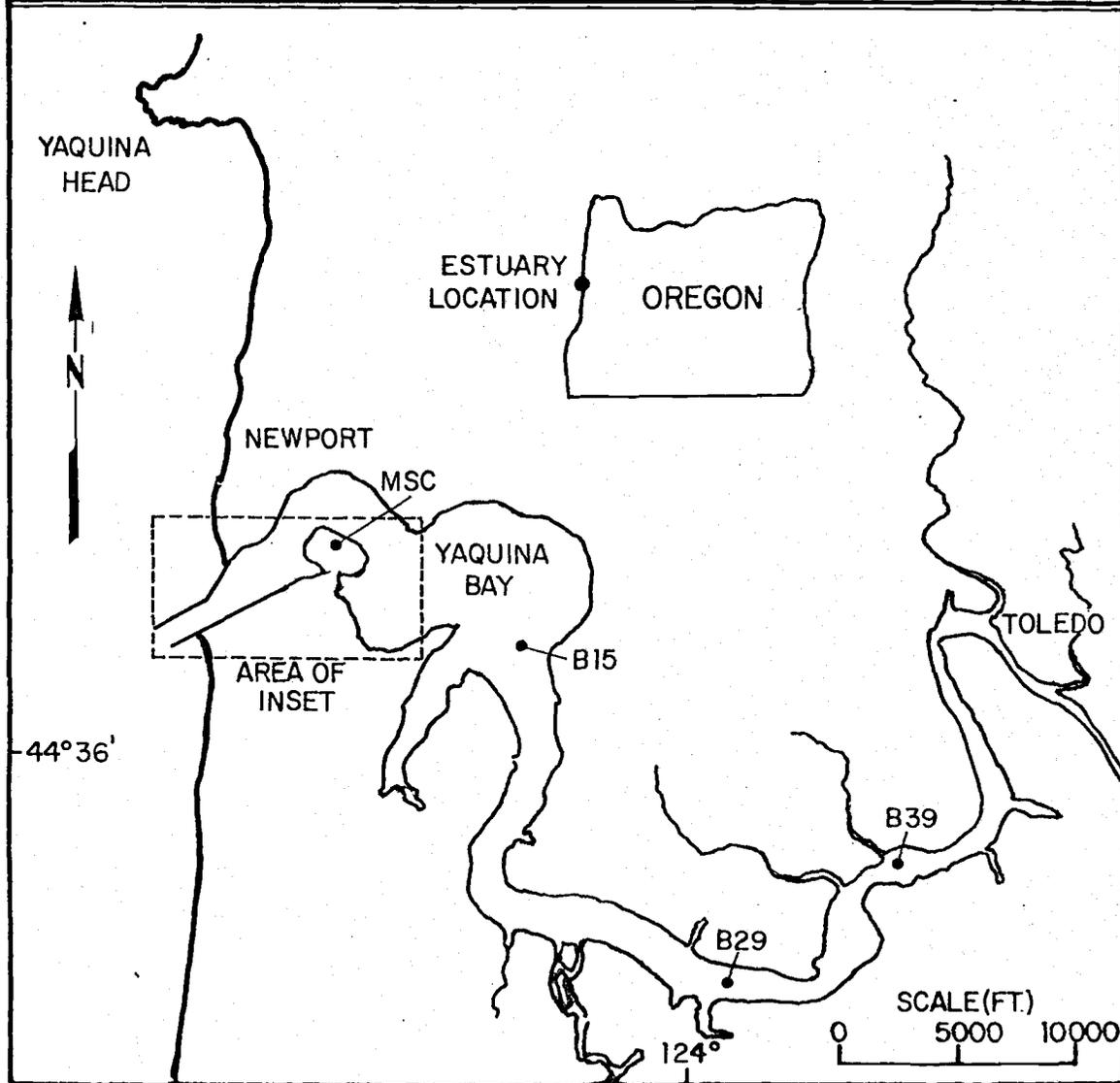
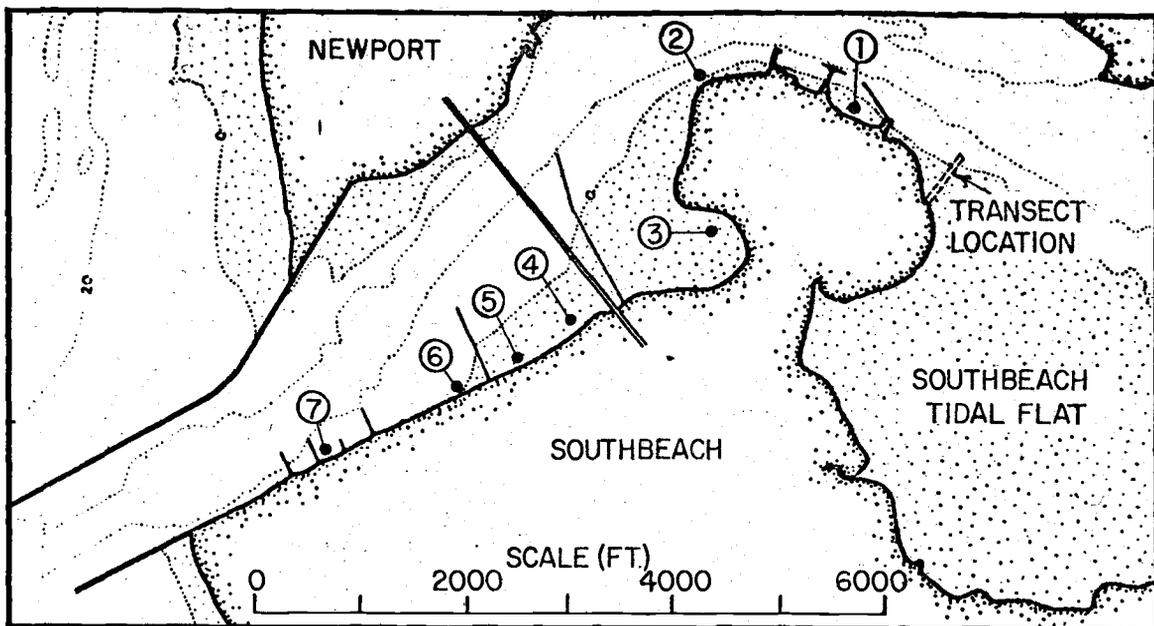


beach varies with the amount of rainfall but may spread out widely over the beach, depending upon the stage of tide and direction of long shore drift. At low tide the fresh water runoff from the creek was observed to be usually restricted to shallow channels 10-20 cm in depth. In the area of the transect freshwater seepage was also frequently observed on the beach between 25 and 100 m from the base of the cliff. The beach is underlain by Nye mudstone (see Figure 9 in Baldwin, 1964) portions of which are exposed during the winter months when up to 4 to 6 feet (1.3 - 2 m) of sand may be eroded from the beach by storms. The sand is generally medium sized and well-sorted, and the particle size distribution is skewed toward the fine fraction. The average grain size of the upper foreshore is smaller than that of the lower foreshore sands. This decrease in particle size is probably due to selective sorting during eolian transport.

3. Yaquina Bay

The other major Oregon study site was located on Yaquina Bay, approximately 300 meters north of Oregon State University Marine Science Center, Newport, Oregon 44°37'04"N 124°03'15"W (see Figure 3). Thum (1972) described this site in detail and the following summary is taken from his work. This area is a slightly sloping (approximately 1.5°) tidal flat composed primarily of marine sediments. Particle size analysis indicated that the sediments on the flat were composed of fine sands. Although there were differences in sediment composition at the different depths and seasons and between stations, the percentage of

Figure 3. Yaquina Bay, Newport, Oregon showing locations of sampling stations and transect area.



fine particles was less than 10% during the winter in the upper flat but often exceeded 20% on the lower flat. The sediment is moderately sorted and is skewed towards the fine fraction.

The salinity in the study area was maximal during August (33.5 ‰). Daily salinity maxima and minima corresponded to periods of high and low tide. The daily range in salinity gradually increased and the total salinity decreased from November through January. In December and January, salinities range from the annual maximum to 0 ‰. High daily variability continued until April when the salinity began to rise. The daily range in salinity was 2-4 ‰ during summer and averaged 10-15 ‰ in winter.

The surface water temperatures at the study area averaged 10.5°C during the summer and rose to about 11.0°C from September to November. Thereafter the temperature decreased monthly until a low of 8.0°C was reached in March, and then increased again to 10.5°C in the spring. Variations as large as 4.0°C in the summer and 1°C to 3°C in the winter corresponded to the biweekly tidal amplitude. The daily range in surface temperature varied from 1°C in the winter up to 7°C in the summer.

A bed of eel grass, Zostera marina, is present throughout the year in the lower intertidal (-3.0 to 0.0 feet). An algal mat of Enteromorpha intestinalis, E. tubulosa and Ulva sp. may also form above the Zostera, and extend up to about +3.0 feet above MLLW during the summer. Bivalves found in this flat (Clinocardium nuttalli, Macoma nasuta, and Tresus capax) add carbonates to the flats, with noticeable

accumulation of shell material at the surface in the high intertidal and in situ in the lower intertidal. The lugworm, Abarenicola in the lower intertidal and the ghost shrimp, Callinassa californiensis in the mid intertidal contribute to reworking of the sediment. This results in a coarser and more homogeneous sediment with large amount of organic material added in the form of their fecal pellets.

The transect studied on this flat was approximately 130 meters long and ranged in elevation from 0.0 to 7.0 feet (MLLW), the vertical limits of Eohaustorius distribution.

4. Other Locations Studied (See Figure 1).

In order to complement the monthly studies conducted at the Lost Creek Beach and Yaquina Bay Sites, collections were also made on several occasions at Beaver Creek, Oregon 44°31'16"N 124°04'18"W, approximately 11 km south of Newport. Collections were also made at several other estuaries on the central Oregon Coast including Big Creek, two km north of Newport, Alsea River, approximately 40 km south of Newport, and Yachats River, approximately 65 km south of Newport. Collecting sites at these other locations were all characterized by relatively clean sands and brackish water.

B. Field Studies

1. Preliminary Surveys

A properly designed sampling program must take into consideration the allocation of sampling units within the sampling area, the

dimensions of the sampling unit (= quadrat size) and the number of sampling units in each sample. The distribution characteristics of the animal to be sampled must be known before making these choices. For this reason it is first necessary to conduct a preliminary survey or to consult other available information on the distribution of the organism one is studying.

In a preliminary study of Eohaustorius spp. at several central Oregon beaches including Lost Creek Beach, Greenley (1969) had previously used a stratified random sampling design, each stratum 100 feet wide and bounded by the horizontal distance that represented a vertical increase of two feet over the stratum below it. Within each stratum three random coordinates were located and samples taken at regular intervals along two axes drawn through the randomly selected points. One of the axes was drawn parallel to the water line, the other drawn perpendicular to it. The number of sampling units per stratum varied between 36 and 70 depending on the area of the stratum and totaled about 500 samples for the transect. Prior to choosing a quadrat size Greenley experimented with several sizes including 75 cm², 184 cm², 625 cm², 1000 cm² and finally chose to use the 184 cm² quadrat size for unstated reasons.

A preliminary examination of Greenley's data revealed that his choice of a stratified random sampling design was probably a correct one since the results of his sampling showed an obvious variability in density of the Eohaustorius species which could be correlated to height on the beach. By stratifying his samples he was able to minimize the

standard error of the mean density for a given total number of samples which resulted in greater precision in estimating the population mean than would have been possible from simple random sampling (Snedecor and Cochran, 1967). It also ensured that all portions of a heterogeneous population were represented in the population statistics. However, locating samples systematically along axes may have inadvertently biased his results by sampling on undetectable physical features such as along a line of buried tidal debris.

Since Greenley did not rationalize his choice of quadrat size or replication, it was necessary to further analyze his data and to complement his survey with an additional preliminary survey of my own.

An examination of his data showed that the distribution of Eohaustorius was not random. The variance to mean ratios or index of dispersion, (I), where $I = \frac{s^2}{\bar{x}}$, was calculated for his data and the results of a χ^2 test indicated ($p \leq .01$) that the distribution was not random. This is not surprising as random or regular distributions are found only infrequently in nature. In addition most other workers, e.g. Dexter (1967), Croker (1966), have shown that amphipods on sandy beaches have a positively contagious or "patchy" distribution. This may be attributed to a number of causes such as uneven distribution of physical factors, some inherent tendency for individuals to aggregate or the result of these young being released from the marsupium and remaining near the parent.

Elliott (1971) discusses the dependence of the final distribution pattern on several characteristics of the "patches", including the

distance between them, the nature of their spatial distribution, and the distribution of individuals within the "patches". He states that one common pattern is due to patches of high density (clumps) on a general background of low density. He suggests that although several mathematical models have been proposed to describe contagious distributions, the negative binomial (Bliss and Fisher, 1953) is probably the most useful. He feels that it can be applied to a wide diversity of contagious distributions and gives some examples (p. 51) that help to explain the models.

Basically, the negative binomial distribution is a counterpart of the positive binomial in which the population mean is not fixed but varies continuously. The derivation of this distribution is described in Bliss and Fisher (1953). The parameters of this distribution are the arithmetic mean, μ , and the exponent k . Elliott (1971) states that

the reciprocal of the exponent k , i.e., $1/k$, is a measure of the excess variance or clumping of individuals in a population. As $1/k$ approaches 0 and k approaches infinity, the distribution converges to the Poisson series. Conversely, if clumping increases, $1/k$ approaches infinity and the distribution converges to the Logarithmic series (Fisher, Corbet and Williams, 1943).

In other words, populations with lower values of k are more patchy than populations with higher k values. The test for agreement with the negative binomial distribution is by comparing the frequencies observed at each "x" with their expected values, ϕ , as computed from the statistics of the sample (Bliss and Fisher, 1953). The application of this test to Greenley's data showed no significant deviation from the fitted negative binomial.

Although it is impossible to relate the negative binomial distribution to any known ecological phenomenon, it is a convenient method for summarizing a set of observations with two parameters. Bliss and Fisher (1953) suggest an adequate fit might serve to justify further statistical analysis such as sequential sampling or a transformation for stabilizing the variance preparatory to an analysis of variance.

A second method of examining distribution patterns is that proposed by Lloyd (1966). Lloyd suggested that mean density is a misleading measure of how crowded animals are if the distribution is positively contagious. He suggested a measure of "mean crowding", \bar{X}^* , defined as the mean number per individual of other individuals in the same quadrat. The statistic, \bar{X}^* , is determined from the equation $\bar{X}^* = \bar{X} + \frac{\bar{X}}{\hat{k}}$, where \hat{k} = an estimate of the parameter, k , from the negative binomial distribution. Lloyd (1966) states:

one can interpret the 'mean crowding' of a patchily-distributed population as that mean density which the population could have, and be no more crowded on the average than it is now, if it had a random distribution.

Populations with higher \bar{X}^* values are more crowded than populations with lower values of \bar{X}^* . Another quantity of interest to Lloyd (1966) was the ratio of the "mean crowding" to the mean density, which he called "patchiness". This ratio $\frac{\bar{X}^*}{\bar{X}} = 1 + \frac{1}{\hat{k}}$ from the above equation. It is here that the negative binomial parameter, k , may acquire some ecological meaning. Lloyd (1966) explains,

The reciprocal of k is that proportion by which 'mean crowding' exceeds mean density. Adding one to the reciprocal of k purports to measure how many times as crowded an individual is, on the

average, as it would have to be if the same population had a random distribution.

Therefore, populations with a higher $\frac{s^2}{\bar{X}}$ ratio are more "patchy" than those with lower $\frac{s^2}{\bar{X}}$ values. Once it was determined that the population of Eohaustorius spp. had a contagious distribution, it was then necessary to ascertain how many samples of what quadrat size should be used to most efficiently estimate population parameters. Efficiency is defined as the relative number of samples required to give estimates of equal precision (Elliott, 1971). The problems of sampling a contagious distribution are unique, however, and Elliott (1971) states that:

Several workers (e.g., Beall, 1939; Finney 1944; Taylor, 1953) have investigated the effects of the size of the sampling unit on the efficiency of sampling, and they conclude that a small unit is more efficient than a larger one when the dispersion of a population is contagious. The advantages of a small sampling unit over a larger unit are: (1) more small units can be taken for the same amount of labor in dealing with the catch; (2) as a sample of many small units has more degrees of freedom than a sample of a few large units, the statistical error is reduced; and (3) since many small units cover a wider range of the habitat than a few large units, the catch of the small units is more representative. [...] It must also be remembered that with a small sampling unit, the sampling error at the edge of the unit is proportionally greater.

Lloyd (1966) feels that in deciding upon a sample size a number of different sizes should be used in a preliminary survey. The means and variances from the results of each sample size are compared and the best sample size to use is the one in which the variance to mean ratio approaches unity. He also stresses the importance of many smaller

size samples.

In the final analysis an investigator can use any of a number of different size sampling units provided that he takes a sufficient number of them to accurately estimate the population mean. His objective, however, should be to maximize the efficiency of his sampling program.

There are several methods of estimating the number of samples (n) required for a specified degree of precision (Steele and Torrie, 1960; Elliott, 1971). They require that estimates of the mean and variance be available and for the investigator to specify how large an error can be tolerated in the estimate of the population mean. Elliott (1971) has modified the general formula:

$$n = \frac{s^2}{D^2 \bar{X}^2}$$

where $D = \frac{\text{standard error}}{\text{arithmetic mean}}$ or $\frac{1}{\bar{X}} \frac{s^2}{n}$

which becomes $D = \frac{1}{X} \frac{\bar{X}}{n} + \frac{\bar{X}^2}{nk} = \frac{1}{nx} + \frac{1}{nk}$

and $n = \frac{1}{D^2} \left(\frac{1}{\bar{X}} + \frac{1}{k} \right)$. N.B. The numerical value of D is apparently set before entering it in this formula.

This formula requires that in addition to an estimate for \bar{X} , an estimate for k be available. When dealing with the results of series of several samples, Elliott (1971) recommends that a common k (k_c) be calculated to

use in estimating the number of samples required. A common k (k_c) can be calculated from the statistics x' and y' which are used to calculate a moment estimate of k where,

$$x' = \bar{X}^2 - \frac{s^2}{N}$$

$$y' = s^2 - \bar{X}$$

$$\text{and } k = \frac{x'}{y'} = \frac{\bar{X}^2 - \frac{s^2}{N}}{s^2 - \bar{X}}$$

After calculating y' and x' for each series of samples, k_c is equal to the slope of a straight line function expressing the average relationship of the two variables, i.e.,

$$\frac{1}{k_c} = \frac{\Sigma y'}{\Sigma x'} \quad \text{or} \quad k_c = \frac{\Sigma x'}{\Sigma y'}$$

In order to decide the number and size of samples to be used in this survey I began by supplementing Greenley's results from the four different quadrat sizes he used, 75 cm², 184 cm², 625 cm² and 1000 cm², with preliminary samples of two additional sizes, 38 cm² and 128 cm² and additional samples of the 75 cm² and 625 cm² size used by Greenley. I resampled with the last two quadrat sizes since initial examination of his data showed that these samples had variances that were closest to the mean in value. I then compared the results of all quadrat sizes by calculating mean, variance, variance to mean ratio and \hat{k} . In addition, I calculated a common k (k_c) for each group of samples and estimated the number of samples of that quadrat size which would be required (using a grand mean for each sample size) to reliably estimate the population

mean within a standard error equal to 20% of the mean.

The results indicated that while there was still variability within each sample size there would be fewer samples required if the sample size of 128 cm² were used. The results of Greenley's 625 cm² sample were somewhat enigmatic and were definitely atypical of the distribution usually found. The relatively small area he sampled on the beach (all 40 samples were contiguous and only covered about 2-1/2 m² of beach) undoubtedly biased his results.

Although the results of this comparison showed that the number of 128 cm² samples required would be four, I increased the number of samples to ten in order to be conservative in the error allowed, and also to take into consideration both the decreased density and resulting increase of patchiness at the boundaries of the E. brevicuspis distribution. The larger number of samples would also compensate for the fact that the area of stratum could change slightly from month to month depending on the profile of the beach. After three months of sampling an increase of density of E. brevicuspis in the middle of the beach prompted a re-evaluation of the choice of sample size and frequency. Recalculation indicated that the quadrat size could be decreased to 75 cm² and still achieve the same efficiency (i.e., number of samples required to reliably estimate the population statistics) achieved with the 128 cm² sample size.

The ratio of the variance (s^2) to the mean (\bar{X}) was calculated from the statistics of the ten replicate samples per strata to give an Index of Dispersion I where $I = \frac{s^2}{\bar{x}}$. This ratio will approximate unity

when the population is distributed randomly, i.e., there is agreement with a Poisson series. Values of this ratio less than 1.0 indicate a population tending towards uniform dispersion whereas values greater than 1.0 indicate a contagious or clumped dispersion.

The statistics, \bar{x} and \hat{k} , were then calculated for E. brevicuspis, E. washingtonianus at Lost Creek Beach and E. estuarius at Yaquina Bay. The statistic, k , was estimated using a moment estimate of k (Bliss and Fisher, 1953) where:

$$k = \hat{k} = \frac{\bar{x}^{-2}}{s^2 - \bar{x}} \text{ for samples where } n > 50, \text{ and}$$

$$k = \hat{k} = \frac{\bar{x}^{-2} - s^2}{s^2 - \bar{x}} \text{ for samples where } n < 50 \text{ (Elliott, 1971).}$$

2. Physical Factors

a. Lost Creek Beach

Samples for interstitial salinity and sediment analysis were taken on 18 August 1971 and 27 January 1972 at 50, 150, 250 and 450 feet seaward from the base of the sea cliff. These distances corresponded approximately to +13, +10, +9 and +7 feet above MLLW in August and +11.5, +7, +4 and +2 above MLLW in February. The differences in elevation were caused by erosion of sediment from the beach between August 1971 and January 1972.

Duplicate salinity samples were taken at each station from a depth of 8 cm in the sand. A pilot hole was first made in the sand with a pencil, a syringe tipped with an airstone inserted and about 30 ml of water withdrawn. These samples were titrated for chlorinity on an Aminco-Cotlove Chloride Titrator (American Instrument Co., Silver Springs, Maryland) and the results converted to salinity.

Triplicate sediment samples were taken from each station with a test tube corer inserted to a depth of 10 cm into the sand. Sediment analysis was conducted using a settling tube for the coarse fraction (> 62 μ diameter). The proportion of the fine fraction (< 62 μ diameter) was negligible (< 1%) in all sediment samples and was therefore not quantified. Overall size of the coarse fraction was expressed by the graphic mean (Carver, 1971) where:

$$M_z = \frac{(\phi \text{ at 16th percentile} + \phi \text{ at 50th percentile} + \phi \text{ at 84th percentile})}{3}$$

Sorting was expressed by the Inclusive Graphic Standard Deviation (σ_I) (Carver, 1971) where:

$$\sigma_I = \frac{\phi \text{ at 84th percentile} - \phi \text{ at 16th percentile}}{4} + \frac{\phi \text{ at 95th percentile} - \phi \text{ at 5th percentile}}{6.6}$$

b. Yaquina Bay

No interstitial salinity or sediment samples were taken at this transect because Thum (1972) had previously made a rather complete survey of the values and the variability of parameters that could be expected. Correlation between the distribution of E. estuarius and the physical factors at this location, was not attempted.

3. Methods for General Population Sampling

General collections were made monthly from February 1971 through February 1972, at both the Lost Creek Beach transect and the Yaquina Bay transect, using a stratified random sampling design. Prior to sampling, waterproof cards were made for each sampling unit to be collected. Upon each card was listed the date collected, stratum collected and the random coordinates for that specific sampling unit. For example, "21 VIII 71, 5,15 V" referred to a sampling unit taken in stratum V on August 21, 1971 at the random coordinates 5 and 15. The random coordinates were selected successively from a random numbers table. Only numbers 0 through 20 were used for coordinates.

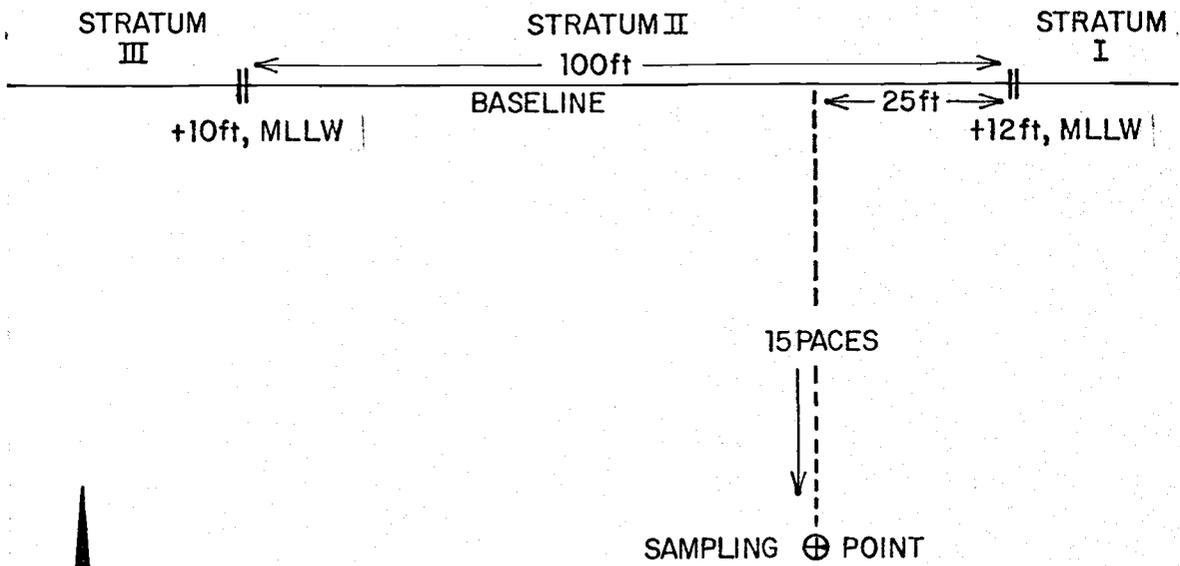
Upon arriving at the sampling location a vertical profile of the beach was taken using a hand level and stadia rod. Beach profiles for each month were started from the same point. At Lost Creek Beach a mark was gouged in the sea cliff; at the Yaquina Bay transect a stake was placed in the dunes above the high water line. A table of predicted tide times and heights (USCGS, 1970; 1971) was used to approximate the starting points of the survey. These points were adjusted by consulting

the tide recorder at the Oregon State University Marine Science Center on the days of the surveys. Since the sampling locations were near this tide gauge a reasonably accurate base point could be estimated and surveying begun from there. However, 13 minutes were subtracted from the times recorded at the Marine Science Center to estimate times of tides at Lost Creek Beach. Upon completing the survey, the beach profile was quickly sketched and strata for each increase of two feet delineated. A marked line was then laid out across the beach from the sea cliff to the water line and distances along the line, representing the bounds of each stratum, marked with a stake. Generally seven strata were delineated on Lost Creek Beach above MLLW. When possible, one stratum was sampled below MLLW. At the Yaquina Bay transect three strata were delineated.

Within each stratum 10 samples were collected, each sample being located by the pair of random coordinates referred to above. For each set of coordinates, the first referred to the proportion of the distance from the uppermost to lowermost boundaries of the stratum; the second number referred to the number of paces to proceed southward (westward at Yaquina Bay) to the precise sampling point. For example "5,15" indicated that the point lay 5/20 or 25% of the distance from the upper to the lower boundary of the stratum and 15 paces in a southerly direction (see Figure 4).

Upon reaching the sampling point the sampling unit was taken by pushing the sampling corer into the sand to a depth of 15 cm at the point where the pacer's right foot stopped. The core of sand was re-

Figure 4. Schematic of method of random sampling point location.



moved by placing a flat shovel under the can and lifting it up from the sand. The sand collected in the core was placed in a plastic bag with the tag identifying the sampling unit and sealed and placed next to the sampling location. An assistant collected the bagged samples for processing as described later. In cases when the sampling location was on exposed mudstone, no sample was taken and a zero was recorded. This occurred only on a few occasions, however, and in no instance were there any fewer than 5 cores taken in a stratum. On two occasions the lower strata on Lost Creek Beach could not be collected, once (March 1971) because the lower portion of the beach was denuded of sand; the second time (November 1971) because the tidal elevation was increased by a storm.

4. Special Studies

Several special field studies were conducted during the course of the year to examine certain aspects of Eohaustorius distribution. These included intensive studies of intraspecific dispersion; an examination of their vertical distribution within the sand; studies to ascertain the limits of each of the species locally both in and around rivers and offshore; and, an examination of their distribution within the water column during high tide.

On 14 July 1971 an intensive sampling program was conducted at Lost Creek Beach in the portion of the beach where E. washingtonianus and E. brevicuspis overlapped in their distribution. A 20 ft by 20 ft plot was laid out and within it 20 randomly located cores of 38 cm² area were

taken to a depth of 15 cm. The purpose of this sampling was to determine whether the two amphipod species were found closely together in an area inhabited by both. It was also designed to compare the degree of "patchiness" of the distribution of these species.

Studies to describe the distribution of both E. washingtonianus and E. brevicuspis within the sand were conducted along the Lost Creek Beach transect on 13 July and 18 August 1971 and on 30 January 1972. In each study stations were selected at intervals along the transect and duplicate 38 cm² samples taken to a depth of 16 cm. The core was removed from the corer and divided into several two cm transverse sections. Eohaustorius spp. found in each of these sections were returned to the laboratory where they were identified and counted. The studies in August and January were taken in conjunction with the transect taken for sediment and interstitial salinity and utilized the same stations.

On two occasions during August 1971 day and night plankton tows were made on a flooding tide over portions of the beach where Eohaustorius were known to inhabit. These tows were made to determine whether these amphipods swam into the water column in order to migrate up and down the beach with the waves. The plankton tows were made in the surf zone using an approximately one mm mesh bag attached to a pole. I was dressed in a wet suit with a weight belt for stability and made near-bottom tows of approximately 25 meters in length before the net was brought up and examined. On neither of the occasions were any Eohaustorius caught in the net, although both the isopod, Cirolana hartfordi and the amphipod, Dogielinotus loquax, normally found in the same part

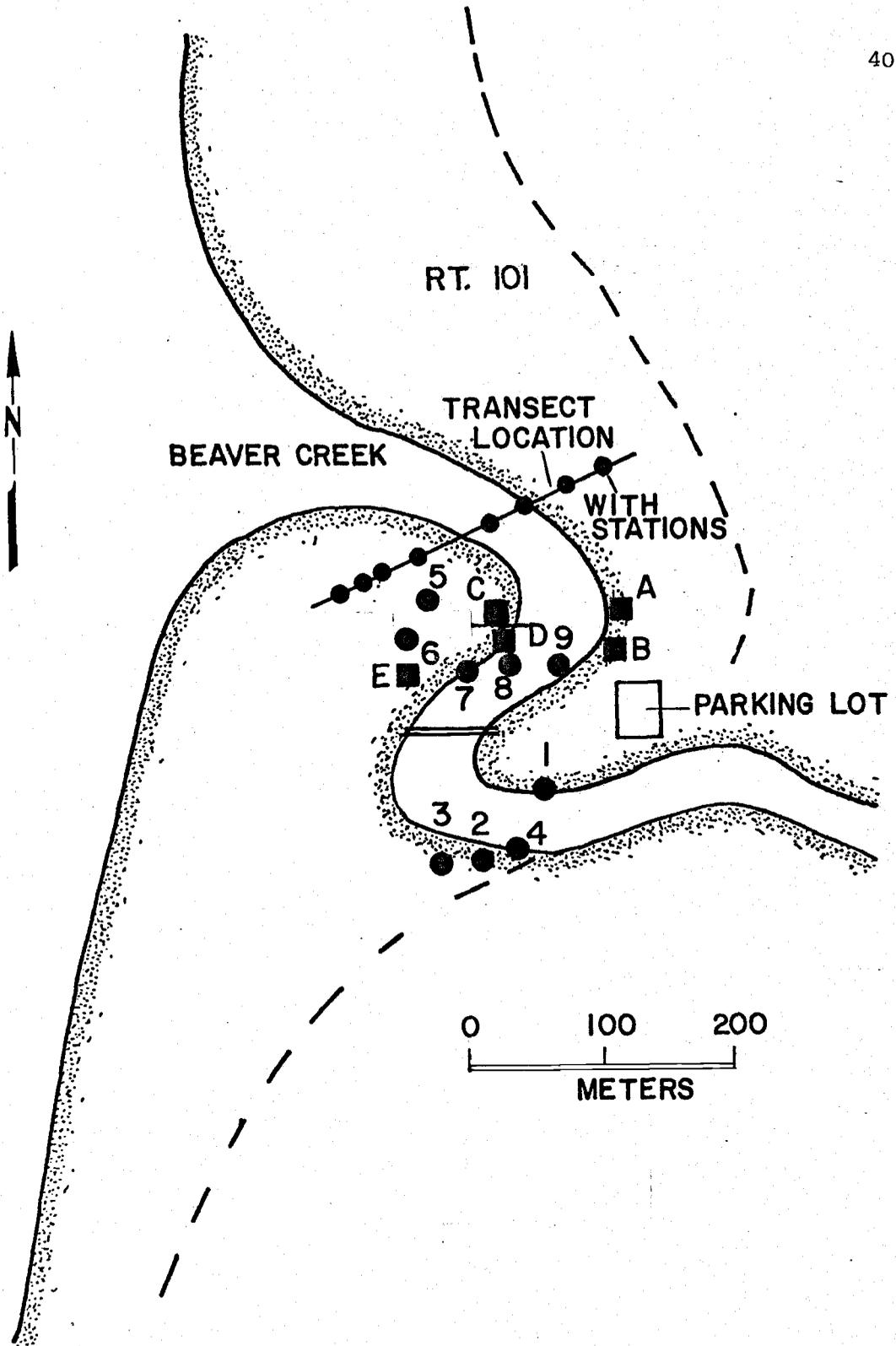
of the beach as Eohaustorius brevicuspis, were found in the sample. This type of sampling for Eohaustorius was therefore suspended.

In order to further define the local distributional limits of the four Eohaustorius spp., several collections were made in places other than the Yaquina Bay and Lost Creek Beach transects. On two occasions during July 1971 cruises were made on the R.V. Paiute up Yaquina Bay to marker 39, approximately 10 km from the Marine Science Center, (see Figure 3) and immediately offshore from Lost Creek Beach. On each cruise qualitative samples were collected using a small biological dredge fitted with an approximately one mm mesh net bag. The dredge was towed for approximately five minutes and then retrieved. The contents were sieved and examined for Eohaustorius spp. Any collected were returned to the laboratory for preservation and identification.

Another survey involved taking samples along the shore of Yaquina Bay from the site of the Yaquina Bay transect seaward toward the mouth of the Bay out to the end of South Jetty. Seven stations (see Figure 3) were sampled qualitatively using a shovel. Sediment was collected and sieved on location. Eohaustorius spp. retained in the sieve were placed in vials and returned to the laboratory for preservation and identification.

Surveys were conducted on 22 July 1971 and on 10 August 1971 at Beaver Creek (Figure 5). On 22 July 1971 a transect was established running from mean high water across the mouth of Beaver Creek and down to MLLW. Duplicate cores of 75 cm² area were taken at indicated intervals (see Figure 5) along this transect to a depth of 15 cm. On 6 July

Figure 5. Beaver Creek, Lincoln County, Oregon, showing sampling transect and stations.



1971 nine stations were qualitatively sampled with a shovel (Stations 1-9, Figure 5) in the vicinity of Beaver Creek above the high water line. On 10 August five additional stations (Stations A-E, Figure 5) were sampled similarly near the creek bed just above the high water line. Sediment and animals retained in each core were placed in a plastic bag and returned to the laboratory for sieving, identification and enumeration.

On 20 February 1972 another survey was conducted to sample additional estuaries along the central Oregon coast. During this survey the following locations were sampled: Alsea River, Big Creek, Yachats River and Beaver Creek (see Figure 1). In each location a qualitative sample was taken by passing several shovels full of sediment through a one mm sieve. All Eohaustorius spp. retained on the sieve were placed in a vial and returned to the laboratory for preservation and identification.

5. Associated Fauna

Only those animals collected in the monthly population samples were identified and enumerated. No additional samples were taken to describe the resident fauna although general observations revealed additional species normally missed by the sampling.

C. Laboratory Studies

1. Processing of Samples

Upon return to the laboratory the samples were placed, still in the plastic bags, into a cold room at an approximate temperature of 15°C until they could be processed the following day. The samples were sieved on a 1.00 mm mesh brass screen and all animals retained on the sieve were removed with forceps. The live specimens, both the amphipods and members of other taxa, were placed in a vial containing 5% formalin buffered with hexamethylanamine.

At a later time all the specimens collected in each sample were identified using a dissecting microscope and enumerated. During identification all Eohaustorius spp. were placed over a scaled grid that was attached to the bottom of the counting chamber, identified to species and measured. The lengths of the animals were measured to the nearest 0.5 mm, from the tip of the rostrum to the end of the telson, while the animal was extended uncurled on its back.

Since haustoriid amphipods are not very dimorphic sexually, the sex of each Eohaustorius was determined by examination for testicular papillae in males or for oostegites (brood plates) in females. Female Eohaustorius were categorized into four stages depending upon the development of their oostegites (Crocker, 1966; Dexter, 1967). Stage I females were characterized by having oostegites as buds smaller than their branchial plates. Stage II females had oostegites larger than their branchial plates. Stage III females had oostegites larger than their branchial plates but lacked marginal setae. Stage IV females had

fully developed oostegites with marginal setae and were considered to be mature. Those females bearing young were categorized as gravid. The eggs in the marsupium of each gravid female were counted to determine fecundity. Since eggs were often found free in the sample vial, the marsupium of each gravid female was examined closely and notes made as to whether it appeared full or could have been missing some eggs. Only those females whose marsupia appeared to retain their full complement of eggs were used in fecundity estimates. Mature males were defined as males with complete setation, fully developed testicular papillae, and 3.5 mm or larger.

A total of 18,488 Eohaustorius spp. from the monthly population sampling was processed in this manner. Approximately 4000 additional Eohaustorius spp. from other special surveys were similarly examined. From this information, the following statistics were calculated for each species:

- 1) mean density per square meter for each stratum and month for all developmental stages combined;
- 2) mean density per square meter for each stratum and month for mature females (Stage III and gravid);
- 3) mean density per square meter for each stratum and month for mature males;
- 4) mean fecundity by size of female by month;
- 5) total fecundity per square meter for each stratum and month;
- 6) size-frequency composition of the population by month;

- 7) percent gravid females of total females by month; and,
- 8) ratio of males to females for each stratum and month.

2. Laboratory Maintenance

An experiment was conducted to determine the laboratory conditions best suited to keep these animals in healthy condition for accurate physiological tolerance measurements. In this experiment individuals of E. estuarius and E. brevicuspis were brought in from the field and placed in several fingerbowls of the size later used for tolerance measurements.

The fingerbowls were kept in the cold room at approximately 15°C. Of the four fingerbowls two were filled with a half an inch of beach sand and an inch of water. One of these was aerated. The other two fingerbowls were filled only with water. One of these latter two bowls was also aerated. The water used in these experiments was collected at the same location as were the animals. The beach sand was also collected with the animals. Aeration was provided by airstones at the ends of lines supplied from the central air system in the laboratory. All experimental conditions were tested in duplicate with ten to 20 animals in each fingerbowl. During the test the animals were examined periodically and any mortality noted. Mortality was determined by prodding moribund animals with a blunt probe. Those that showed no reaction were removed from the dish with a wide bore pipette, placed in a cooled depression slide and examined under a dissecting microscope. Those displaying no heartbeat were removed from the experiment. The

experiment was terminated at the end of 186 hours. The results indicated that there was very little mortality in any of the dishes until about 60 hours. After that the animals in the dishes with sand survived better, but the amphipods were harder to find in the dishes with sand since they could burrow in it. Aeration did not noticeably increase survival.

On the basis of this experiment sand was not used in the dishes in the physiological tolerance experiment. Not only might sand add a confounding effect to a salinity tolerance experiment but it required sieving the sand to find the animals, exposing them to additional handling. The final experiments were run for only 48 hours since it appeared that all the amphipods stayed relatively healthy for that period of time. A preliminary salinity tolerance experiment was conducted to ensure that my suppositions were correct. Ten individuals of E. brevicuspis were placed into each of four fingerbowls previously filled with water of 100%, 70% and 30% seawater and in fresh dechlorinated water. The animals were maintained at 15°C and examined daily for a week. Mortality was assessed as before.

3. Salinity-Temperature Tolerance Experiment

The tolerance of Eohaustorius estuarius, E. washingtonianus and E. brevicuspis to 20 different combinations of temperature and salinity was tested. The design included four temperatures: 5, 11, 15 and 21°C and five salinities: 0, 6, 14, 23 and 28 ‰. The seawater dilutions used were made up from seawater collected at Lost Creek Beach

(28 ‰) and variously diluted with dechlorinated water to yield the intermediate salinities. Pure, dechlorinated water was used for the 0 ‰. Salinities were verified with a hydrometer. Fingerbowls with approximately 150 ml of water at one of the five salinities were placed into each of four temperature control rooms.

The amphipods were collected from locations where it had been previously established that only one of the species was found. They were brought back to the laboratory and kept in large glass containers holding sand and water from the place where the amphipods were collected. After two days of holding at 12°C, which approximated the environmental seawater temperature at that time, they were sieved from the sand and placed in the experimental containers. The three species were tested separately. Ten amphipods of each species were placed into each temperature and salinity combination and the experiment was duplicated. The amphipods were examined and mortality recorded at 3, 6, 9, 12, 24 and 48 hours of exposure. Criteria for mortality was the same as discussed previously. After 48 hours each amphipod was examined to verify species and determine sex.

The percent survival at each of the six intervals for all combinations of temperature and salinity was fitted by multiple regression analysis to the quadratic model of Box and Youle (1955) where:

$$Y = b_0 + b_1X_1 + b_2X_2 + b_{11}X_1^2 + b_{22}X_2^2 + b_{12}X_1X_2$$

where y = percent survival

X_1 = temperature (°C)

x_2 = salinity (‰)

b_0 = constant

b_1 = linear effects of temperature

b_2 = linear effects of salinity

b_{11} = quadratic effects of temperature

b_{22} = quadratic effects of salinity

b_{12} = interaction effect of temperature and salinity

The results of equations were used to generate response surface estimations of percent survival and 10% contour intervals of survival were plotted. Regression coefficients were tested for significance. Survival of each species over the 48 hour period was plotted for each experimental temperature and salinity.

4. Laboratory Feeding

All species were successfully kept in the laboratory for as long as three months. Although no effort was made to control their diet during these periods, beach sand was periodically changed in the containers. Animals were periodically examined under the dissecting microscope to ascertain whether they were feeding. On one occasion several animals were maintained in a container without sand for two weeks and periodically fed a monoculture of the phytoflagellate, Isocrysis sp. provided by Dr. Cristopher Bayne. The guts of these animals were examined microscopically at the end of the two weeks to determine whether they had fed on the algae.

D. Zoogeographical Study

Since the literature on the genus Eohaustorius is rather limited, it was necessary to examine other collections in order to describe the wider geographical distribution of the Oregon species and to elucidate their zoogeographical relationship to other described species. Specimens in the United States National Museum were kindly sent to me by Dr. J. L. Barnard. These specimens were from collections in Puget Sound, Washington, from Oregon, and from several locations along the California coast including four samples from "Velero" cruises in 1956 and 1959 taken in 30-40 meters of water off Point Conception, California and further south. Dr. E. L. Bousfield, National Museum of Natural Sciences, Ottawa, provided Eohaustorius specimens collected from Prince William Sound, Alaska to Southern Oregon during 1955 and 1970 (e.g. Bousfield, 1967; 1963; 1968). Mr. Peter Slattery provided samples collected near the Moss Landing Marine Laboratories in Moss Landing, California and Dr. C. D. Levings, Pacific Environmental Institute, West Vancouver, British Columbia, provided samples collected from the Fraser River estuary, British Columbia. All specimens were examined using the same morphological criteria previously used to describe the Oregon species (Bosworth, 1973). Notes were made on the tidal elevation, salinity and temperature at which they were collected. The distributions of the Eohaustorius species found in Oregon were then plotted on a map.

III. OBSERVATIONS AND RESULTS

A. Physical Factors

1. Lost Creek Beach

Measurements of interstitial salinity (Table I) during August 1971 showed that interstitial water in the upper portion (+10 ft MLLW) of the beach was less saline than that of the rest of the beach, where salinity was near that of the surf. At the uppermost station (+12 ft MLLW) the sand was dry and no water could be extracted from the sediment. During the survey in February 1972 the uppermost station (+11.5 ft MLLW) had the lowest interstitial salinity on the beach (Table I). In both surveys the lowest interstitial salinities coincided with the area where the sand appeared saturated, apparently the intersection of the water table with the beach surface.

The average grain size and degree of sorting of three replicate sediment samples taken from each station is shown in Table I. During both sampling periods and at all stations the substrate was characterized as very well-sorted sand with average diameter between 1 and 2 ϕ .

Figure 6 shows the profile of the transect at Lost Creek Beach at successive sampling intervals. It shows that the beach had a relatively even slope when measured on February 6, 1971. During the latter part of February several severe storms washed much of the sand from the lower portion of the beach and there was only sufficient sand on the upper portion (+10 - +14 ft MLLW) of the beach to provide a suitable

TABLE I. SALINITY AND SEDIMENT CHARACTERISTICS AT LOST CREEK BEACH,
AUGUST 1971 AND FEBRUARY 1972.

AUGUST 1971

FT FROM CLIFF	FT ABOVE MLLW	SALINITY ($^{\circ}/\infty$)	GRAIN SIZE ($Mz_1 \phi$)	SORTING ($\sigma_I \phi$)
50'	13	No sample	1.83	.28
150'	10	29.8	1.73	.27
250'	9	32.6	1.74	.25
400'	7	33.0	1.75	.27
Surface Water		33.1		

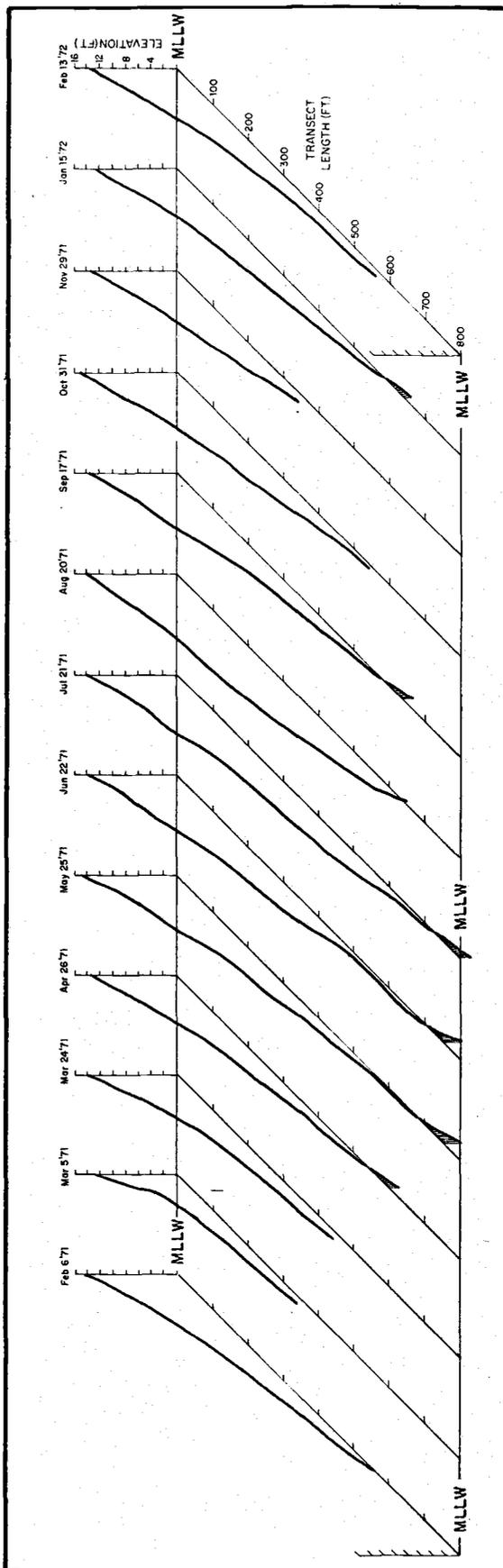
FEBRUARY 1972

FT FROM CLIFF	FT ABOVE MLLW	SALINITY ($^{\circ}/\infty$)	GRAIN SIZE ($Mz_1 \phi$)	SORTING ($\sigma_I \phi$)
50'	11.5	24.2	1.96	.24
150'	7	28.8	1.77	.28
250'	4	28.4	1.81	.24
400'	2	28.5	1.74	.23
Surface Water		28.5		

$\sigma < .35 \phi$ = very well sorted distribution

$Mz_1 \phi = 1-2$ = medium sized sand

Figure 6. Vertical profile of Lost Creek Beach, February 1971 - February 1972.



habitat for burrowing amphipods. A profile was not taken at that time but several samples collected in the upper portion showed that E. brevicuspis was present but at relatively low densities. Sand was gradually deposited back on the beach and on March 5, 1971 the beach profile measured again prior to sampling. This profile showed that while the depth of the sand was increasing on the middle beach the profile was degraded from what it had been in early February. Sand was added continually and on April 26, 1971 the shape of the beach was similar to what it had been prior to the storms in late February. Net deposition of sand on the beach continued through August 1971. During the late spring and summer months the beach profile steepened and there was some evidence of a berm developing at about +10 ft MLLW in June and July. In July the tidal debris line was at approximately +10.5 ft MLLW and the sand was dry above it. As more sand was deposited the berm became more apparent in the beach profile. From September 1971 through February 1972 there was net erosion on the beach which was first evident on the lower portion of the beach. By February 1972 the net erosion from more severe storms had affected the upper portion of the beach and the profile appeared similar to what had been measured the previous February.

2. Yaquina Bay Station

Thum (1972) documented interstitial salinity and sediment characteristics at this location on an adjoining transect during several of the months (February through May 1971) of this study.

Profiles of my transect were taken starting in July 1971 after Thum had completed his work. The results of these beach profiles are compared to Thum's June 1971 profile in Figure 7. The results showed that there was little net deposition or erosion on the beach. The little that did occur was greatest in the upper and lower portion of the beach.

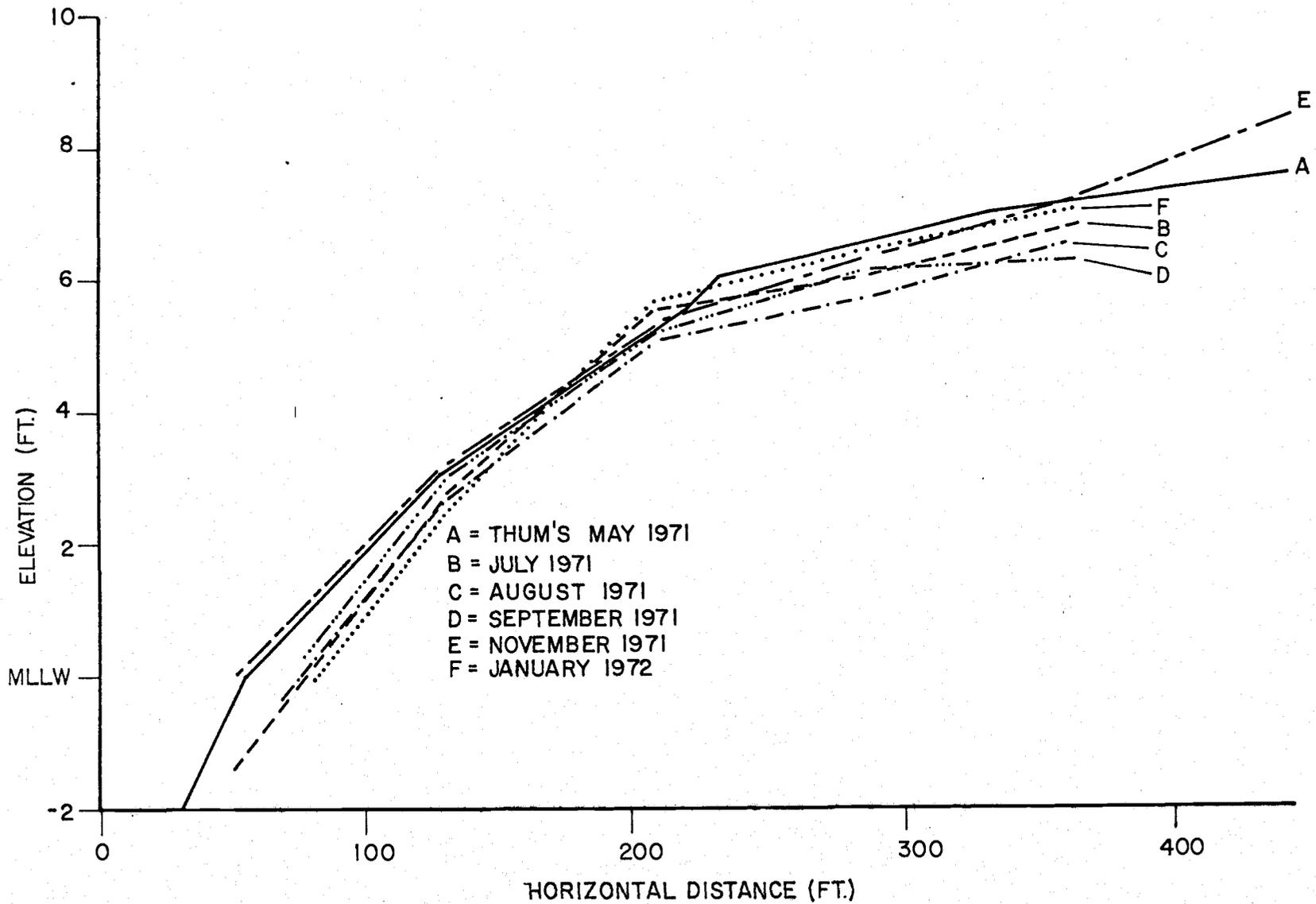
B. Intraspecific Dispersion

Values for Index of Dispersion, I , are tabulated for E. brevicuspis (Appendix 1, Table I) and E. washingtonianus (Appendix 1, Table II), at Lost Creek Beach and E. estuarius (Appendix I, Table III) at Yaquina Bay. Significance of differences from unity were evaluated by chi square where $I_{(n-1)} = \chi^2$ with $(n-1)$ degrees of freedom (Elliott, 1971). The results indicated that in the majority of cases all three Eohaustorius spp. exhibited a contagious dispersion.

Estimates of k for E. brevicuspis (Appendix 1, Table IV) ranged from 0.11 to 46.22. Generally highest values for k indicating least contagion were found coincident with the center of E. brevicuspis distribution (Appendix 1, Table V). Lowest values of k were generally found at the highest and lowest ends of the distribution of E. brevicuspis where density was lowest and some of the replicate sampling units were empty.

Estimates of k for E. washingtonianus (Appendix 1, Table VI) ranged from 0.11 to 1.0. Negative values for k may occur when the mean exceeds the variance. In these instances the distribution does not fit

Figure 7. Vertical profile of transect at Yaquina Bay sampling area.



the negative binomial and the values are, therefore, meaningless and were included just for reference. Again, there was some tendency for the value of k to increase with increasing density (Appendix 1, Table VII).

Estimates of k for E. estuarius (Appendix 1, Table VIII) ranged from 0.19 to 3.66. There is some correspondence between highest k values and highest densities (Appendix 1, Table IX) although the relationship is not consistent.

The parameters "mean crowding" (\bar{X}^*) and "patchiness" ($\frac{\bar{X}^*}{\bar{X}}$), as suggested by Lloyd (1966), were calculated for all three Eohaustorius spp. The variability in these parameters for all populations is shown in Appendix 1, Tables X-XV. One can see that the most crowded animals are not necessarily those found where the density was greatest (see Appendix 1, Tables V, VII, IX). There is a general trend for all three species to be more "patchy" at the ends of their distribution, implying that there is some active behavioral mechanism leading to their positive contagion.

The results of the study on 14 July 1971 when cores of 38 cm² were taken in a 20 ft x 20 ft area with E. brevicuspis and E. washingtonianus both present are shown in Figure 8 and Table II. E. washingtonianus exhibits a more contagious distribution than E. brevicuspis. Both species were found in all but three of the 20 samples. In all cases but one, E. brevicuspis was more abundant.

Figure 8. Frequency distribution of Eohaustorius brevicuspis and E. washingtonianus in area of overlapping distribution.

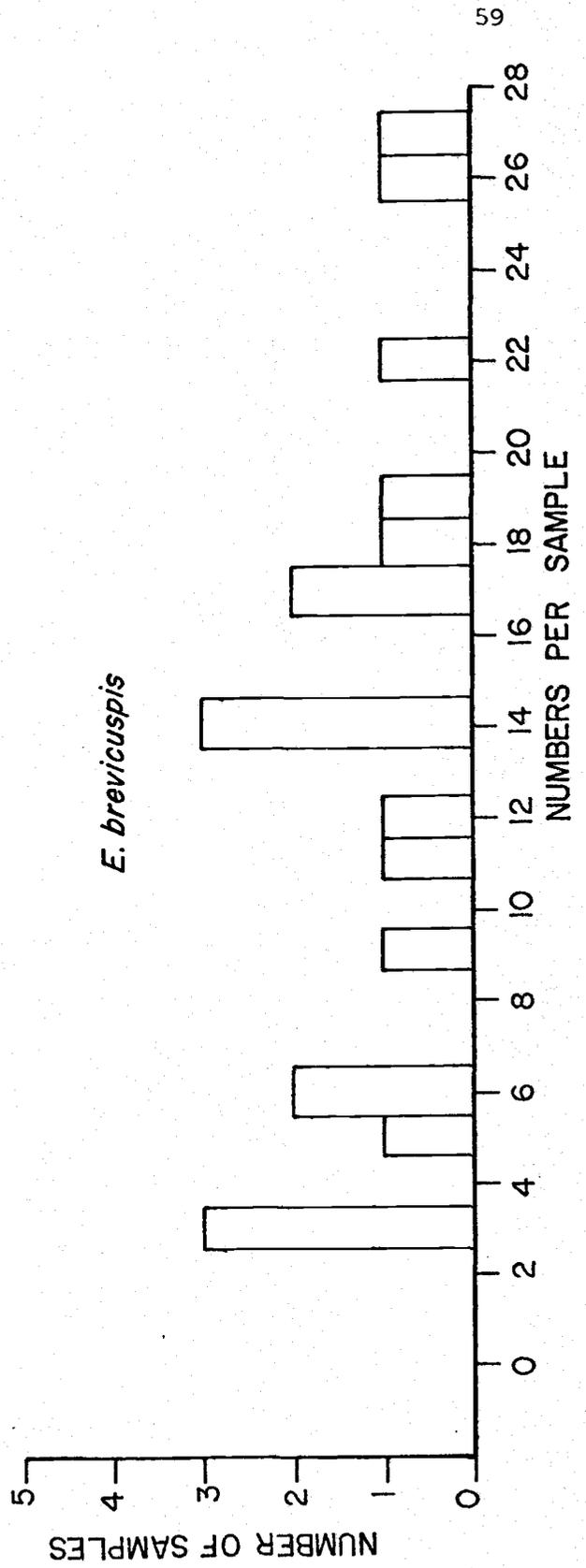
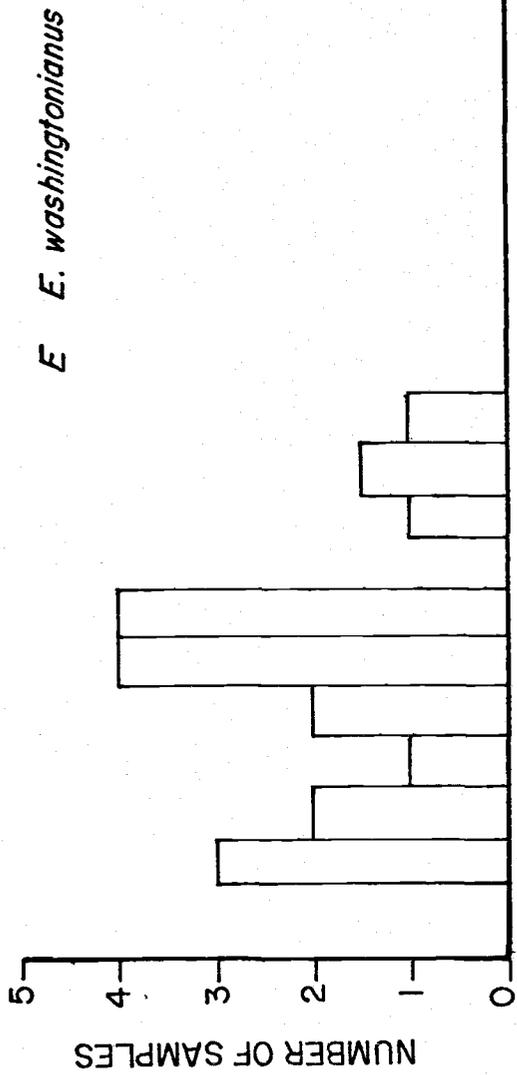


TABLE II. RESULTS OF SAMPLES TAKEN IN AREA WHERE E. WASHINGTONIANUS AND E. BREVICUSPIS OVERLAPPED IN THEIR DISTRIBUTION.

NUMBER OF INDIVIDUALS PER SAMPLE		
<u>SAMPLE NUMBER</u>	<u>E. BREVICUSPIS</u>	<u>E. WASHINGTONIANUS</u>
1	17	3
2	19	5
3	6	4
4	18	2
5	3	1
6	14	4
7	17	9
8	6	0
9	13	8
10	14	5
11	26	5
12	27	8
13	3	0
14	3	0
15	5	7
16	22	5
17	9	4
18	14	3
19	11	1
20	12	4
TOTAL	259	78
	$\bar{x} = 12.95$	$\bar{x} = 3.75$
	$s^2 = 53.94$	$s^2 = 21.38$
	$\hat{k} = 4.03$	$\hat{k} = .74$
	$\frac{\bar{X}^*}{\bar{X}} = 1 + \frac{1}{\hat{k}} = 1.25$	$\frac{\bar{X}^*}{\bar{X}} = 1 + \frac{1}{\hat{k}} = 2.35$

C. Interspecific Distribution

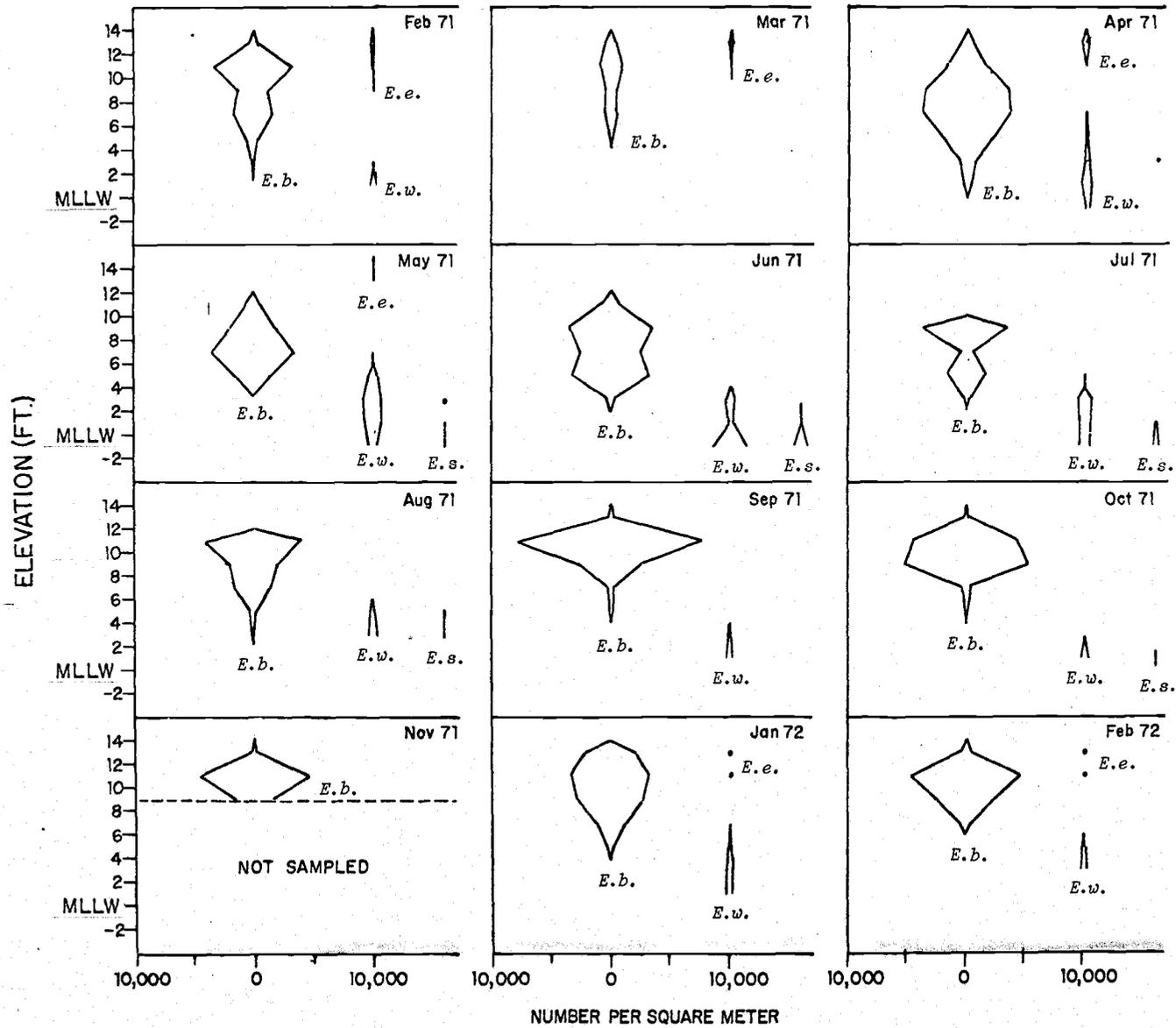
1. Vertical Distribution in the Intertidal Zone

The zonation or vertical intertidal range of Eohaustorius spp. on the Lost Creek Beach transect throughout the study period is shown in Figure 9. Eohaustorius brevicuspis was generally found throughout the intertidal area from +4 to +12 ft above MLLW. Highest densities (up to 15,000/m²) were found in the mid intertidal from +6 to +11 ft. The lowest abundance of all four species was found in March, approximately a month after sands had been eroded from the beach in a storm. By April the abundance had surpassed that found prior to the February storm. During April E. brevicuspis was found down to MLLW, lower on the beach than any other time of the year. From May through August no E. brevicuspis were found above +12 ft, and in July none were found above +10 ft. Sand above these elevations was apparently not regularly immersed during those months as this was above the highest reach of the small summer waves and was dry. During June there was a bimodality in their distribution which became more pronounced in July. In the lower beach the distribution of E. brevicuspis overlapped to varying degrees with the upper portion of the distribution of E. washingtonianus.

Eohaustorius washingtonianus was distributed from the subtidal up to about +6 ft above MLLW in the lower intertidal. Between +4 and +6 ft both E. washintonianus and E. brevicuspis were occasionally found together, particularly during late spring and summer. Usually, however, the density of E. brevicuspis was relatively low in these regions of

Figure 9. Zonation of Eohaustorius spp. at Lost Creek Beach.
February 1971 - February 1972.

E.b. = E. brevicuspis
E.w. = E. washingtonianus
E.s. = E. sawyeri
E.e. = E. estuarius



overlap. Highest abundances (up to $2600/m^2$) of E. washingtonianus were found in the late spring and summer although they were always much less abundant than E. brevicuspis. The distribution of E. washingtonianus also overlapped with the upper range of E. sawyeri.

Eohaustorius sawyeri was only collected occasionally and was found generally around MLLW. It is apparently an obligate subtidal species. Abundances only reached about $240/m^2$.

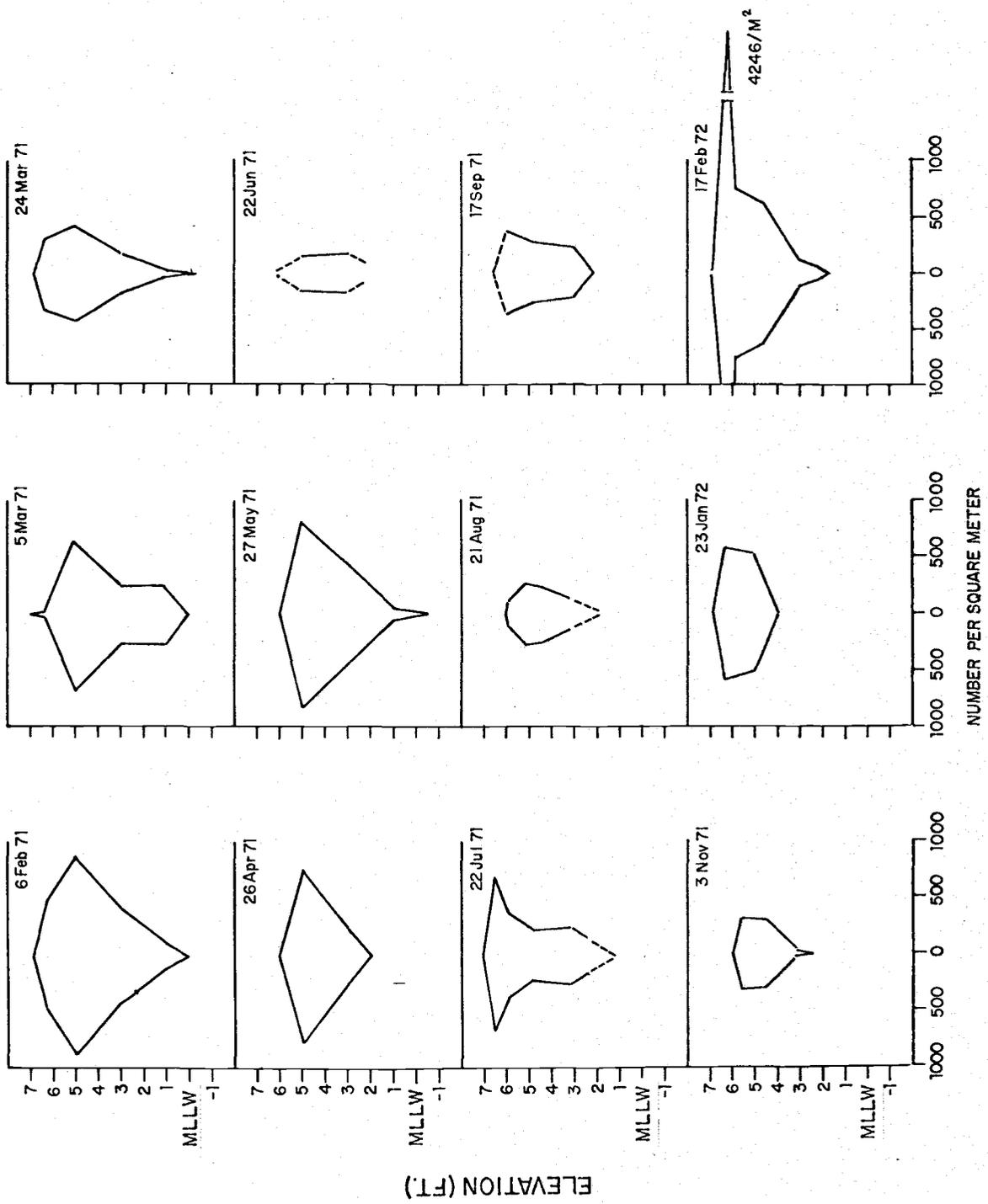
Eohaustorius estuarius was collected in the upper intertidal area only during the winter and early spring. They were found in low numbers, usually one or two in all the samples taken from +10 to +14 ft.

The zonation of E. estuarius at the Yaquina Bay study area is shown in Figure 10. It was usually found from about +2 to +6 ft but occasionally was found up to +7 ft and down to below MLLW. Highest abundancies were found from +4 to +6 ft during February of 1971 and 1972. Densities reached about $4200/m^2$ in February 1972. Abundance was lowest during the summer and fall.

2. Vertical Distribution Within the Sediment

The results of four studies of vertical distribution of Eohaustorius spp. within the sand at Lost Creek Beach are shown in Appendix 2, Figures 1, 2, 3 and 4. Except for one occasion during the July 1971 sampling when E. brevicuspis was found exclusively on the surface at the +8 ft station (Appendix 2, Figure 1) the majority of individuals of both species were found between 4 and 12 cm deep. The samples taken at +8 ft in July were within a zone of saturated sand and

Figure 10. Zonation of Eohaustorius estuarius at Yaquina Bay sampling area, February 1971 - February 1972.



large numbers of Eohaustorius spp. were observed crawling on the wet sand. Results of sampling on a very cold day (27 January 1972) did not reveal any tendency for the amphipods to be deeper in the sand at low tide on cold days (Figure 3).

3. Geographical Distribution of Eohaustorius spp.

The distribution of E. brevicuspis, E. washingtonianus, E. estuarius and E. sawyeri is presented in Appendix 2, Figures 5, 6, 7 and 8, respectively. Data from Oregon are primarily from Greenley (1969) and this study although some records are from the collections in the Canadian and U. S. National Museums. Data outside Oregon are chiefly from Bousfield's collections north of Oregon and from collections south of Oregon now in the U. S. National Museum. These data are supplemented by several samples contributed by biologists mentioned previously.

Eohaustorius washingtonianus is found north to Prince William Sound, Alaska. It is found south in Oregon to at least Coos Bay. It appears to be the most abundant species of Eohaustorius in the Puget Sound, Washington area where the species was originally found by Thorsteinson (1941). There is some indication from collecting records that the vertical distribution of this species on sandy beaches becomes lower the farther south it is found (Bousfield, unpublished).

Eohaustorius brevicuspis is the dominant Eohaustorius spp. in the mid intertidal in Oregon and Washington. It was also found intertidally in samples from Tomales Bay, California. Presumably it also lives intertidally throughout northern California. Northward its dis-

tribution apparently ends in northern Washington at the entrance to Puget Sound. It was not found in any of several samples taken from within Puget Sound or on Vancouver Island, British Columbia.

Eohaustorius sawyeri was found in samples from as far south as Moss Landing, California, where it was found in the shallow subtidal (-20 meters) to as far north as the southwest shores of Vancouver Island, British Columbia. It was generally collected in the lower intertidal in the Puget Sound area but appears to be found further subtidally in the southern extent of its range.

Eohaustorius estuarius is found as far south as Moss Landing, California, north to the Queen Charlotte Islands and Hecate Straits, on the central British Columbia coast. It apparently is found in the same habitats throughout its range, i.e., large estuaries and at the mouths of small freshwater streams draining into the ocean. It is found intertidally throughout its range and subtidally in and near mouths of estuaries in Oregon and California. It is probably also found subtidally in the northern parts of its range.

Insufficient samples are available from most parts of the eastern Pacific coastline other than Oregon to detail the distributional relationships among these four Eohaustorius spp. The few locations from which both intertidal and subtidal collections are available are characterized by zonation differences similar to those found at Lost Creek Beach.

At least three other species of Eohaustorius were found in the collections examined. Of these E. sencillus was found subtidally in

about 30 meters of water off Newport, Oregon (Barnard, 1971). It was also found in subtidal collections from other locations along the California coast (Barnard, 1957). Eohaustorius sp. (the form described as E. washingtonianus by Barnard, 1957) was found in subtidal collections from southern California. Another undescribed species was found in some intertidal collections from central British Columbia. The zoogeographic relationships between these species and those found in Oregon are complex and can only be resolved with further collections.

I made other collections at several locations around Newport, Oregon to determine the distributional boundaries of the four Oregon species I was studying.

Only one specimen of E. estuarius was collected in dredge samples from various localities in the Yaquina estuary in January 1971. During July 1971, however, several specimens were collected in several locations in the estuary. Dr. W. Scott Gray (personal communication) also reported the presence of Eohaustorius sp. at several locations in the Yaquina estuary. Although these were not examined, it is assumed they were E. estuarius. No Eohaustorius were collected in any of the dredge samples taken directly offshore of Lost Creek Beach.

Several samples were taken at intertidal stations along the shore of Yaquina Bay and in some small brackish streams behind Oregon State University Marine Science Center. Specimens of E. estuarius were collected at all stations except Station 3 (see Figure 3). Station 3 was characterized by muddy sand substrate. The reducing layer was within a 5 cm of the sand surface. Specimens of E. brevicuspis were

collected along with E. estuarius at Station 7. The ratio of the two species was approximately four E. estuarius to one E. brevicuspis.

Results of samples taken at Beaver Creek, Oregon are shown in Appendix 2, Figure 9. Specimens collected at all sampling locations below mean high-water were all E. brevicuspis, even those collected in the creek bed. Specimens collected in and along the banks of Beaver Creek above the high water mark were all E. estuarius. Stations sampled within 20 ft of Beaver Creek near the high water mark contained both E. brevicuspis and E. estuarius. Densities of both species ranged from several hundred to about 5500 individuals per square meter.

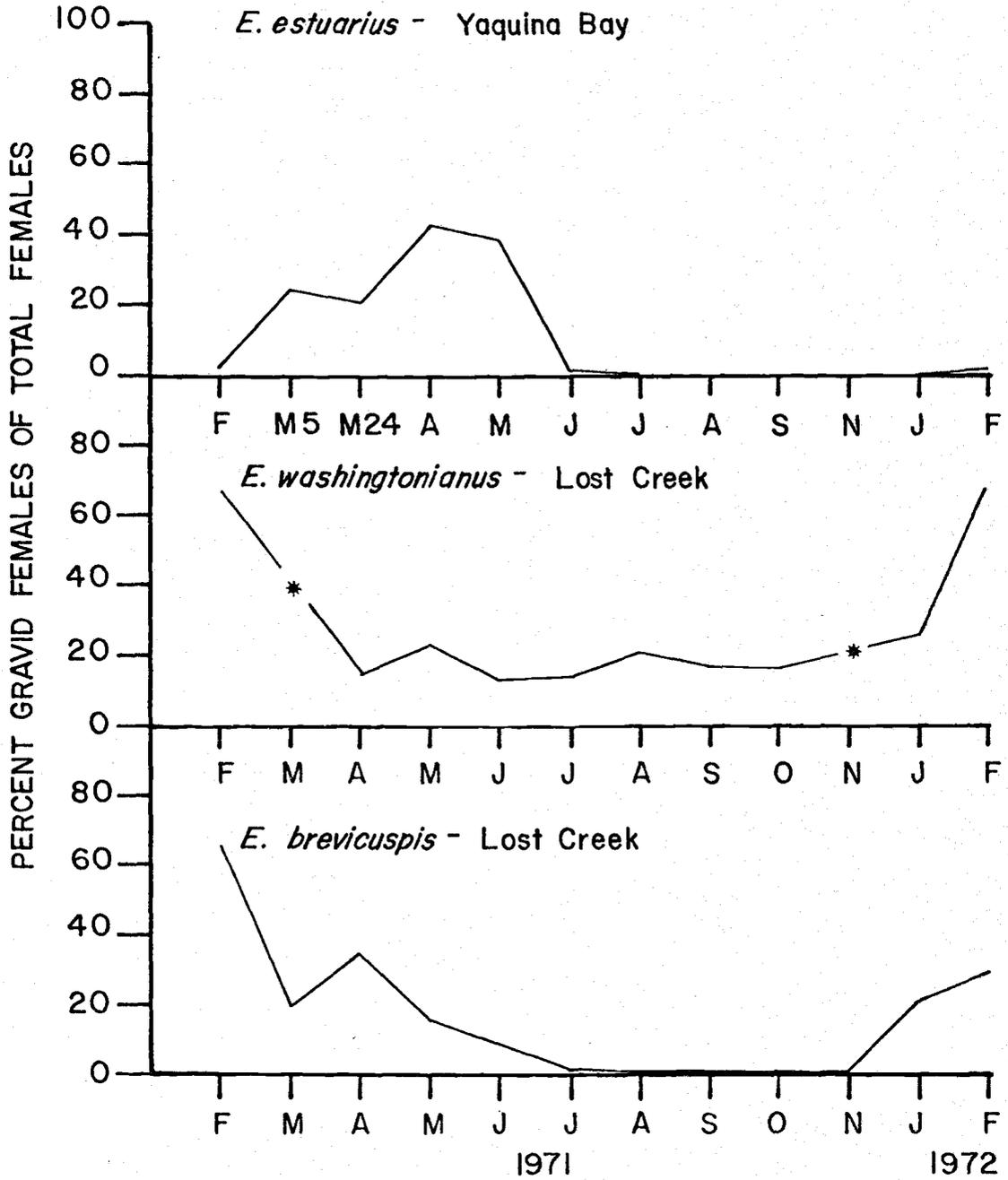
Samples were collected in Big Creek, Alsea River and Yachats River (Figure 1) in February 1972. E. estuarius was abundant at all locations. No other Eohaustorius species were collected at these locations.

D. Population Biology

1. Reproductive Cycle

The nature of the reproductive cycle of E. estuarius, E. washingtonianus and E. brevicuspis is given in Figure 11 which shows the seasonal frequency of gravid females. Too few E. sawyeri were found to construct a similar graph. Gravid females of E. estuarius in Yaquina Bay were found from February through July with maximum numbers in April. There was evidence (Appendix 2, Figure 10), however, that populations in different locations may breed at different times. Gravid females of E. washingtonianus were found every month, but the peak percentage was

Figure 11. Percent of gravid females of total females of Eohaustorius spp. by sampling period.



* = Not Sampled

found in February 1971. The percentage then dropped to 10-20% throughout the year until the following February when they again reached a peak of about 67%. Gravid females of E. brevicuspis were primarily found from January through June. Starting with a peak of about 66% in February 1971 the percent of gravid females steadily declined to about 1% in July, a level that stayed fairly constant until January 1972.

The distribution of gravid E. brevicuspis and E. washingtonianus females on Lost Creek Beach is shown in Appendix 1, Table IV. During the breeding peak of E. brevicuspis there is a trend ($p \approx .05$, Kendall's coefficient of concordance, Tate and Clelland, 1957) for a higher percentage of gravid females at the lower strata. At the same time these data show that there are fewer total females inhabiting these lower strata. There were no consistent trends in the distribution of gravid E. washingtonianus females.

2. Size and Growth

Appendix 2, Figures 11-13 show the percentage length composition for E. brevicuspis, E. washingtonianus and E. estuarius, respectively. These figures include animals of both sexes and all sizes collected. Data for E. brevicuspis and E. washingtonianus are from samples collected at Lost Creek Beach. Data for E. estuarius are from the samples collected at Yaquina Bay. In interpreting these graphs one should bear in mind that these amphipods are generally 2 mm long before they are broad enough to be retained on the 1.00 mm sieve that was used. Following the peak of reproductive activity of E. brevicuspis in Febru-

ary through May when the percentage of small amphipods (< 3 mm) is around 20 to 25%, an increase in recruitment to the 2 and 2.5 mm class begins in July when it reached 31%. This increase continued until about October when these classes made up about 57% of the population. The percentage of amphipods in these size classes then decreased to around 37% in January and February 1972. Because breeding activity ceases in June, the percentage of the larger classes decreases rapidly from August through October. The number of mature males decreases more rapidly than the females. This suggests that individuals breed for a short period and then die.

It is difficult to estimate growth rates from these data. Since the highest percentage of 2 and 2.5 mm amphipods is in October, it would seem that E. brevicuspis requires approximately seven to eight months to reach a 2.5 mm size. Growth appeared to be more rapid just prior to spawning again in January 1972. The 3.5 mm class seems to be consistently less abundant than the 3 and 4 mm class. This may be adventitious, an artifact of rounding off while measuring or may represent a size when growth is fastest.

The reproductive peak of E. washingtonianus in February is followed by a rapid decrease in larger individuals during the following three months. The percentage of smaller amphipods (< 3 mm) reaches a maximum in June, four months later, suggesting faster growth in this species than in E. brevicuspis. Gravid females smaller than 4 mm were not found, in contrast to a large number of gravid females smaller than 4 mm in E. brevicuspis. Individuals of E. washingtonianus tended to

reach a larger size, in general, than those of E. brevicuspis. Breeding continued throughout the year and smaller individuals (< 3 mm) were recruited to the population at a fairly constant rate. Interpretation of the data for the last four months of sampling was difficult because the small numbers of individuals collected may have introduced greater variability into the results.

The reproductive peak of E. estuarius in the spring was followed by a rapid and pronounced recruitment into the 2 and 2.5 mm classes in July. This coincided with a rapid decrease in the larger size classes. Recruitment continued at a fairly constant rate for the rest of the study period. Since no further reproduction in the intertidal collections was observed, this was puzzling. Intertidal collections of E. estuarius in other estuaries along the coast showed that there was a large percentage of gravid females present during February at Alsea River and Big Creek but that Yachats River, Beaver Creek and Yaquina Bay had very few or no gravid females (Appendix 2, Figure 10). Exchange between the intertidal and subtidal populations of this species has probably confounded the results of length-frequency data gathered for the intertidal population.

3. Sex Ratio

The ratio of males to females for all strata at each station is shown by sampling period in Appendix 1, Table XVII. Sex ratios for E. brevicuspis ranged from 1:1.03 to 1:2.12. All monthly totals except October were all significantly different ($p \leq .01$, comparison to a

binomial distribution) from a 1:1 ratio. In general, it appeared that ratios in the higher strata indicated a significantly greater ($p \leq .01$) number of females, while ratios in the lower strata indicated a significantly greater number of males, when compared to the total sex ratio for the collecting period. This is particularly true just prior to the initiation of reproductive activity during November, January and February. Ratios of males to females for E. washingtonianus ranged from 1:0.4 to 1:2.21. The monthly totals were not significantly different ($p > .05$) from a 1:1 sex ratio except for April, June and July when there were significantly ($p \leq .01$) more females than males. Numbers of E. estuarius and E. sawyeri at Lost Creek Beach were too low to attach any significance to the ratios observed. Ratios of males to females of E. estuarius at Yaquina Bay were between 1:0.9 and 1:1.94. Generally the ratio was not significantly different ($p > .05$) than a 1:1 ratio. There was no explicable pattern to the variation in the sex ratios of E. estuarius.

4. Fecundity

The mean number of eggs carried in the marsupium for each size female of E. brevicuspis, E. washingtonianus and E. estuarius is shown in Appendix 1, Table XVIII. The number of eggs carried generally increases with the increasing size of the female. The trend is more apparent with E. brevicuspis probably because there were greater numbers of females with undisturbed marsupia to count. There appeared to be a tendency for E. brevicuspis females of the same size to have a greater

number of eggs in January and February 1972 than in February 1971. However, examination of the gravid females suggested that, in general, the determining factor was the physical size of the marsupium. Casual observations also suggested that as the egg hatches and the juvenile begins to mature, some of the young are forced out of the marsupium. The maximum size of juveniles found in the marsupia in any of the species was around 1.5 mm in length. At that size they apparently leave the female. In laboratory observations, young of that size were occasionally seen to leave and re-enter the marsupium as Croker (1968) has previously reported in other haustoriids. It generally took three to four weeks at about 15°C in the laboratory for the juveniles of E. brevicuspis to reach the size where they leave the marsupium.

The total population fecundity per square meter for E. brevicuspis and E. washingtonianus is shown in Appendix 2, Figure 14. These estimates were calculated by multiplying the number in a size class of gravid females by the mean class fecundity (Appendix 1, Table XVIII) and summing the results for each stratum. During the peak of reproduction the population fecundity was highest in the higher intertidal (+6 to +12). This trend is especially pronounced during February 1971 and January and February 1972 when highest fecundity was between 10 and 12 ft above MLLW.

Appendix 1, Table XIX gives the mean size of gravid females of E. brevicuspis, E. washingtonianus and E. estuarius by month. E. washingtonianus is larger and E. estuarius smaller than E. brevicuspis during their respective peaks of reproductive activity. In the spring

when all three species were reproductively active, E. brevicuspis was smaller by about 0.65 mm than E. washingtonianus, and larger by about 0.75 mm than E. estuarius. There was some variability in the magnitude of the size differences throughout the year but, in general, the size relationship remained the same.

The mean size of gravid E. brevicuspis females was smallest when the peak of spawning activity approached, and it increased as spawning activity waned. The mean size of gravid females in February 1972 was about the same as it was in February 1971. Several gravid females 2.5 mm in length were collected each February. These were the smallest reproductively mature females of this species collected.

The mean size of gravid E. washingtonianus was greatest (about 4.8 mm) during February; the mean size then declined to 4.6 mm in April, and remained relatively constant until January 1972, when the average size was only about 3.8 mm. Gravid females found in January 1972 were the smallest on the average. The smallest reproductively mature E. washingtonianus females (3 mm long) were collected during February, only three of this size were found.

The mean size of E. estuarius was smallest during its reproductive peak in late spring. Although the sizes were noticeably larger during other times of the year, the small number of gravid females collected could well have biased these results.

5. Spatial Distribution of Mature Adults By Sex

The zonation of mature males and females of E. washingtonianus and E. brevicuspis on Lost Creek Beach is shown in Appendix 2, Figure 15. Mature females were defined as those with fully developed and setose oostegites whether they were gravid or not. Since there was no similar criterion for males, males 3.5 mm in length were arbitrarily defined as mature. This seemed a reasonable assumption since there did not appear to be any sexual dimorphism in size and most females became mature at about 3.5 mm in length. Appendix 2, Figure 15 shows that there is even less habitat overlap between mature individuals of both species than there is between that of the sexes in the population as a whole. During the months of February, March and April 1971 and January and February 1972, this segregation of mature adults is especially apparent.

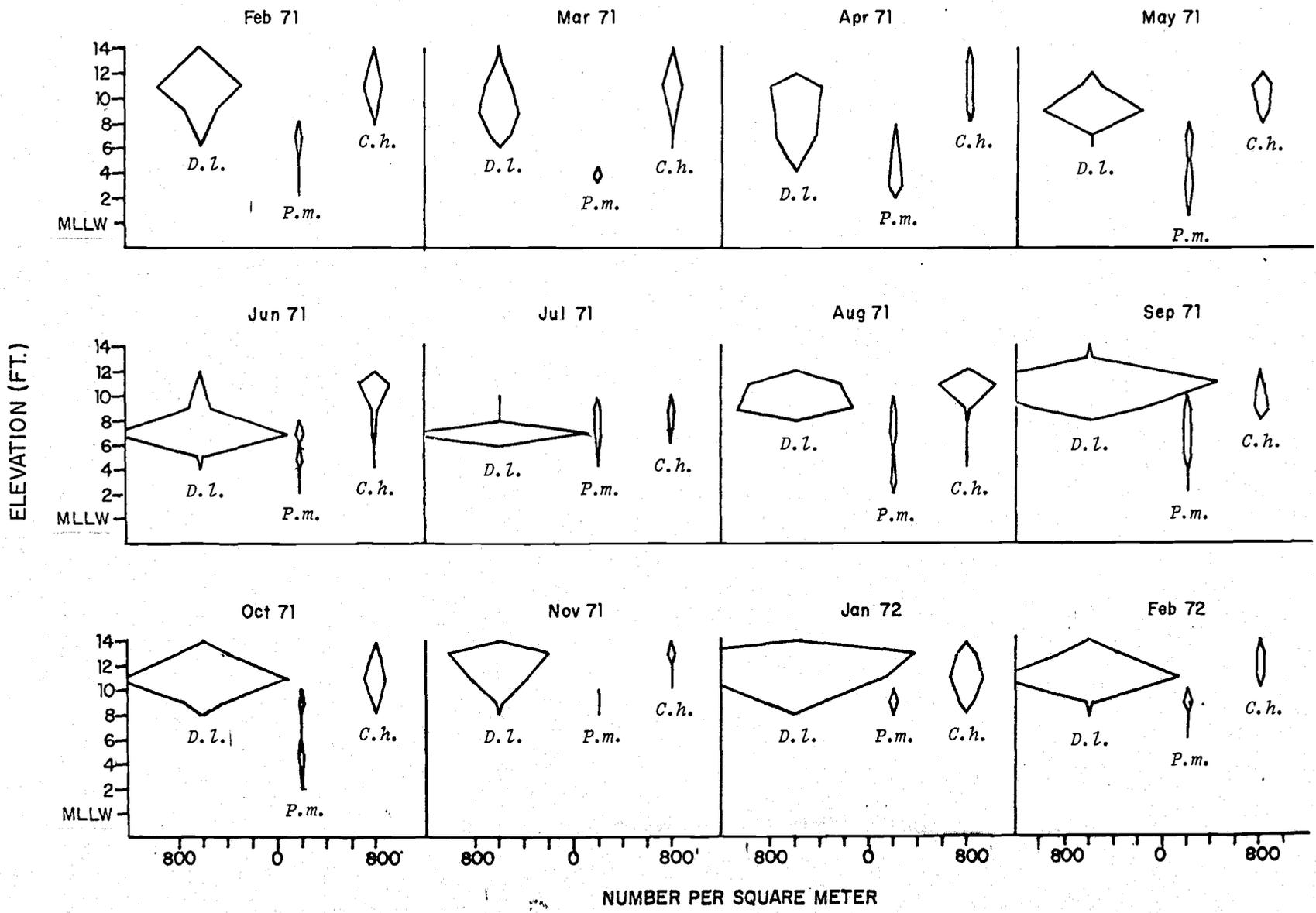
Plankton tows were made during the day and night in the surf when the tide was above mid-tide level to see if Eohaustorius spp. were mating in the water column, but none were found.

E. Associated Fauna

1. Lost Creek Beach

Macrofauna associated with Eohaustorius spp. on Lost Creek Beach were chiefly of two classes, Crustacea and Polychaeta. The zonation of the most abundant species is presented in Figure 12. Of the Crustacea, the most abundant, by far, was the sand-burrowing talitrid,

Figure 12. Zonation of Dogielinotus loquax (D.L.), Paraphoxus milleri (P.m.), and Cirolana hartfordi (C.h.) at Lost Creek Beach, February 1971 - February 1972.



amphipod Dogielinotus loquax Barnard. This species was generally present on the same part of the beach as Eohaustorius brevicuspis. It was found from +5 to +14 ft but had highest densities from +6 to +12 ft. Although no quantitative records were kept, observation of D. loquax specimens in the samples indicated that the spawning peak of this species was April through June. The phoxocephalids, Paraphoxus milleri Barnard and a large unidentified phoxocephalid species were found in low densities in the mid and lower intertidal. The large unidentified species was only collected on four occasions in the lower intertidal zone. The talitrids, Orchestia traskiana Stimpson and Orchestoidea californianus Brandt were frequently seen in the upper intertidal zone above the high tide line but because of their mobility they were only occasionally collected. Another peracaridan, the isopod, Cirolana hartfordi Lockington, was found to be abundant in the upper intertidal. It was most dense between +8 and +12 ft although during their reproductive peak in August 1971 large numbers of small (1 mm) juveniles were observed at the edge of the surf swimming in the thin water layer near the sand. Small mysids, Archaeomysis grebnitzkii Czerniavsky (3-8 mm long) were frequently seen in the lower intertidal but only occasionally collected in samples. One Emerita analoga Stimpson was collected at +4 ft in February 1972. Four pycnogonids of an undescribed species (personal communication, Dr. Joel Hedgpeth) were once collected in one sample near MLLW in June.

The bloodworm, Euzonus mucronata Treadwell, was found abundantly (up to 580/m²) in the upper intertidal where both Dogielinotus

loguax and Eohaustorius brevicuspis were most abundant. The Nephtyd polychaete, Nephtys californiensis Hartman, which is believed to prey on E. mucronata was commonly found in samples although much less frequently than was E. mucronata.

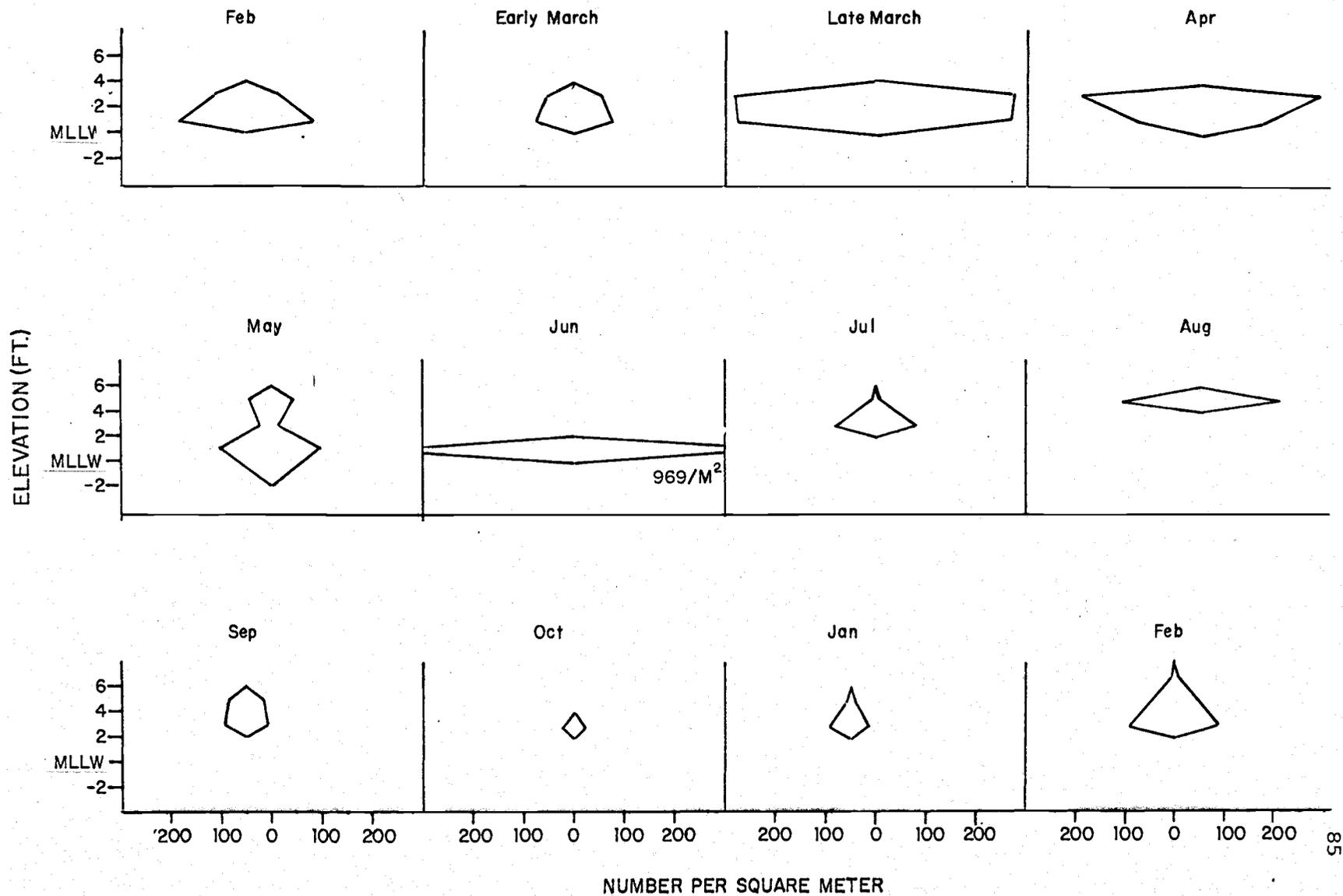
2. Yaquina Bay Transect

The only animal collected abundantly with Eohaustorius estuarius at Yaquina Bay was another small amphipod, the phoxocephalid, Paraphoxus fatigans Barnard. It was present throughout the year primarily below +4 ft MLLW (Figure 13). Although no quantitative records were kept, it was observed that the reproductive peak of this species was in February 1971. Other malacostracans occasionally collected were the corophiid amphipods, Corophium spinicorne Stimpson and C. acherusicum Costa, the isopod Cirolana hartfordi and juvenile ghost shrimp, Callinasa californiensis. Only one or two individuals of these species were collected during each sampling period. Other animals inhabiting the beach but not collected in samples included ghost shrimp adults, C. californiensis Dana; the bivalves, Tresus capax Conrad, Macoma nasuta Conrad and Clinocardium nuttalli Conrad; and the polychaete, Abarenicola sp. Other small polychaetes were occasionally collected.

F. Predators and Parasites

The primary predators of the amphipods at Lost Creek Beach are probably shorebirds and fishes. Although confirmation is lacking because no gut analyses were conducted on potential predators, it was

Figure 13. Zonation of Paraphoxus fatigans at Yaquina Bay transect.



quite obvious that the Sanderling, Crocethia alba and to a lesser extent the Least Sandpiper, Erolia minutilla and the Western Sandpiper, Ereunetes maurie were feeding heavily on amphipods during low tide. Indirect evidence included observations of the shorebirds feeding primarily in the regions of highest density of both Eohaustorius brevicuspis and Dogielinotus loquax; interruption of tracks in sand made by Eohaustorius with "bill marks" and, increased feeding activity of shorebirds on warm, sunny days when Eohaustorius were most frequently seen crawling on the surface of the sand in areas of seepage.

Although there is no direct evidence, it is also possible that several species of fish found in the surf zone may also prey on these amphipods during high tide. These species include the red tail surf perch and striped sea perch, Amphistichus rhodoterus and Embiotoca lateralis respectively, and the juvenile sand sole, Psettichthys melanostictus (personal communication, Dr. Eugene Burreson).

At Yaquina Bay, the Sanderlings were less common than at Lost Creek Beach but both Least and Western Sandpipers are more abundant and were frequently seen pecking in the sand. Since amphipods were less dense at the Yaquina Bay transect, and other animals relatively more abundant, there is not as much evidence that the shorebirds were feeding on amphipods as there was at Lost Creek Beach.

Fish species preying on Eohaustorius estuarius include the Staghorn Sculpin, Leptocottus armatus and probably juvenile English Sole, Parophrys vetulus (Burreson, personal communication).

Eohaustorius estuarius was regularly parasitized by a helminth. The nature of the infection and appearance of the parasite resembled that reported by Sandeman and Burt (1972) and by Bullock and Scott (1975) for infections of other gammarid amphipods by the pseudophyllid, Bothrimonus sturionis. The worm invades the body cavity and begins to grow, apparently displacing organs, until they probably kill the host or pass into a fish or bird when the amphipod is eaten. The worms are quite visible as they are dark and the exoskeleton of E. estuarius, transparent. They begin to coil up as they grow and some amphipods 3-4 mm long were found to harbor worms 13-15 mm in length.

The parasite was found in about 4% of the E. estuarius collected although the incidence of infection varied from 0 to 12.7% throughout the year (Table III). No gravid females were found with the infection. Only two specimens of E. brevicuspis collected from Lost Creek Beach during the whole year were similarly infected. Some of the E. estuarius collected from other small estuaries in Oregon and some collected by Bousfield from the Queen Charlotte Islands, British Columbia were infected in a manner similar to those seen in Yaquina Bay.

G. Laboratory Studies

1. Preliminary Salinity-Tolerance Experiment

The results of the preliminary tolerance experiment showed that E. brevicuspis was capable of surviving in standing sea water at 15°C with no apparent food for at least five days at salinities as low

TABLE III. INCIDENCE OF INFECTION OF EOHAUSTORIUS ESTUARIUS
 BY THE PARASITE, BOTHRIMUM STURIONIS, FEBRUARY 1971 -
 FEBRUARY 1972.

COLLECTING PERIOD	# OF E. ESTUARIUS EXAMINED	% INFECTED
February	336	3.9
Early March	177	4.0
Late March	135	3.0
April	126	12.7
May	139	5.0
June	49	2.0
July	119	0
August	51	3.9
September	93	4.3
November	32	6.3
January	156	1.3
February	<u>232</u>	<u>1.7</u>
	<u>TOTAL: 1645</u>	<u>MEAN: 3.8</u>

as about 10 ‰ (Appendix 2, Figure 16). It also showed that this species suffered total mortality in fresh water after only 17 hours.

2. Salinity-Temperature Tolerance Experiment

The tolerance of Eohaustorius brevicuspis to the 20 temperature-salinity combinations is shown in Appendix 2, Figures 17 and 18. At six hours survival was near 100% except for those tested at the lowest salinity (0 ‰). After six hours, mortality increased to some extent at the other salinities except for those tested at 15°C, the temperature closest to that experienced in their habitat. At 21°C those tested at 6 ‰ experienced about 50% mortality after approximately 24 hours. This effect of a decrease in survival at 6 ‰ on those tested at the highest temperature 21°C is represented by the increased significance of the temperature and salinity interaction in Appendix 1, Table XX at 24 hours.

The multiple regression analysis indicated that the linear effects of salinity contributed significantly to the variability in survival after six hours. At that time 18.8% of the variability was explained by the linear effects of salinity. The quadratic effects of salinity although not significant accounted for another 13.9% of the variability. The entire polynomial,

$$Y\% \text{ survival} = 89.66 - 3.31(T) + 3.62(S) + 0.12(T^2) - 0.10(S^2) + 0.02(TXS)$$

explained 35.6% of the variability after six hours. The linear and quadratic effects of temperature accounted for only 0.3% of the vari-

ability at this time.

At 48 hours the linear effects of salinity accounted 54.9% of the variability; the quadratic effects another 29.5%. The polynomial

$$Y\% \text{ survival} = 8.14 + 2.19(T) + 10.12(S) - 0.14(T^2) - 0.28(S^2) + 0.05(TXS)$$

explained 87.5% of the variability. Of this 0.2% was attributed to the linear and quadratic effects of temperature.

The tolerance of E. washingtonianus to the 20 temperature-salinity combinations is shown in Appendix 2, Figures 19 and 20. Survival of E. washingtonianus was dramatically better at low to moderate temperatures (5-15°C) and higher salinities (23-28 ‰). At six hours the survival at 5, 11 and 15°C was 100% for the three highest salinities tested (14, 23 and 28 ‰). Mortality was increased even at the high salinities when tested at 21°C.

The multiple regression analysis indicated that only the linear and quadratic effects of salinity contributed significantly to the variability at any time (Appendix 1, Table XXI). At six hours 70.9% of variability was explained by the linear effects of salinity. The quadratic effects of salinity accounted for another 23.6% of the variability. The entire polynomial,

$$Y \text{ ‰ survival} = 11.5 + 1.04(T) + 9.26(S) - 0.09(T^2) - 0.24(S^2) + 0.04(TXS)$$

explained 96.0% of the variability after six hours. The linear and quadratic effects of temperature accounted for a total of only 0.1% of the variability at this time.

At 48 hours the linear effects of salinity accounted for 73.6% of the variability; the quadratic effects of salinity another 0.3%. The polynomial,

$$Y\% \text{ survival} = -25.13 + 4.31(T) + 7.12(S) - 0.19(T^2) - 0.09(S^2) - 0.08(TXS)$$

explained 84.7% of the variability, of this 0.7% was attributed to the linear and quadratic effects of temperature.

The tolerance of E. estuarius to the 20 temperature-salinity combinations is shown in Appendix 2, Figures 21 and 22. Mortality occurred in this species only in fresh water (0 ‰) except for less than 10% mortality at 21°C temperature on those tested at 6 ‰.

The multiple regression analysis indicated that the linear and quadratic effects of salinity and the combined effects of temperature and salinity were significant at six hours (Appendix 1, Table XXII). At this time 30.2% of the variability was due to the linear effects of salinity; 22.7% was due to the quadratic effects of salinity; and 11.3% was due to the combined effects of salinity and temperature. The entire polynomial,

$$Y\% \text{ survival} = 96.95 - 0.33(T) + 0.96(S) - 0.02(T^2) - 0.04(S^2) + 0.04(TXS)$$

explained 71.3% of the variability after six hours. The linear and quadratic effects of temperature accounted for 7.1% of the variability at this time.

At 48 hours only the linear and quadratic effects of salinity contributed significantly to the variability (Appendix 1, Table XXII).

The linear effects of salinity accounted for 43.2% of the variability; the quadratic effects of salinity for another 30.5%. The polynomial,

$$Y\% \text{ survival} = 82.07 - 2.26(T) + 4.37(S) + 0.04(T^2) - 0.14(S^2) + 0.05(TXS)$$

explained 78.8% of the variability. Of this only 0.2% was due to the linear and quadratic effects of temperature.

3. Laboratory Maintenance

Successful holding in the laboratory required no special preparation or material. All three species, E. brevicuspis, E. estuarius, and E. washingtonianus, were remarkably easy to keep with minimum care. For short term holding they survived well in seawater from where they were collected. For holding over four or five days, they required feeding and generally the easiest way was to replace the sand in the bowl with fresh beach sand. No aeration was required if care was taken not to overcrowd. Approximately 50 animals per small (four inch) fingerbowl or 500 per large (ten inch) fingerbowl seemed empirically to be a "healthy" density. At these densities there was generally 50-75% survival after two months if the sand was changed at least every five days. Animals that were stressed by lack of food or other "unhealthy" conditions responded lethargically to prodding with a dissecting pin.

In some instances, gravid females would release their eggs or recently hatched juveniles when stressed. In these instances the young would not survive even when placed in optimum conditions.

4. Other Observations

Casual examination of several guts of both recently collected and laboratory maintained Eohaustorius revealed that the majority of their food is probably detritus. Most of the contents were amorphous greenish-brown material. One or two species of diatoms were also found. They readily ate the Isocrysis sp. culture that was fed to them.

IV. DISCUSSION

This study has identified several ecological and physiological differences between four species of the genus Eohaustorius inhabiting the sandy beaches on the central Oregon coast. The results of this study have also identified several population characteristics which together with the ecological and physiological differences contribute to a differentiation of their niches.

The four species, Eohaustorius washingtonianus, E. brevicuspis, E. sawyeri and E. estuarius although found in close proximity throughout most of their range have their maximum densities in different portions of their habitat. Eohaustorius estuarius is most abundant in brackish water habitat; E. brevicuspis in the high and mid intertidal regions on exposed beaches; E. washingtonianus in the low intertidal and shallow subtidal in both exposed and sheltered habitat; and, E. sawyeri in the shallow subtidal on exposed coasts.

In addition to habitat segregation, other mechanisms which contribute to the maintenance of reproductive isolation between the species include the timing of the reproductive cycle and isolation of mature adults of the different species during reproductive peaks.

Other biological differences among these species include: brood size; population reproductive potential; maximum size; sex ratio distribution; salinity and temperature tolerance; predators; and, associated fauna.

Eohaustorius brevicuspis is found in the high and mid intertidal on most exposed sandy beaches along the central Oregon coast. A

similar distribution was found at Beaver Creek during this study and Greenley (1969) and Bousfield (unpublished field notes) found essentially the same distribution at other local beaches. Maximum densities were generally above mean high water in the surf zone. During August 1971 and February 1972 when salinity measurements were taken, the maximum densities were in the area of fresh water seepage (see Table I and Figure 9). The gravid females during the beginning months of the reproductive activity are smaller than those found gravid near the end of reproductive activity (Appendix 1, Table XIX). However, the difference in size is not substantial. The strong seasonal peak in reproductive activity (Figure 11) and the fact that the percentage of mature animals in the population decreases after reproduction ceases (Appendix Figure 11) suggests that this species has a univoltine generation and lives for about one year. This appears to be the most common life cycle found in the Haustoriinae (Croker, 1966; Dexter, 1967; Sameoto, 1969; Bousfield, 1973).

The majority of the mature and gravid females were found in the upper intertidal where they generally outnumber the males significantly (Appendix Table XVII). However, a greater percentage of the females found in the lower portion of their intertidal range were gravid. This is perhaps a reflection of the fact that male E. brevicuspis significantly outnumbers the females there.

Eohaustorius brevicuspis was probably preyed upon primarily by birds, especially the Sanderling and the Least and Western Sandpiper, although the evidence is only circumstantial. Other workers (Croker,

1966; Dexter, 1967; Sameoto, 1969; Mills, 1967) have also suggested that pipers and plovers were probably responsible for a good deal of the predation on intertidal populations of Haustoriinae and other amphipods. It is possible that the cirolanid isopod, Cirolana hartfordi could also play some role in limiting this species. Although cirolanids are generally considered to be scavengers (Ricketts, et al., 1968), they are quite voracious and will even attack wader's legs (Dahl, 1953). Sameoto (1966) reports seeing them attacking and eating juvenile haustoriids in aquaria.

In salinity-temperature tolerance studies E. brevicuspis was tolerant of a wide range of salinities for long periods of time at intermediate temperatures. Only fresh water caused high mortality. At the highest temperature (21°C) there was significant mortality caused by exposure to 6 ‰ water. As indicated by the response surface curves (Appendix 2, Figure 18) E. brevicuspis can survive up to six hours in a broad range of temperature-salinity combinations. After six hours the range of salinities in which 100% survival can be expected narrows. After 24 hours the higher temperatures begin to contribute to mortality and this effect continues throughout the 48 hours.

E. washingtonianus was found in maximum abundances in the lower intertidal at Lost Creek Beach. It is found in a similar position on other exposed beaches in Oregon (Greenley, 1969; Bousfield, unpublished field notes). The extent of the subtidal distribution on these beaches is unresolved.

E. washingtonianus reaches its peak of reproductive activity on Lost Creek Beach approximately the same time of the year that E. brevicuspis does, i.e., the winter months (Figure 11). E. washingtonianus differs from E. brevicuspis, however, by the fact that in E. washingtonianus a certain proportion of the population (12-23%) is gravid throughout the year. The average size of gravid females was largest in February 1971 and generally declined throughout the year until February 1972. Average size during February 1972 was smaller than during the previous February. After the peak in reproduction in February 1971, there was decrease in larger individuals as they presumably died. Rapid and continuous recruitment to various size classes in this species suggests that they are faster growing than E. brevicuspis.

Since smaller numbers of E. washingtonianus were collected and also considering that those collected may only have been a portion of a population that extended subtidally, speculation on the nature of its life cycle is tentative. It may be that E. washingtonianus has a life cycle similar to that of Bathyporeia pelagica, a shallow subtidal species described by Fincham (1971). B. pelagica shows almost a continuous breeding cycle phased by the tides. However, in the spring the cycle is reinforced by the spring rise in temperature to give an intense reproductive period. In Oregon it is likely that if temperature stimulates an intense reproductive period in January or February, low temperatures rather than high temperatures are responsible. Temperatures along the Oregon coast generally are lowest in December through February (Bourke et al., 1971). A second possibility is that low dissolved oxygen levels

provide the stimulus to begin reproductive activity. Burt et al., (1959) reported that low dissolved oxygen concentrations are found in the winter months, whereas at other times during the year there is supersaturation of oxygen. The facts that E. washingtonianus does not display a prolonged high plateau of reproductive activity, and that size of gravid females decreases throughout the year, suggest that a low level of reproductive activity is maintained throughout the year by individuals reaching sexual maturity.

Average size of E. washingtonianus at maturity is 0.5-1.0 mm larger than E. brevicuspis (Appendix 2, Figures 11 and 12). Their larger size may result from this species being able to feed throughout a greater part of the tidal cycle. Since fecundity increases with size, gravid E. washingtonianus on the average carry more eggs than E. brevicuspis (Appendix 1, Table XVIII). However, since E. washingtonianus are far less abundant than E. brevicuspis, total population fecundity is lower (Appendix 2, Figure 14).

The distribution of sexes of E. washingtonianus reveals no consistent trends. On the whole, there are more females than males but only in three of the months was the difference significant (Appendix Table XVII).

Although some of the birds that presumably prey on E. brevicuspis also indiscriminately eat E. washingtonianus at low tide, the lower distribution of the latter suggests that predation by fish, e.g., surf perches and sand sole may be more important in these populations. Whether any invertebrates prey on E. washingtonianus is unknown. Ciro-

lana hartfordi is not generally found this low on the beach but a large (10-15 mm) unidentified phoxocephalid, may possibly prey on E. washingtonianus. Sand shrimp, Crago sp., which move in with the tide, may also prey on this species more than on E. brevicuspis in the upper intertidal.

The salinity-temperature tolerance experiments revealed that E. washingtonianus had better survival in low to intermediate temperatures and high salinities. It was evident that this species was quite stenotopic compared to E. brevicuspis and its low survival in temperatures and salinity regimes not found in its more constant low intertidal and subtidal habitat reflected this even after only six hours (Appendix 2, Figures 19 and 20).

Eohaustorius sawyeri was found in the shallow subtidal portion of Lost Creek Beach. Greenley (1969) found it distributed similarly on other nearby beaches. This species is apparently an obligate subtidal species in Oregon and to the south. Slattery (personal communication) reports that it is found subtidally as deep as 20 meters off Moss Landing, California. My lack of success in collecting it in subtidal dredge samples and the relatively low numbers collected on Lost Creek Beach precluded obtaining information on its population ecology similar to that found for E. brevicuspis and E. washingtonianus. In addition, not enough individuals could be collected to include them in the salinity tolerance experiment. The nature of their distribution suggests, however, that they would probably be fairly stenotopic.

Eohaustorius estuarius was found intertidally in several estuaries on the central Oregon coast. Eohaustorius estuarius was also found subtidally in both Yaquina Bay and Beaver Creek, the only two estuaries where subtidal collections were made. Bousfield (unpublished field notes) also reports their presence intertidally in several other estuaries from Oregon to northern British Columbia. Slattery (personal communication) reports that it is found subtidally off Moss Landing.

There is evidence that E. estuarius in Yaquina Bay are eaten by staghorn sculpin and probably by juvenile english sole (Burreson, personal communication). Birds also may prey on this species in the intertidal portion of their range. Eohaustorius estuarius was also infected by a small helminth. The effect of this parasite on the population of E. estuarius is difficult to evaluate. Since no parasitized females were ever found to be ovigerous, it is probable that the parasite either sterilizes the female or causes the release of the eggs if they are fertilized. Since the highest percentage (12.7%) of parasitized individuals (Table III) were found in April, coincident with the peak of reproductive activity, the effect of this infection on the population could have been substantial. The disappearance of parasitized animals by July could mean that the parasites have killed their host or that parasitized individuals because of behavioral changes or decreased mobility were differentially selected by predators as reported by Stark (1965) for Gammarus zaddachi. It is presumed that E. estuarius serves as the alternate host for this parasite while the primary host is probably a fish, perhaps the staghorn sculpin. The fact that other

Eohaustorius spp. were not parasitized by this worm suggests that its primary host is some estuarine vertebrate.

The amount of migration between the intertidal and subtidal populations in Yaquina Bay was not documented. The results of size-frequency histograms (Appendix 2, Figure 13) suggest, however, that there is some migration. The fact that the only evidence of reproduction of the E. estuarius intertidal population occurred during the spring and juveniles were recruited to the intertidal population throughout the year suggests that there is definitely some interchange between the populations. Some evidence suggests that the population of E. estuarius found in the Yaquina Bay area may not be typical of populations in other areas. Densities in other locations, e.g. Beaver Creek and Big Creek, were found to be higher than at the Yaquina Bay study area. Even other locations within Yaquina Bay, particularly the small creeks behind the Marine Science Center, had higher densities. In addition, there may be differences in life cycle phenomena among estuaries as was shown for the timing of their reproductive peaks (Appendix 2, Figure 10).

There were insufficient numbers of gravid E. estuarius retaining their full brood after the sorting process to determine whether the size of gravid females increased during the reproductive period. Without this information it is difficult to substantiate whether this species is univoltine. The nature of the curve for reproductive activity (Figure 11) and the fact that the percentage of larger sized animals decreases after spring breeding, suggests that the intertidal population

at the Yaquina Bay study area has only one brood per year and that adults die after reproducing. The continued recruitment of juveniles to the population throughout the year suggests that reproductive activity of the subtidal population is either out of phase with the intertidal population, or like E. washingtonianus sustains a low-level of reproductive activity throughout the year.

The salinity-temperature tolerance experiment proved that E. estuarius is a eurytopic species, well adapted to tolerating a wide variation in salinity and temperature. The results showed that, except at extremely cold and hot temperatures, E. estuarius could tolerate pure freshwater for up to six hours (Appendix Figure 21); slightly longer than the period between successive low and high tides on this coast. Mortality in fresh water was not 100% at any temperature tested even after 48 hours. Lowest estuarine salinities near the bottom occur at low tide, and this species could therefore survive regular winter salinity fluctuations between high and low tide periods.

The reproductive cycles of Eohaustorius spp. testify to adaptations which maintain populations on sandy beaches separated by the rivers or rocky headlands of the Oregon coast. An understanding of these adaptations may also help to explain how estuaries and sandy beaches in the North American-Pacific region were originally populated in the absence of any extensive and stable interconnection (Bousfield, 1970). Reproductive activity of E. brevicuspis and E. washingtonianus and to some extent E. estuarius occurs during the winter and early spring months when rains and storms erode sandy beaches and subject

small freshwater streams to more "flushing" than at other times during the year. The coincidence of the peak of the reproductive cycle with the time of greatest habitat instability could well be an adaptation ensuring dispersal of young to other locations. Dispersal to and colonization of new habitats cannot be as rapid as in species with a meroplanktonic stage, but it is easy to see how a species could disperse several miles per generation using this strategy. Bousfield (1970) discusses this possibility and notes that the distribution of the more mature individuals in the upper intertidal and the juveniles in the lower intertidal may facilitate this mechanism. It is not surprising that species which provide maximum protection of their young by brooding still require a dispersal stage to recolonize depopulated habitat areas.

A second evolutionary advantage of the peaking of reproduction cycle during the winter is that the early spring is generally one of the most productive times of the year. The availability of phytoplankton to newly arrived young must result in some selective advantage. Steele and Steele (1975) in their comprehensive study of the genus Gammarus in the northwestern Atlantic stressed the importance of timing of release of the brood to coincide with optimal conditions:

In terms of strategy, it makes little difference if larger or smaller young are produced or whether they emerge from one brood or several, or if parents are annual or perennial, unless the young are released at a time when they can survive.

In addition, Kanneworff (1965), in studies of the amphipod, Ampelisca macrocephala, concluded that the fastest growing period and release of the young was correlated with phyto- and zooplankton blooms. Since

Eohaustorius spp. are filter feeders it would be highly adaptive for young to be produced at a time when they would be best able to make use of seasonal productivity. Nutrient runoff and increased solar radiation lead to an eventual increase in phytoplankton production along the Oregon coast in the spring. Since haustoriids can make use of detritus and phytoplankton, mostly diatoms, (Croker, 1966; Dexter, 1967; Sameoto, 1969a and Bousfield, 1970) it follows that spring must be the most productive time of the year for Eohaustorius. My observations that they can feed successfully on Isocrysis and Dexter's (1967) success at maintaining haustoriids in the laboratory by feeding them phytoplankton cultures, suggest that live phytoplankton as well as interstitial detritus can be important in their diet.

The fact that the mean size of the gravid females of all species was smaller at the onset of reproductive activity than later on during the reproductive time of year (Appendix Table XIX) also suggests that it is an extrinsic stimulus, perhaps decreased temperature or low dissolved oxygen levels, that triggers breeding activity. The only instance where this does not pertain is with E. washingtonianus. During the February 1971 peak the mean size was at its greatest, whereas during the February 1972 peak the mean size was the smallest. Information on reproductive activity prior to the February 1971 peak would aid in interpreting this apparent contradiction.

The significance of the clumped distribution of the Eohaustorius species is not readily interpretable. The fact that "patchiness" increased where density was lowest (Appendix Tables III, VII, IX, XI,

XIII and IV) suggests that there is an active mechanism operating which results in a clumped distribution. Whether this mechanism is behavioral, related to microhabitat differences or the result of the organism's sexual biology was not resolved by this study. The results of an intensive sampling in a 20 ft x 20 ft section of beach where both E. brevicuspis and E. washingtonianus were present, indicated that although E. brevicuspis was more abundant, the distribution of E. washingtonianus was more contagious. This result suggests some form of species recognition among E. washingtonianus but this inference must remain in the realm of speculation. Little information on the significance of intraspecific dispersion was gained from this study except that all Eohaustorius species were patchily distributed and that patchiness increased at the boundaries of the species' distributions. Dexter (1967) and Croker (1966) and other workers have observed that the haustoriid species they studied also had a "patchy" distribution.

The abundance and persistence of the species of Eohaustorius on these central Oregon beaches is an indication of the success attained by these and other malacostracans on sandy beaches throughout the world (Dahl, 1953; Bousfield, 1970; and Croker, 1975 among others). The consistent differences between the four Oregon species in such characteristics as distribution and sexual biology, attests to the adaptive radiation that has occurred in this genus. The ecological relationship between these Eohaustorius species has many of the characteristics displayed by the Bathyporeia complex in the northeastern Atlantic (Vader, 1965; Fincham, 1970; Fish and Preece, 1971; and McGrorty, per-

sonal communication) and by polygeneric groups of Haustoriinae along the eastern Atlantic (Croker, 1966; Dexter, 1967; and Sameoto, 1969a, b, c among others). The study of amphipods on sandy beaches has, in general, revealed, as Dexter (1967) put it:

(Obvious conclusions are) that the intertidal sand habitat regardless of its uniform appearance to the casual observer offers a variety of niches with enough diversity to allow several morphologically similar species to coexist, and conversely, that morphologically similar species of haustoriid amphipods exhibit enough ecological niche variety to occupy a fairly uniform habitat.

Most studies of niche diversity and competition between species of fossorial amphipods on sandy beaches have shown that the several genera of haustoriids investigated do display sufficient differences in niche requirements to suggest to the investigator that competition may be decreased by these differences. The observation of sympatry in the Bathyporeia complex in the northeastern Atlantic and of the Eohaustorius complex found in Oregon implies that competition among these sibling species may be more intense because of their phyletically closer relationship. This study of Eohaustorius spp. has shown that not only is there evidence of differences in the biology of these species but also indirectly that there is rather intense competition between them.

The stability of the distributional zones of the four species throughout a variety of changing environmental conditions suggests that zones result from active competition between species having differential fitnesses for different habitats. As Hutchinson (1957) noted:

The general evidence of considerable stability under most environmental conditions would suggest competitive action of some sort is nearly always of significance.

Several characteristics of species populations discovered in this study undoubtedly contribute to the distributional characteristics observed. The absence in these species and most other Haustoriinae (Croker, 1966; Dexter, 1967; and Sameoto, 1969a) of pelagic mating helps to keep the zones autonomous. It was also found that the characteristics of the species populations in the zones of overlap probably work to prevent interspecific mating. Although there is only a little overlap between E. washingtonianus and E. brevicuspis (Figure 9), it was observed that when only sexually mature individuals are considered, the overlap and hence the chance of interspecific mating becomes further decreased (Appendix 2, Figure 15). This also results in a maximumization of size differences in this portion of the beach. McGrorty (personal communication) also observed minimum spatial overlap of Bathyporeia populations during times of reproductive activity. He concluded that because of this competition could be expected to be minimized.

The observed distribution of the sexes of E. brevicuspis offers additional evidence that spatial segregation of these species is the result of an active mechanism. Appendix 1, Table XVII indicates that the sex ratio of E. brevicuspis is skewed significantly toward females in the upper intertidal and significantly toward males in the lower intertidal, closest to the zone of overlap with E. washingtonianus. This phenomenon has been found in other mid-intertidal haustoriids, e.g., Neohaustorius schmitzi (Dexter, 1967). This displacement of sex ratio in Eohaustorius brevicuspis has several results which may act in concert to increase reproductive success of E. brevicuspis and to

maintain the segregation from E. washingtonianus. It permits the brooding female and recently hatched juvenile to inhabit the less rigorous part of the habitat. It also decreases intraspecific competition for resources, since it is only necessary to have sufficient males available for fertilization. Any more males would presumably result in competition for some resource, i.e., food or space. In his study of Ampelisca spp., Mills (1967) observed that:

Kinne feels that displacement of the sex ratio of Gammarus duebeni towards the males in suboptimal conditions may have a great adaptive significance, since if males are more resistant than females under those conditions they may maintain species in an area by occupying space until more favorable conditions allow the relative number of females to increase. In addition the presence of relatively large numbers of females could interfere with the success of a competing species of the same genus, since it has been observed that males of one species of Gammarus will mate with females of closely related species but that the cross is sterile. Thus by mating with the females of competing species, G. duebeni males might reduce egg production of those species.

Following this reasoning, E. brevicuspis may have evolved distributional characteristics which maximize the protection of brooding females while at the same time minimizing the chance that sterile matings occur.

The fact that the distributional relationship between E. brevicuspis and E. washingtonianus is actively acquired by the species can be partially demonstrated by changes in distributional pattern after a storm in February 1971 which eroded a great deal of sand off Lost Creek Beach. As soon as sand began to be deposited on the beach again in March 1971 it was observed that the two species assumed much the same distribution they had displayed prior to the storm. It was noted (Fig-

ure 9) that in April and May E. washingtonianus was distributed higher on the beach than it had been the previous February. There was an adjustment in the species distributions, presumably reflecting competition or differential fitness, until the following September when almost no overlap between the species occurred. This situation continued generally until February 1972 when sampling ended. Dexter (1967) reported a similar phenomenon when the normally low intertidal Acantho-
haustorius millsii extended its zone of maximum concentration upwards following a reduction in abundance of the mid intertidal Neohaustorius schmitzi after heavy rains in June 1966. By the end of that summer, the two species had readjusted their distribution to what it was prior to the storm.

Other evidence of competition or differential fitness among the species consists of the segregation of E. brevicuspis and E. estuar-
ius around the mouths of estuaries. At Lost Creek Beach E. estuar-
ius was only found on the upper beach during winter and early spring when storms increased runoff of Lost Creek so it spread over the beach during low tide. After the stormy season subsided, E. estuar-
ius was no longer found on Lost Creek Beach (Figure 9). This was also quite evident at Beaver Creek where studies during August showed that E. estuar-
ius was found only in the creek above approximately mean high water. E. estuar-
ius was the only species found in or beside the creek bed from the MHW (mean high water) level down to MLLW level (Appendix 2, Figure 9). In several samples taken along the shores of Yaquina Bay (Figure 3), E. brevicuspis was collected near the end of south jetty but nowhere fur-

ther inside the bay. Examination of Bousfield's specimens and field data (unpublished) reveal that this relationship is similar in other parts of Oregon and in Washington. It would be interesting in further studies to see how far from the mouth of larger estuaries, such as Yaquina Bay, subtidal populations of E. estuarius are found. Information provided by Mr. Peter Slattery (personal communication) indicates that near Moss Landing, California, E. estuarius is found off the mouth of a river out to about 10 meters depth.

Of course, much of the competitive success of the three species, E. washingtonianus, E. brevicuspis and E. estuarius, in the variety of habitats that they actively or passively colonize can probably be directly attributed to their ability to tolerate the physical regimes they encounter. Results of the temperature-salinity tolerance experiment indicated, as one would expect a priori, that those species living in habitats where changes in temperature and salinity are the greatest have the greatest ability to tolerate them. This has been shown for many organisms and studies of temperature and salinity tolerances of amphipods are no exception (Croker, 1966; Dexter, 1967; Sam-eoto, 1969c, McCrorty, 1971 personal communication). Conversely, the species living in habitats where the magnitude of physical changes are relatively small have little ability to tolerate broad extremes of salinity and temperature. It is unlikely that E. washingtonianus would be as successful as E. brevicuspis in the high intertidal habitat where it might be exposed to salinity changes from rain or temperature changes from insolation for as much as 12 hours. This is true in spite of the

fact that both these species are found from 4 to 10 cm beneath the sand surface where environmental extremes are mitigated (Johnson, 1965; Croker, 1966). Using the same argument, it is unlikely that E. brevicuspis would be as successful in an estuarine environment as is E. estuarius. Results of the temperature-salinity experiment showed that although E. brevicuspis could tolerate a wide range of temperature and salinity over the short term, after 12 hours its tolerance of lower salinities would be expected to decrease (Appendix 2, Figure 18). Of course, E. estuarius would be physiologically capable of tolerating the range of salinities and temperature that E. brevicuspis and E. washingtonianus encounter, so some other factor must limit its distribution in these habitats. Although this limiting factor was not identified in this study, one could speculate that it might be related to exposure to an open coastal environment, some characteristic of the substrate, availability of a preferred food, or to competition. One would also have to speculate about E. brevicuspis exclusion from the lower intertidal and subtidal habitats. Although it seems physiologically capable of tolerating the temperature and salinity regimes, the lack of some other environmental requirement may decrease its relative fitness for that habitat.

The sympatry of E. brevicuspis with other malacostracans, i.e., Dogielinotus loquax, Paraphoxus milleri and Cirolana hartfordi as well as the polychaete, Euzonus mucronata represents an interesting and more classical case of reduction of competition in sympatric species by niche diversification. In this instance, several mechanisms which act to

reduce competition between these species can be identified. Of the three gammarids on Lost Creek Beach, E. brevicuspis is a relatively small, 3.5-5 mm, filter feeding and relatively deeply burrowing (Bousfield, 1970) amphipod. D. loquax is a larger 10-15 mm, probably epistrate feeding amphipod which is only capable of shallow burrowing (Bousfield, 1970). Paraphoxus milleri is an intermediate-sized 8-12 mm possibly carnivorous amphipod (Bousfield, 1970) which is much less abundant than either of the above two species. The peak of E. brevicuspis reproductive activity is in the winter months, whereas D. loquax bred somewhat later in the spring. It was not established when P. milleri bred. The polychaete E. mucronata which is very abundant in the area of maximum concentration of both E. brevicuspis and D. loquax is a deposit feeder (Ricketts, et al., 1968). The isopod, C. hartfordi is generally a scavenger (Ricketts, et al., 1968) and breeds in the late summer.

Similar adaptations for niche diversification are present in the Yaquina Bay area. Here, as in other sheltered areas, the proportion of bivalves and polychaetes to malacostracans is higher than upon exposed beaches (Croker et al., 1975; Eleftherion and Nicholson, 1975). However, the characteristics that are present which reduce competition are the same. Differences in feeding type and size are readily apparent here. The species most closely related to E. estuarius are Corophium spp. and Paraphoxus fatigans. Neither species seem sufficiently abundant in the same zone as E. estuarius to pose a serious competitive problem. The corophids on this beach were fairly rare as they generally

prefer a higher organic content in the substrate. Paraphoxus fatigans generally was found in the lower intertidal where the higher organic content and finer sediment (Thum, 1972) presumably restricts the distribution of E. estuarius.

This study has identified instances where indirect evidence of competition between the species of the genus Eohaustorius exist. However, as Croker (1966) noted:

It would appear that it is not the amount of [niche] overlap that is of primary importance for the operation of what has been termed competitive exclusion, but instead the lack of niche diversity with regard to limiting factors (Mayr, 1963; King, 1964).

However, resources for which these haustorid species compete or limiting factors which result in segregation of their populations were not identified in this study. Some possibilities are that these species are limited by the availability of food or space or by predatory pressures.

It is doubtful that the haustoriids on these beaches are limited strictly by the availability of food. Not only is there evidence that herbivores are generally not food-limited (Hairston, et al., 1960), but also as Bousfield (1970) points out,

Waters flooding the sandy beaches contain virtually the same rich supply of nutrient food materials that supports the wealth of sessile filter-feeding organisms on adjacent rocky shores.

On Lost Creek the high abundance of macroinvertebrates in the zone near mean high water suggests that this is a food rich area. In addition, the evidence that these species maintain virtually the same abundance throughout the year would tend to indicate that detritus or plankton

abundance, the availability of which varies throughout the year, does not act directly to limit their populations.

It is also doubtful that food is limiting in the lower intertidal areas of these exposed beaches. Not only is the same amount of food available from the waters that cover the beach at high tide, but there are fewer individuals with similar food requirements competing for it. It is also doubtful that availability of interstitial organic matter is any different from the upper intertidal area. Croker *et al.* (1975) found no significant differences in organic carbon and total nitrogen concentrations between upper and lower levels of exposed northern New England beaches. Bousfield (personal communication) stated that one might even expect a greater amount of organic content in the lower beach sand because of its generally finer sand composition. He also suggested (personal communication) that

lower densities of haustoriids in the lower intertidal area may be the result of greater exposure to predators, not only fishes, but to other crustaceans (e.g., Crago) that move in and out with the tide.

Space may well be a limiting factor in the zone near mean high water on Lost Creek Beach. The very high abundances of the macroinvertebrates there probably results in a large number of intra and interspecific encounters. Although it has been observed that several adaptations have been evolved to diversify the niches of species living there, a finite limit to the space available in this zone must exist. The fact that there is little variation in time of the total abundance of several of the species living there may be indicative of space

limitation. It is obvious, however, that, while the availability of space may operate to limit populations in the upper intertidal, there is ample space for more macroinvertebrates in the lower intertidal.

The limiting factors on E. estuarius in estuarine environments may be to some extent different from those operating on the species living on exposed beaches. Certainly the organic contents of the substrate will have some effect since haustoriids generally prefer "clean" sands (Crocker, 1966; Bousfield, 1970). The estuarine environment is typically characterized by a greater availability of detritus, so it seems unlikely that E. estuarius is directly limited by food. The generally lower density of E. estuarius and the fact that there are fewer species of similar size and food preferences suggests that E. estuarius is not involved in any intense competition for its preferred food. The relatively lower density, at least at the Yaquina Bay station also suggests that there is not as much of a space restriction as there may be on E. brevicuspis in the upper intertidal of exposed beaches. Predation, including parasitism, may play more of a role in limiting the population of E. estuarius than E. brevicuspis. Predation by the abundant staghorn sculpin and the incidence of parasitism leads to this conclusion.

Much ecological evidence must be gathered, however, before these speculations on factors limiting the populations of Eohaustorius spp. can be confirmed or dismissed. As with other habitats, the interaction between the organisms living on sandy beaches and their relationship to physical factors are often subtle and difficult to measure.

It is certainly obvious that there are several complex mechanisms that determine the characteristics of the populations described in this study. Evidence presented here has helped to understand how these species succeed in the sandy beach environment and how they interact with their congeners. It is hoped that this study has also presented some ideas which will stimulate further research into the relationship between these species and their success in the sandy beach habitat.

Some of the problems which need resolution include:

- 1) Identification of resources for which the Eohaustorius spp. are competing or factors which limit their population;
- 2) Further identification of relationship between morphology, feeding behavior and niche (this work is presently in progress);
- 3) Whether patchy distribution is actively or passively acquired;
- 4) Determination of the subtidal range of lower intertidal and subtidal species;
- 5) Determination of mechanics by which intertidal distribution of E. brevicuspis and E. washingtonianus is adjusted after storms which erode sand from beaches;
- 6) More detailed comparison of E. estuarius population in Yaquina Bay with other populations in other estuaries.

V. SUMMARY AND CONCLUSIONS

1. Sibling species of the genus Eohaustorius on sandy beaches differed with respect to:

- a. Ecology: abundance, density, habitat with highest density zonation on the beach, degree of patchiness;
- b. Population dynamics: size at maturity, timing of reproductive periods, fecundity, population reproductive potential, and sex ratios;
- c. Physiology: tolerance to combinations of salinity and temperature.

The species were similar with respect to: gross morphology, distribution within the sediment; and presence in relatively clean beach sand.

2. There was a tendency for all three species measured, E. brevicuspis, E. washingtonianus and E. estuarius to have a greater degree of patchiness where their density was lowest. In a region of overlap between E. brevicuspis and E. washingtonianus, the former was more abundant but the latter had a higher degree of patchiness.

3. Distribution of the four species remained relatively constant throughout the year. On Lost Creek Beach E. brevicuspis was most abundant between +6 and +10 ft above MLLW which coincided with the intersection of the water table and the beach; E. washingtonianus was most abundant between the lower subtidal to +4 ft above MLLW; E. sawyeri was collected only occasionally and was found generally around MLLW. In Yaquina Bay, E. estuarius was most abundant between +2 and +6 ft MLLW.

4. Vertical zonation within the sand was about the same for both E. brevicuspis and E. washingtonianus, both being found most abundantly between 4 and 12 cm deep.

5. Examination of other collections of Eohaustorius spp. along the North American Pacific coast revealed that the distributional characteristics observed for these species in Oregon was similar throughout their range.

6. Eohaustorius brevicuspis had its peak of reproductive activity in the winter and early spring months. Percentage of gravid females in the population of this species was less than 1 per cent during the summer and early fall. Eohaustorius washingtonianus had its peak of reproductive activity at about the same time as E. brevicuspis, however, about 20 per cent of the females in this population were gravid throughout the rest of the year. The peak of E. estuarius reproductive activity occurred in the spring. There were virtually no gravid females in the Yaquina Bay population of this species in the summer and fall. Insufficient numbers of E. sawyeri were collected to determine when it reproduced.

7. Eohaustorius brevicuspis probably has a univoltine generation with mature individuals dying soon (1-2 months) after breeding. Individuals of Eohaustorius washingtonianus may breed more than once before they die, however, it is doubtful whether individuals that breed during the winter peak survive to breed the succeeding winter. It is more likely they breed once during the winter and then again (one or more times) during the summer and fall. Mature females of E. washingtonianus

are larger on the average (approximately .75 mm) than E. brevicuspis. Eohaustorius estuarius probably has a univoltine generation although the fact that there was probably interchange between the intertidal and subtidal populations makes this conclusion tentative. Mature females of E. estuarius were smaller (.65 mm) on the average than E. brevicuspis.

8. The ratio of E. brevicuspis males to females ranged from 1:1.03 to 1:2.12. The sex ratios in upper intertidal were significantly skewed towards females, whereas the sex ratios in the lower intertidal was significantly skewed towards males. Ratios of males to females for E. washingtonianus ranged from 1:0.4 to 1:2.21 although the differences were generally not significantly different from a 1:1 ratio. Ratios of males to females of E. estuarius at Yaquina Bay were between 1:0.9 and 1:1.94. The differences were generally not significantly different from a 1:1 ratio.

9. Fecundity of all species increased with size. Females of the largest species, E. washingtonianus, carried between 8 and 15 eggs on the average; females of E. brevicuspis between 5 and 10 eggs on the average; and, E. estuarius about the same number as E. brevicuspis. Juveniles reached approximately 1.5 mm in length before leaving the marsupium in all species. It took about three to four weeks at about 15°C in the laboratory for juveniles of E. brevicuspis and E. estuarius to reach the size when they left the marsupium.

10. Spatial overlap between populations of E. brevicuspis and E. washingtonianus was minimal when only mature individuals were considered. This was particularly true during the winter months when repro-

ductive activity in the two species was at its maximum.

11. Dominant faunal associates of Eohaustorius spp. on Lost Creek Beach included the amphipods, Dogielinotus loquax and Paraphoxus milleri; the isopod, Cirolana hartfordi; and, the blood worm, Euzonus mucronata. These species were most abundant in the upper intertidal area. The dominant faunal associates of Eohaustorius estuarius included the amphipod, Paraphoxus fatigans; the isopod, Cirolana hartfordi; the ghost shrimp, Callinasa californiensis; the bivalves, Tressus capax, Macoma nasuta, Clinocardium nuttalli and the polychaete, Abarenicola sp.

12. Major predators of E. brevicuspis are several species of pipers and plovers; E. washingtonianus, because of its lower distribution on the beach, is probably more preyed upon by fishes or other crustaceans during high tide; E. estuarius in Yaquina Bay is probably preyed upon by both shorebirds and fishes and also parasitized by a helminth that resembles a pseudophyllid tapeworm. Incidence of infection was as high as 12% of mature E. estuarius during the reproductive peak and averaged 4% during the year. No gravid parasitized females were ever found.

13. The three species, E. brevicuspis, E. washingtonianus and E. estuarius were exposed to a variety of salinity and temperature combinations in a laboratory experiment designed to discover any differences in salinity and temperature tolerance among them. E. estuarius proved to be the most tolerant to temperature and salinity extremes; E. washingtonianus, the least tolerant. The effect of salinity on survival was more significant than temperature.

14. It was concluded that the timing of the reproductive peak of E. brevicuspis, E. washingtonianus and E. estuarius may result in two adaptive advantages: 1) the coincidence of the peak of the reproductive cycle with the time of greatest habitat instability may well be an adaptation to ensure dispersal of young to other habitats and may help to explain how the beaches and estuaries of the North American-Pacific region were originally populated in the absence of any extensive and stable interconnections; 2) the coincidence of the peak of the reproductive cycle during the most productive time of the year may enhance the survival of the recently hatched juveniles.

15. The stability of the distributional zones of the four species throughout a variety of changing environmental conditions suggests that competitive action may be of significance.

16. This study has identified several characteristics of these species which serve to differentiate their respective niches and has verified that they warrant specific rank not only because of their morphological differences but also because of their reproductive isolation and other ecological differences.

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APPENDIX 1

TABLE I. INDEX OF DISPERSION (I) FOR E. BREVICUSPIS AT LOST CREEK BEACH TRANSECT.
FEBRUARY 1971 - FEBRUARY 1972.

STRATA	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	JAN	FEB
+12 - +14	20.59	32.78	10.19	X	X	X	X	1.82*	6.42	1.57*	37.41	13.30
+10 - +12	61.08	7.64	22.22	22.43	17.37	X	26.81	20.03	16.56	33.69	9.37	16.56
+ 8 - +10	14.17	6.95	11.75	2.22**	3.79	96.14	58.06	62.33	32.01	30.89	5.46	7.64
+ 6 - + 8	81.97	5.84	2.69	2.11**	5.75	14.14	15.16	3.12	5.07	I	6.45	6.57
+ 4 - + 6	20.60	5.88	2.52**	4.14	16.66	13.73	3.75	2.91	1.88*	I	6.98	0
+ 2 - +14	2.05**	I	6.36	2.37**	9.11	2.00**	0	0	0	I	0	0
MLW - + 2	0	I	3.18	0	0	0	0	0	0	I	0	0
TOTAL ALL STRATA	61.26	12.63	22.88	17.34	21.35	76.97	45.23	92.18	62.63	54.82	21.46	35.05

X = above surf zone

* = not significantly different from Poisson at .05 level

I = not sampled

** = not significantly different from Poisson at .01 level

TABLE II. INDEX OF DISPERSION (I) FOR E. WASHINGTONIANUS AT LOST CREEK BEACH TRANSECT.
FEBRUARY 1971 - FEBRUARY 1972.

STRATA	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	JAN	FEB
+4 - +6	0	I	3.51	16.88	.78*	3.05	14.64	0	0	I	2.92	3.69
+2 - +4	.89*	I	6.24	15.59	10.94	13.56	9.93	4.53	1.11*	I	5.33	5.24
MLW - +2	4.52	I	7.77	16.23	9.12	28.25	I	4.08	5.07	I	3.84	I
Below MLW	I	I	2.69	11.27	48.21	14.27	I	I	I	I	I	I
TOTAL	7.04		5.86	14.23	33.91	16.58	11.31	4.02	4.46		4.01	4.32

I = not sampled

* not significantly different from Poisson at .05

TABLE III. INDEX OF DISPERSION (I) FOR E. ESTUARIUS AT YAQUINA BAY TRANSECT.
FEBRUARY 1971 - FEBRUARY 1972

STRATA	FEB	5 MAR	24 MAR	APR	MAY	JUN	JUL	AUG	SEP	NOV	JAN	FEB
+6 and above	18.31	1.44*	14.11	0	0	I	28.17	2.44**	0	0	40.75	13.77
+4 - +6	21.13	37.15	12.87	9.91	4.21	3.42	6.14	12.06	15.78	7.39	13.53	15.02
+2 - +4	8.45	5.49	5.77	7.42	9.51	4.33	.58*	2.88**	5.86	.57*	0	3.02**
Below +2	4.43	7.77	1.11*	0	1.99**	I	I	I	I	I	I	2.16**
TOTAL	14.93	23.70	9.11	17.19	14.80	3.75	15.42	9.01	12.72	5.92	25.55	30.50

I = not sampled

* = not significantly different from Poisson at .05

N.B. = total number of samples in
each strata may vary

** = not significantly different from Poisson at .01

TABLE IV. ESTIMATES OF \hat{k} FOR E. BREVICUSPIS AT LOST CREEK BEACH TRANSECT.
FEBRUARY 1971 - FEBRUARY 1972.

STRATA	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	JAN	FEB
+12 - +14	.27	.11	.53	X	X	X	X	1.24	.18	3.04	.75	.50
+10 - +12	.68	1.89	.96	.35	.57	X	2.27	6.03	4.16	1.97	5.76	4.41
+ 8 - +10	1.30	.97	4.65	24.16	18.78	.46	.41	.52	2.38	.71	9.60	5.06
+ 6 - + 8	.19	1.09	32.29	46.22	8.22	.50	1.61	.37	.60	I	3.35	1.36
+ 4 - + 6	.32	.51	20.64	37.92	2.87	1.79	.63	.53	.18	I	.72	0
+ 2 - + 4	.33	I	1.93	.71	.38	1.80	0	0	0	I	0	0
MLW - + 2	0	I	.68	0	0	0	0	0	0	I	0	0
TOTAL	.29	.61	1.16	1.39	1.51	.29	.67	.35	.48	.58	1.44	.88

X = above surf zone

I = not sampled

Estimates is by moments where $\hat{k} = \frac{\overline{x^2} - \frac{s^2}{n}}{s^2 - \bar{x}}$

\hat{k} for strata totals where $n > 50 = \frac{\overline{x^2} - \frac{s^2}{n}}{s^2 - \bar{x}}$ as recommended by Elliott (1971)

TABLE V. ESTIMATES OF MEAN (\bar{x}) PER M² FOR E. BREVICUSPIS AT LOST CREEK BEACH TRANSECT.
FEBRUARY 1971 - FEBRUARY 1972.

STRATA	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	JAN	FEB
+12 - +14	7.5	6.8	5.9	X	X	X	X	1.2	1.6	1.9	31.0	7.5
+10 - +12	47.1	13.3	22.7	9.7	11.1	X	61.4	116.8	66.2	67.9	49.0	70.2
+ 8 - +10	18.6	6.5	51.2	29.6	52.8	53.2	30.1	38.4	76.9	24.4	43.3	34.4
+ 6 - + 8	23.5	5.8	54.7	51.3	39.6	8.0	24.3	1.1	3.4	I	18.9	7.2
+ 4 - + 6	8.4	3.1	31.6	22.0	46.6	24.2	2.1	1.3	.5	I	5.0	0
+ 2 - + 4	.6	I	11.0	1.2	4.0	2.2	0	0	0	I	0	0
MLW - + 2	0	I	1.8	0	0	0	0	0	0	I	0	0
TOTAL	17.18	7.13	25.56	27.76	30.78	21.90	29.45	31.76	29.72	31.40	29.46	29.83

X = above surf zone

I = not sampled

TABLE VI. ESTIMATES OF \hat{k} (k) FOR E. WASHINGTONIANUS AT LOST CREEK BEACH TRANSECT.
 FEBRUARY 1971 - FEBRUARY 1972.

STRATA	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	JAN	FEB
+4 - +6	0	0	.34	.16	-1.05	.13	.22	0	0	I	.42	.31
+2 - +4	-1.10	I	.53	.70	.55	.59	.59	.18	1.00	I	.39	.23
MLW - +2	.72	I	.59	.63	.11	.21	I	.61	.34	I	.46	I
Below MLW	I	I	.25	.40	.32	.41	I	I	I	I	I	I
TOTAL	2.00		.50	.59	.19	.35	.47	.50	.20		.51	.54

I = not sampled

TABLE VII. ESTIMATES OF MEAN (\bar{x}) PER M² FOR E. WASHINGTONIANUS AT LOST CREEK BEACH TRANSECT. FEBRUARY 1971 - FEBRUARY 1972.

STRATA	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	JAN	FEB
+4 - +6	0	0	1.2	4.2	.3	.8	4.5	0	0	I	1.1	1.2
+2 - +4	.2	I	3.4	11.7	6.6	8.8	6.3	1.1	.2	I	2.2	1.5
MLW - +2	3.0	I	4.8	11.3	1.8	7.2	I	2.3	1.9	I	1.7	I
Below MLW	I	I	.7	5.2	19.7	6.9	I	I	I	I	I	I
TOTAL	1.6		2.58	8.10	7.10	5.93	5.40	1.70	1.05		1.67	1.35

I = not sampled

TABLE VIII. ESTIMATES OF \hat{k} FOR E. ESTUARIUS AT YAQUINA BAY TRANSECT
 FEBRUARY 1971 - FEBRUARY 1972.

STRATA	FEB	5 MAR	24 MAR	APR	MAY	JUN	JUL	AUG	SEP	NOV	JAN	FEB
+6 and above	.33	-.34	.19	0	0	I	.20	.76	0	0	.19	2.24
+4 - +6	.46	.13	.26	1.25	3.66	.73	.71	.21	.33	.54	.51	.64
+2 - +4	.66	.51	.44	.43	.48	.71	-8.75	.72	.50	-1.00	0	.33
Below +2	.31	.33	1.86	0	.16	I	I	I	I	I	I	.18
TOTAL	.46	.18	.31	2.33	.45	.82	.95	.26	.34	.27	.27	.34

I = not sampled

TABLE IX. ESTIMATES OF MEAN (\bar{x}) PER M² FOR E. ESTUARIUS AT YAQUINA BAY
TRANSECT. FEBRUARY 1971 - FEBRUARY 1972.

STRATA	FEB	5 MAR	24 MAR	APR	MAY	JUN	JUL	AUG	SEP	NOV	JAN	FEB
+6 and above	7.6	.3	4.8	0	0	I	10.2	1.5	0	0	8.7	32.0
+4 - +6	12.8	9.9	6.3	11.4	12.2	2.1	4.3	3.9	6.4	4.7	7.8	10.7
+2 - +4	6.1	3.4	2.7	3.5	6.5	2.8	3.8	1.8	3.3	.5	0	1.7
Below +2	1.7	3.8	.3	0	.5	I	I	I	I	I	I	.8
TOTAL	6.93	5.40	2.80	6.30	6.95	2.45	5.95	2.55	4.65	1.60	7.80	11.60

I = not sampled

TABLE X. ESTIMATES OF \bar{x}^* FOR E. BREVICUSPIS AT LOST CREEK BEACH TRANSECT
 $(\bar{x}^* = \bar{x} + \frac{\hat{x}}{k}$, SEE TEXT) = "MEAN CROWDING", FEBRUARY 1971 -

FEBRUARY 1972.

STRATA	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	JAN	FEB
+12 - +14	35.3	68.6	17.0	X	X	X	X	2.2	10.4	2.5	72.3	22.5
+10 - +12	116.4	20.3	46.3	37.4	0.6	X	88.4	136.2	82.1	102.4	57.5	86.1
+ 8 - +10	32.9	13.2	62.2	30.8	55.6	168.9	103.5	112.2	109.2	58.8	47.8	41.1
+ 6 - + 8	147.2	11.1	56.4	52.4	44.4	24.0	39.4	4.1	9.1	I	24.5	12.5
+ 4 - + 6	34.7	9.2	33.1	22.6	62.8	37.7	5.4	3.8	3.2	I	11.9	0
+ 2 - + 4	2.4	I	16.7	2.9	14.5	3.4	0	0	0	I	0	0
MLW - + 2	0	I	4.4	0	0	0	0	0	0	I	0	0

X = above surf zone

I = not sampled

TABLE XI. ESTIMATES OF $\frac{\bar{x}^*}{\bar{x}}$ FOR E. BREVICUSPIS AT LOST CREEK BEACH TRANSECT

$$\left(\frac{\bar{x}^*}{\bar{x}} = 1 + \frac{1}{\hat{k}}, \text{ SEE TEXT}\right), \text{ I.E., "PATCHINESS", FEBRUARY 1971 -}$$

FEBRUARY 1972.

STRATA	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	JAN	FEB
+12 - +14	4.7	10.1	2.9	X	X	X	X	1.8	6.6	1.3	2.3	3.0
+10 - +12	2.5	1.5	2.0	3.9	2.8	X	1.4	1.2	1.2	1.5	1.2	1.2
+ 8 - +10	1.8	2.0	1.2	1.0	1.1	2.2	3.4	2.9	1.4	2.4	1.1	1.2
+ 6 - + 8	6.3	1.9	1.0	1.0	1.1	3.0	1.6	3.7	2.7	I	1.3	1.7
+ 4 - + 6	4.1	3.0	1.1	1.0	1.4	1.6	2.6	2.9	6.6	I	1.4	0
+ 2 - + 4	4.0	I	1.5	2.4	3.6	1.6	0	0	0	I	0	0
MLW - + 2	0	I	2.5	0	0	0	0	0	0	I	0	0

X = above surf zone

I = not sampled

TABLE XII. ESTIMATES OF \bar{x}^* FOR E. WASHINGTONIANUS AT LOST CREEK BEACH TRANSECT
 $(\bar{x} = \bar{x} + \frac{\bar{x}}{k})$ = "MEAN CROWDING", FEBRUARY 1971 - FEBRUARY 1972.

STRATA	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	JAN	FEB
+4 - +6	0.0	0	4.7	30.4	0.0	7.0	25.0	0	0	I	3.7	5.1
+2 - +4	0.0	I	9.8	28.4	18.6	23.7	17.0	7.2	0.4	I	7.8	8.0
MLW - +2	7.2	I	12.9	29.2	18.2	41.5	I	6.1	7.5	I	5.4	I
-2 - MLW	I	I	3.5	18.2	81.3	23.7	I	I	I	I	I	I

I = not sampled

TABLE XIII. ESTIMATES OF $\frac{\bar{x}^*}{\bar{x}}$ FOR E. WASHINGTONIANUS AT LOST CREEK BEACH TRANSECT

$$\left(\frac{\bar{x}^*}{\bar{x}} = 1 + \frac{1}{\hat{k}}\right) = \text{"PATCHINESS", FEBRUARY 1971 - FEBRUARY 1972.}$$

STRATA	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	JAN	FEB
+4 - +0	0	3.9	7.3	0	8.7	5.5	0	0	I	3.4	3.2	
+2 - +4	0	I	2.9	2.4	2.8	2.7	2.7	6.6	2.0	I	2.6	5.3
MLW - +2	2.4	I	2.7	2.6	10.1	5.8	I	2.6	3.9	I	3.2	I
-2 - MLW	I	I	5.0	3.5	4.1	2.4	I	I	I	I	I	I

I = not sampled

TABLE XIV. ESTIMATES OF \bar{x}^* FOR E. ESTUARIUS AT YAQUINA BAY TRANSECT

$$(\bar{x}^* = \bar{x} + \frac{\bar{x}}{k}) = \text{"MEAN CROWDING", FEBRUARY 1971 - FEBRUARY 1972.}$$

STRATA	FEB	5 MAR	24 MAR	APR	MAY	JUN	JUL	AUG	SEP	NOV	JAN	FEB
+6 and above	30.6	0	30.1	0	0	I	61.2	3.5	0	0	54.5	46.3
+4 - +6	40.6	86.1	34.2	20.5	15.5	5.0	10.4	22.5	25.8	13.4	23.1	27.4
+2 - +4	15.3	10.1	8.8	11.6	20.0	6.7	3.34	4.3	9.9	0	0	6.9
Below +2	7.2	15.3	0.5	0	3.6	I	I	I	I	I	I	7.0

I = not sampled

TABLE XV. ESTIMATES OF $\frac{\bar{x}^*}{\bar{x}}$ FOR E. ESTUARIUS AT YAQUINA BAY TRANSECT

$$\left(\frac{\bar{x}^*}{\bar{x}} = 1 + \frac{1}{\hat{k}}\right) = \text{"PATCHINESS"}, \text{ FEBRUARY 1971 - FEBRUARY 1972.}$$

STRATA	FEB	5 MAR	24 MAR	APR	MAY	JUN	JUL	AUG	SEP	NOV	JAN	FEB
+6 and above	4.0	0	6.3	0	0	I	6.0	2.3	0	0	6.3	1.5
+4 - +6	3.2	8.7	4.8	1.8	1.3	2.4	2.4	5.8	4.0	2.9	3.0	2.6
+2 - +4	2.5	3.0	3.3	3.3	3.1	2.4	0	2.4	3.0	0	0	4.0
Below +2	4.2	4.0	1.5	0	7.3	I	I	I	I	I	I	6.6

I = not sampled

TABLE XVI. REPRODUCTIVE CYCLE OF E. BREVICUSPIS AND E. WASHINGTONIANUS AT LOST CREEK BEACH.
 NUMBERS INDICATE PERCENTAGE GRAVID FEMALES OF TOTAL FEMALES GIVEN IN PARENTHESES

E. BREVICUSPIS

STRATA	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	JAN	FEB
+12 - 14'	1.9(52)	20.9(86)	15.0(40)	I	I	I	I	0 (9)	0 (9)	0 (16)	11.1(278)	8.2(61)
+10 - 12'	68.8(544)	18.4(125)	24.1(170)	0 (71)	0 (88)	I	0 (367)	0.4(654)	0 (358)	0.8(446)	22.2(414)	27.6(554)
+ 8 - 10'	57.8(185)	10.4(67)	35.7(373)	20.6(218)	3.2(347)	0 (338)	1.2(166)	1.5(188)	0.8(371)	0 (178)	26.6(240)	44.9(118)
+ 6 - 8'	76.9(247)	30.8(52)	28.3(364)	33.4(334)	16.6(247)	2.1(46)	2.6(115)	0 (1)	0 (13)	I	38.8(18)	60.0(10)
+ 4 - 6'	66.0(47)	23.8(21)	54.2(131)	34.5(58)	12.8(266)	5.7(105)	7.4(22)	16.6(6)	0 (2)	I	40.0(5)	0
+ 2 - 4'	50.0(2)	I	62.1(29)	33.3(3)	15.0(20)	0 (17)	0 (2)	0	0	I	0	0
MLW - 2'	<u>100.0(2)</u>	<u>I</u>	<u>25.0(12)</u>	<u>0 (1)</u>	<u>0</u>	<u>0</u>	<u>I</u>	<u>0</u>	<u>I</u>	<u>I</u>	<u>0 (3)</u>	<u>I</u>
TOTAL	65.5(1089)	19.7(351)	33.5(1120)	15.8(685)	9.2(968)	1.4(506)	1.0(672)	0.8(858)	0.4(753)	0.6(640)	20.5(958)	29.2(743)

E. WASHINGTONIANUS

STRATA	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	JAN	FEB
+ 6 - + 8'	0	0	0 (1)	0 (2)	0	0	0	0	0	I	0 (1)	0 (1)
+ 4 - 6'	0	0	0 (10)	17.4(23)	0 (1)	0 (4)	25.0(20)	0	0	I	14.3(7)	71.4(7)
+ 2 - 4'	100 (1)	I	20.0(25)	24.6(57)	36.1(36)	28.8(52)	18.4(38)	0 (7)	0 (1)	I	37.5(8)	71.4(7)
MLW - 2'	65.4(26)	I	10.3(29)	31.9(72)	0 (13)	2.6(38)	I	30 (10)	20.0(5)	I	50.0(4)	I
- 2 - MLW	<u>I</u>	<u>I</u>	<u>33.3(6)</u>	<u>0 (24)</u>	<u>7.0(128)</u>	<u>13.0(46)</u>	<u>I</u>	<u>I</u>	<u>I</u>	<u>I</u>	<u>I</u>	<u>I</u>
TOTAL	66.7(27)		13.7(73)	23.3(176)	12.4(178)	15.7(140)	20.7(58)	17.6(17)	16.7(6)		26.1(23)	67.7(15)

I = not sampled

TABLE XVII. RATIO OF MALES TO FEMALES OF EOHAUSTORIUS SPP. AT EACH ELEVATION ON LOST CREEK BEACH AND YAQUINA BAY FEBRUARY 1971 - FEBRUARY 1972. NUMBERS INDICATE NUMBER OF FEMALES TO EACH MALE.

E. BREVICUSPIS

STRATA	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	JAN	FEB
+12 - +14	1.73 ³	3.58 ^{2,5}	2.11 ²	X	X	X	X	3.00 ¹	1.29 ¹	5.33 ²	8.69 ^{2,5}	4.36 ^{2,5}
+10 - +12	2.61 ^{2,5}	1.36 ¹	2.54 ²	2.73 ^{2,5}	3.83 ^{2,5}	X	1.49 ²	1.27 ²	1.18 ¹	1.91 ²	5.38 ^{2,5}	3.74 ^{2,5}
+ 8 - +10	1.67 ²	1.76 ²	2.68 ^{2,5}	2.80 ^{2,5}	1.92 ²	1.74 ^{2,4}	1.23 ¹	0.96 ¹	0.93 ¹	2.70 ²	1.24 ^{1,5}	0.52 ^{2,4}
+ 6 - + 8	1.75 ²	1.21 ¹	1.99 ²	1.87 ^{2,4}	1.66 ²	1.35 ¹	0.89 ^{1,5}	0.10 ^{3,5}	0.62 ¹	I	0.11 ^{2,5}	0.16 ^{2,4}
+ 4 - + 6	0.53 ^{2,5}	0.72 ^{1,5}	0.71 ^{3,5}	0.36 ^{2,5}	1.33 ²	0.77 ^{1,5}	4.40 ^{2,4}	0.86 ¹	0.67 ¹	I	0.11 ^{2,5}	I
+ 2 - + 4	0.29 ¹	I	0.36 ^{2,5}	0.33 ^{1,5}	1.00 ¹	3.40 ³	0	0	0	I	0	0
MLLW - + 2	0	I	2.00 ¹	0	0	0	0	0	0	I	0	0
TOTAL (ALL STRATA)	1.85 ²	1.55 ²	1.65 ²	1.51 ²	1.69 ²	1.37 ²	1.31 ²	1.18 ²	1.03 ¹	2.12 ²	1.85 ²	1.65 ²

E. WASHINGTONIANUS

STRATA	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	JAN	FEB
+ 4 - + 6	0	0	5.00 ¹	1.21 ¹	1.00 ¹	1.00 ¹	1.05 ¹	0	0	I	1.75 ¹	1.14 ¹
+ 2 - + 4	0.50 ¹	I	2.78 ³	0.95 ¹	1.20 ¹	1.44 ¹	1.52 ¹	1.75 ¹	1.00 ¹	I	0.57 ¹	0.88 ¹
MLLW - + 2	1.10 ¹	I	1.53 ¹	1.76 ²	2.60 ¹	1.12 ¹	I	0.77 ¹	0.36 ¹	I	0.31 ¹	I
- 2 - MLLW	I	I	2.00 ¹	1.16 ¹	1.86 ²	1.92 ³	I	I	I	I	I	I
TOTAL (ALL STRATA)	1.08 ¹		2.21 ²	1.19 ¹	1.70 ²	1.43 ²	1.32 ¹	1.00 ¹	0.40 ¹		0.70 ¹	1.15 ¹

TABLE XVII. (Continued)

E. ESTUARIUS

STRATA	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	JAN	FEB
TOTAL (ALL STRATA)	1.37 ³	1.18 ¹ 1.11 ¹	1.42 ³	0.93 ¹	1.70 ¹	1.25 ¹	0.70 ¹	1.27 ¹	10.00 ¹	I	1.94 ²	1.32 ¹

¹ Not significant

² significantly different from 1:1 sex ratio at $\alpha = .01$

³ significantly different from 1:1 sex ratio at $\alpha = .05$

⁴ significant at .05 from sex ratio of total population for that collecting period

⁵ significant at .01 from sex ratio of total population for that collecting period

X = above surf zone

I = not sampled

TABLE XVIII. MEAN FECUNDITY OF DIFFERENT SIZE FEMALES OF EOHAUSTORIUS SPP. BY MONTH
 [mm ±1 S.D. (SAMPLE SIZE)], FEBRUARY 1971 - FEBRUARY 1972.

1971

E. BREVICUSPIS
 LOST CREEK BEACH

SIZE (mm)	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP
3	5.05±.94(20)							8.00±0 (1)
3.5	5.99±1.28(87)							
4	7.05±2.43(97)	4.5 ±1.00(3)	7.20±2.10(5)	8.00±1.41(2)	7.25±.96(4)		9.00±1.73(3)	7.00±1.41(2)
4.5	8.75±1.83(8)	±	8.78±0.97(9)	9.00±1.41(2)	7.75±.96(4)		10.00±0 (1)	13.00±0 (1)
5	13.00±0 (2)				9.00±0 (1)			

1971

E. WASHINGTONIANUS
 LOST CREEK BEACH

SIZE (mm)	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP
3.5								
4			13.00±0 (13)				11.20±4.82(5)	9.00±1.41(2)
4.5	8.33±2.08(3)		11.50±2.12(2)	9.80±1.48(5)	9.83±1.33(6)	10.00±0 (1)	11.00±0 (1)	
5	7.83±2.12(6)		13.00±4.24(2)	13.80±2.49(5)	16.75±4.99(4)	14.50±3.15(6)	11.50±2.10(2)	
5.5					19.00±0 (1)		15.00±0 (1)	
6					15.00±0 (1)			

1971

E. ESTUARIUS
 YAQUINA BAY

SIZE (mm)	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP
3				7.00±0 (1)	6.50±.71(2)			
3.5		5.00±1.41(2)	7.67±1.52(3)	6.50±0.71(2)	8.33±1.53(3)			
4	7.00±0 (2)							
4.5	7.67±1.15(3)	10.50±4.95(2)						
5								

E. BREVICUSPIS
 LOST CREEK BEACH

1972

SIZE (mm)	OCT	NOV	JAN	FEB
3			6.73±1.09(13)	5.60±1.20(5)
3.5	8.00±0(1)	8.00±0(1)	6.97±1.19(31)	7.62±1.50(13)
4		7.00±0(1)	8.62±1.52(35)	8.67±0.89(12)
4.5			10.75±2.06(4)	11.00±0 (2)

E. WASHINGTONIANUS
 LOST CREEK BEACH

1972

SIZE (mm)	OCT	NOV	JAN	FEB
3.5			6.00±0 (1)	
4			9.33±1.15(3)	8.67±0.58(3)
4.5				14.50±2.12(2)
5				

TABLE XIX. MEAN SIZE OF GRAVID EOHAUSTORIUS SPP. BY MONTH
 [mm \pm 1 S.D. (sample size)], FEBRUARY 1971 -
 FEBRUARY 1972.

	<u>E. BREVICUSPIS</u> LOST CREEK BEACH	<u>E. WASHINGTONIANUS</u> LOST CREEK BEACH	<u>E. ESTUARIUS</u> YAQUINA BAY
FEB	3.58 \pm .00 (692)	4.82 \pm .01 (17)	4.10 \pm .04 (5)
5 MAR			3.50 \pm 1.0 (2)
24 MAR	3.76 \pm .00 (69)	I	3.51 \pm .14 (17)
APR	3.93 \pm .00 (371)	4.60 \pm .02 (10)	3.41 \pm .01 (16)
MAY	3.92 \pm .00 (108)	4.67 \pm .00 (41)	3.17 \pm .00 (29)
JUN	4.01 \pm .00 (89)	4.67 \pm .01 (23)	3.21 \pm .01 (12)
JUL	4.00 \pm .00 (7)	4.30 \pm .01 (22)	4.00 \pm .00 (1)
AUG	4.00 \pm .01 (6)	4.45 \pm .03 (10)	0
SEP	3.93 \pm .03 (7)	4.33 \pm .03 (3)	0
OCT	3.50 \pm .08 (3)	4.50 \pm .00 (1)	I
NOV	3.38 \pm .06 (4)	I	0
JAN	3.61 \pm .00 (195)	3.78 \pm .02 (7)	0
FEB	3.54 \pm .00 (217)	3.95 \pm .03 (10)	4.00 \pm .00 (2)

I = not sampled

0 = no gravid females present

TABLE XX. STATISTICAL ANALYSIS OF SURVIVAL OF E. BREVICUSPIS AFTER 6, 12, 24 AND 48 HOURS OF EXPOSURE TO 20 TEMPERATURE SALINITY COMBINATIONS.

6 HOURS		
VARIABLE	+ STATISTIC (14 d.f.)	SIGNIFICANCE LEVEL
T	-0.79	n.s.
S	1.81	0.10
T ²	0.76	n.s.
S ²	-1.74	n.s.
TXS	0.21	n.s.
12 HOURS		
VARIABLE	T-STATISTIC (14 d.f.)	SIGNIFICANCE LEVEL
T	0.28	n.s.
S	6.52	0.01
T ²	-0.61	n.s.
S ²	-6.13	0.01
TXS	0.72	n.s.
24 HOURS		
VARIABLE	T-STATISTIC (14 d.f.)	SIGNIFICANCE LEVEL
T	-1.59	n.s.
S	3.16	0.01
T ²	0.88	n.s.
S ²	-3.73	0.01
TXS	1.94	0.10
48 HOURS		
VARIABLE	T-STATISTIC (14 d.f.)	SIGNIFICANCE LEVEL
T	0.64	n.s.
S	6.20	0.01
T ²	-1.13	n.s.
S ²	-5.75	0.01
TXS	0.76	n.s.

TABLE XXI. STATISTICAL ANALYSIS OF SURVIVAL OF E. WASHINGTONIANUS AFTER 6, 12, 24 AND 48 HOURS OF EXPOSURE TO 20 TEMPERATURE SALINITY COMBINATIONS.

6 HOURS		
VARIABLE	T-STATISTIC (14 d.f.)	SIGNIFICANCE LEVEL
T	0.56	n.s.
S	10.51	0.01
T ²	-1.23	n.s.
S ²	-9.11	0.01
TXS	1.31	n.s.
12 HOURS		
VARIABLE	T-STATISTIC (14 d.f.)	SIGNIFICANCE LEVEL
T	.63	n.s.
S	4.97	0.01
T ²	-0.82	n.s.
S ²	-2.86	0.05
TXS	-0.30	n.s.
24 HOURS		
VARIABLE	T-STATISTIC (14 d.f.)	SIGNIFICANCE LEVEL
T	-0.26	n.s.
S	8.54	0.01
T ²	-0.41	n.s.
S ²	-6.84	0.01
TXS	1.21	n.s.
48 HOURS		
VARIABLE	T-STATISTIC (14 d.f.)	SIGNIFICANCE LEVEL
T	1.04	n.s.
S	3.60	0.01
T ²	-1.26	n.s.
S ²	-1.52	n.s.
TXS	-1.01	n.s.

TABLE XXII. STATISTICAL ANALYSIS OF SURVIVAL OF E. ESTUARIUS
AFTER 6, 12, 24 AND 48 HOURS OF EXPOSURE TO 20
TEMPERATURE SALINITY COMBINATIONS.

6 HOURS		
VARIABLE	T-STATISTIC (14 d.f.)	SIGNIFICANCE LEVEL
T	-0.40	n.s.
S	2.47	0.05
T ²	-0.56	n.s.
S ²	-3.32	0.01
TXS	2.37	0.05
12 HOURS		
VARIABLE	T-STATISTIC (14 d.f.)	SIGNIFICANCE LEVEL
T	-1.13	n.s.
S	3.63	0.01
T ²	-0.16	n.s.
S ²	-4.37	0.01
TXS	2.45	0.05
24 HOURS		
VARIABLE	T-STATISTIC (14 d.f.)	SIGNIFICANCE LEVEL
T	0.25	n.s.
S	0.45	n.s.
T ²	-1.23	n.s.
S ²	-1.45	n.s.
TXS	2.31	0.05
48 HOURS		
VARIABLE	T-STATISTIC (14 d.f.)	SIGNIFICANCE LEVEL
T	-1.06	n.s.
S	4.28	0.01
T ²	0.53	n.s.
S ²	-4.49	0.01
TXS	1.37	n.s.

APPENDIX 2

Figure 1. Vertical distribution within the sand of Eohaustorius brevicuspis and E. washingtonianus at Lost Creek Beach on 13 July 1971.

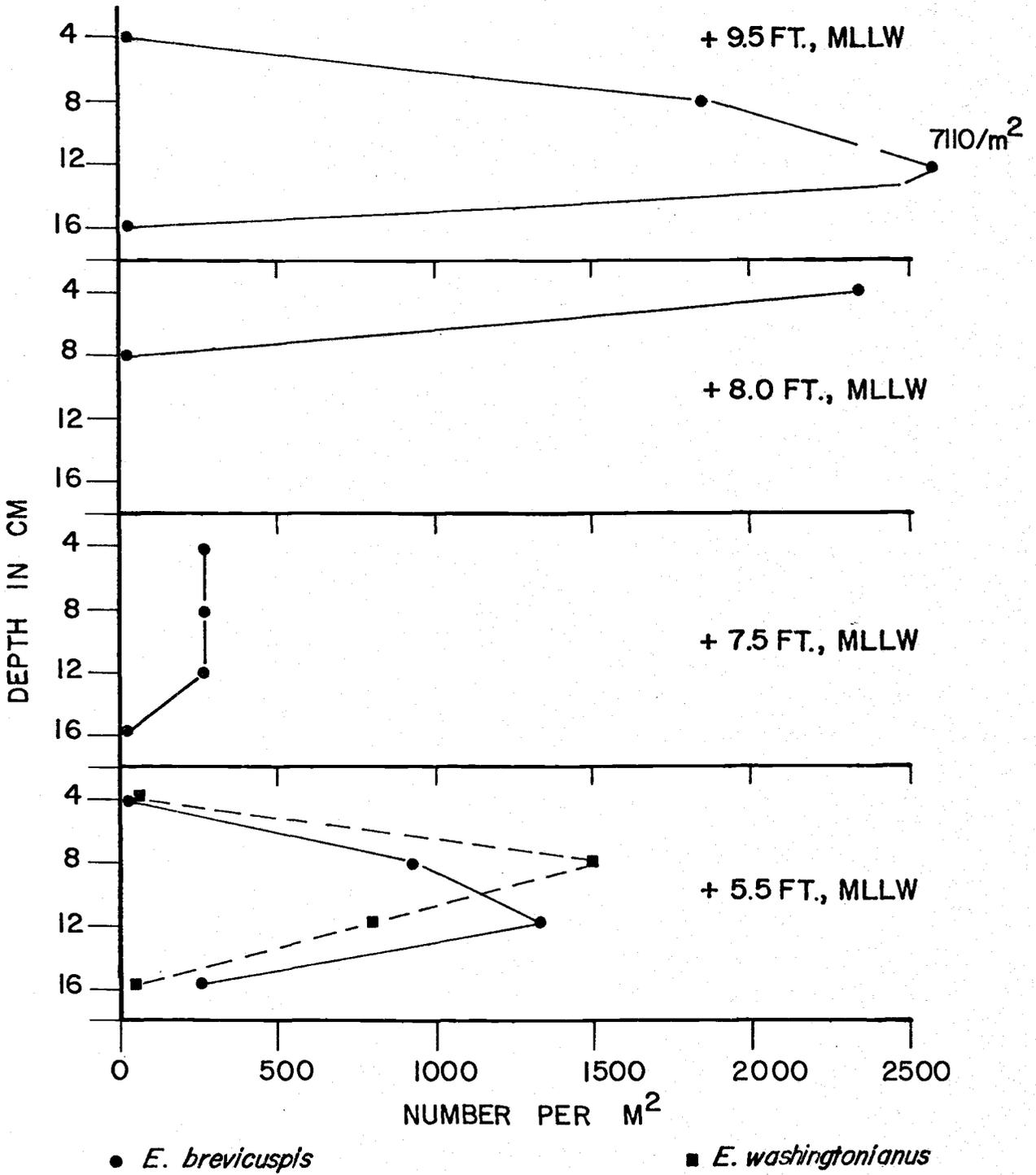


Figure 2. Vertical distribution within the sand of Eohaustorius brevicuspis and E. washingtonianus at Lost Creek Beach on 18 August 1971.

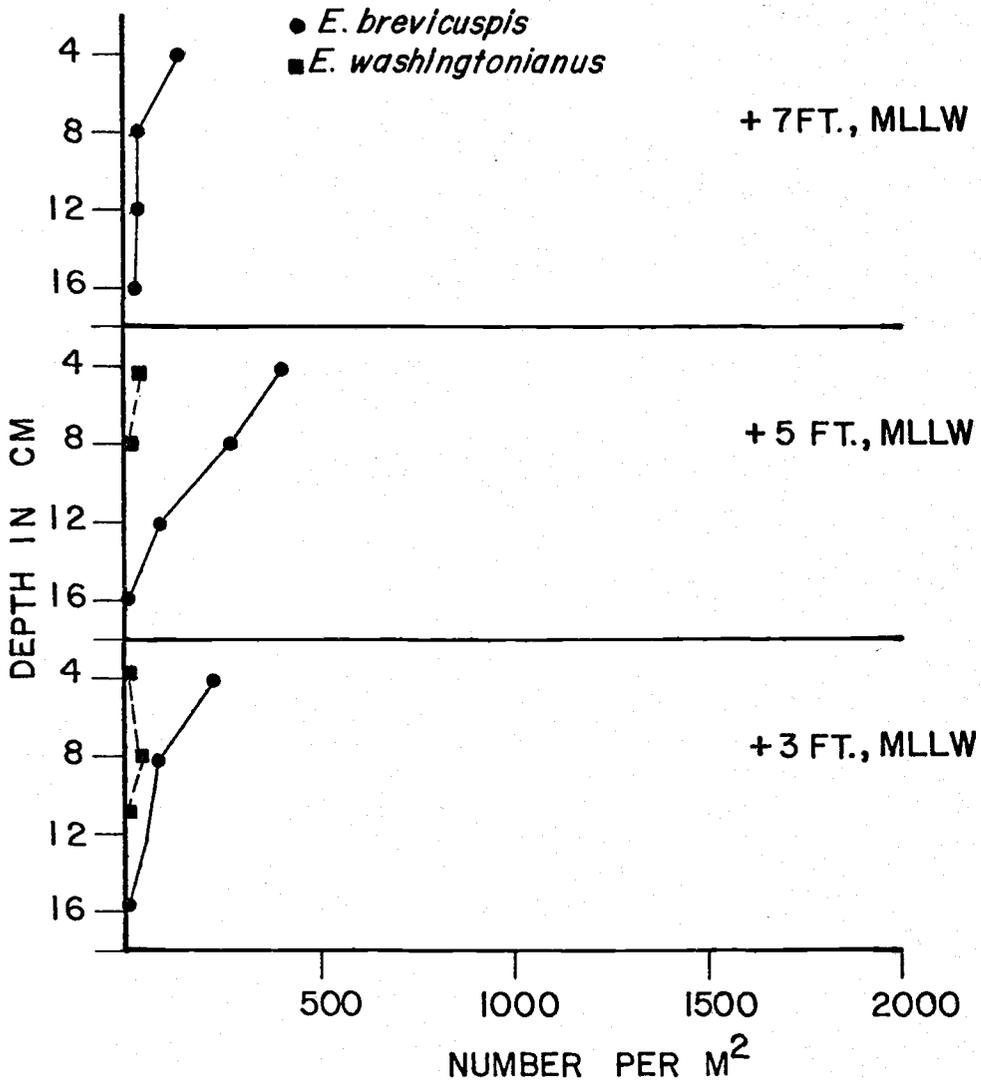


Figure 3. Vertical distribution within the sand of Eohaustorius brevicuspis at 7.5 ft above MLLW on Lost Creek Beach, 27 January 1972. (Average of six replicate samples).

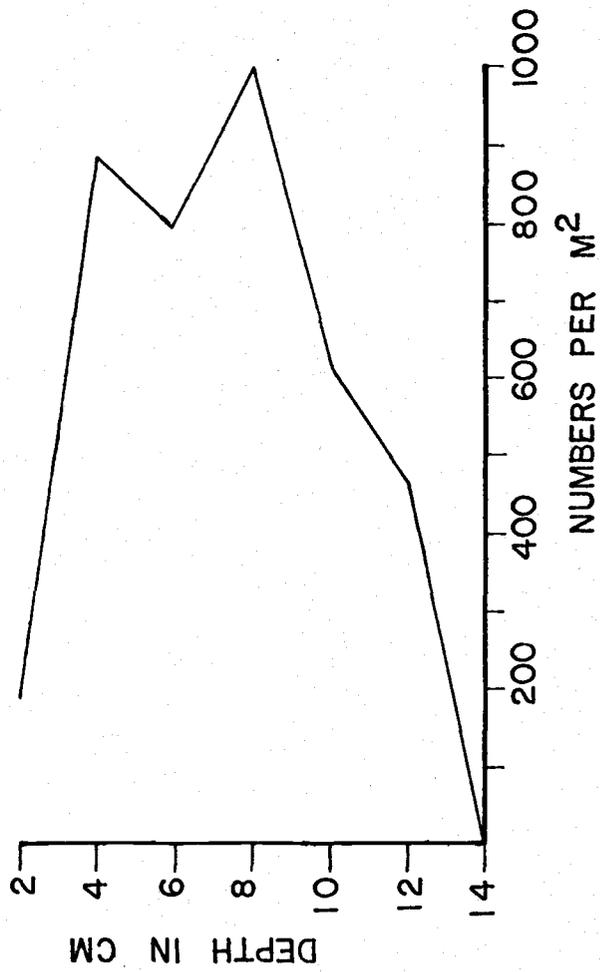


Figure 4. Vertical distribution within the sand of Eohaustorius brevicuspis and E. washingtonianus at Lost Creek Beach on 30 January 1972.

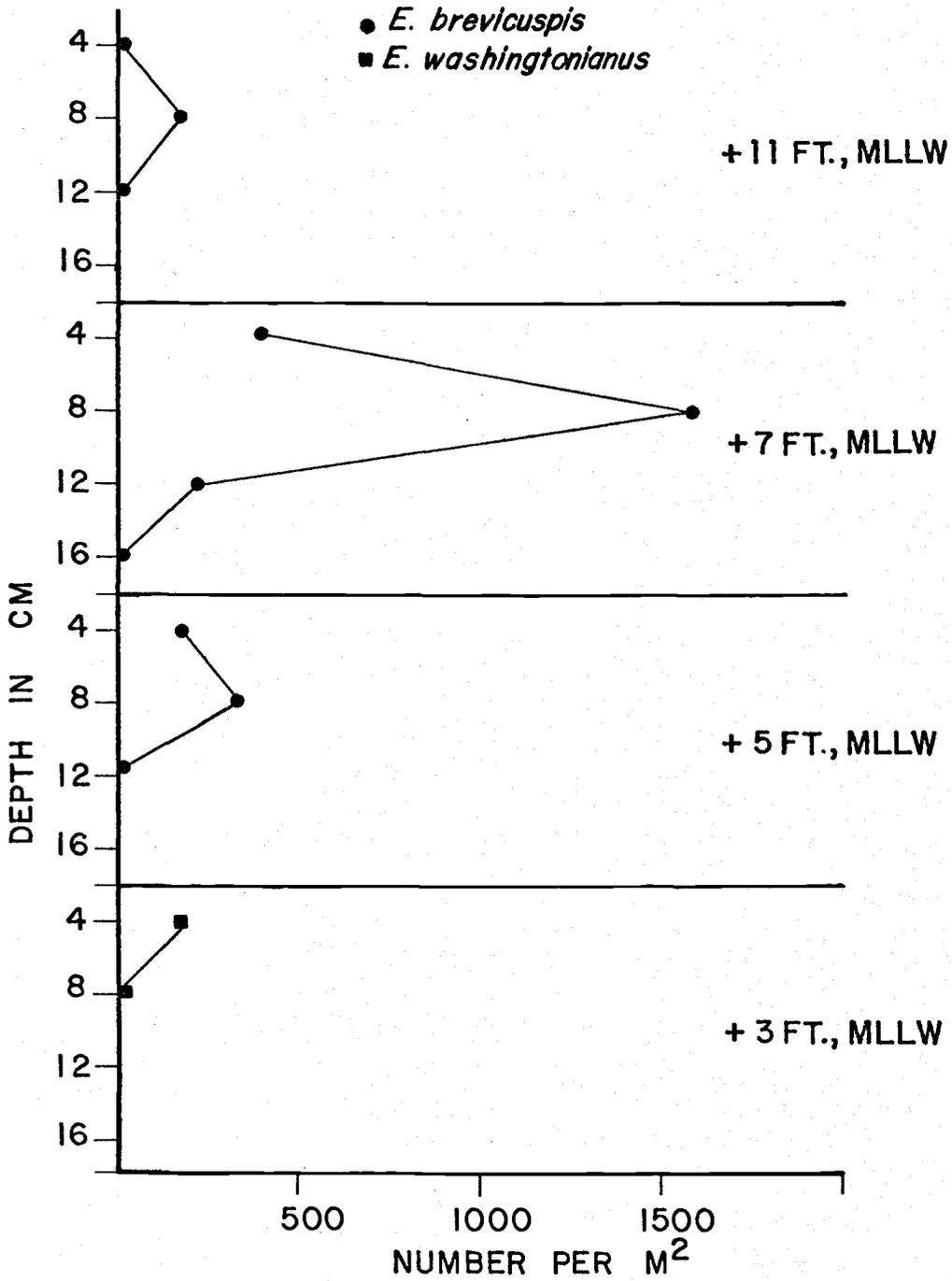


Figure 5. Distribution of Eohaustorius brevicuspis along
North American-Pacific Coast.

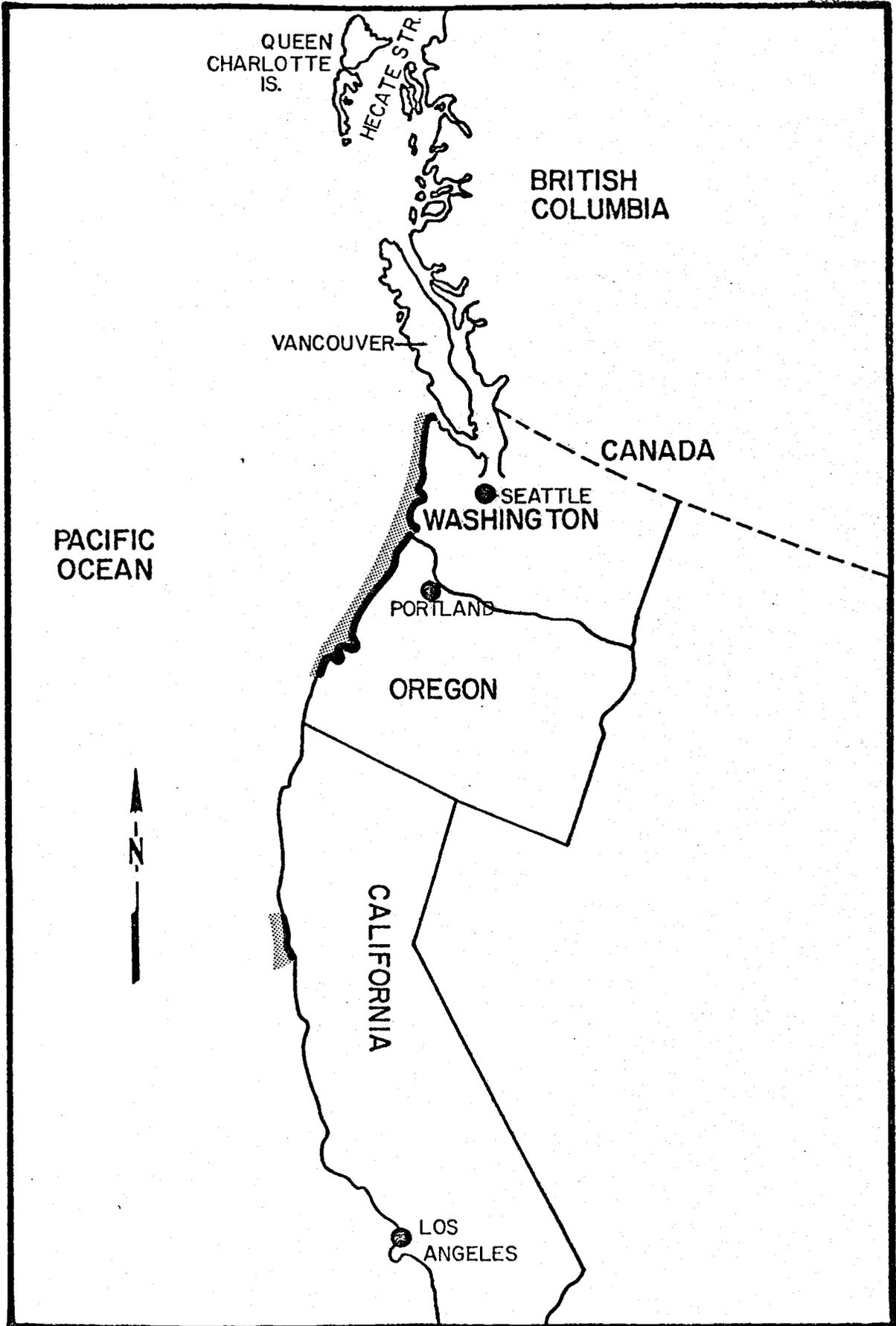


Figure 6. Distribution of Eohaustorius washingtonianus along North American-Pacific Coast.

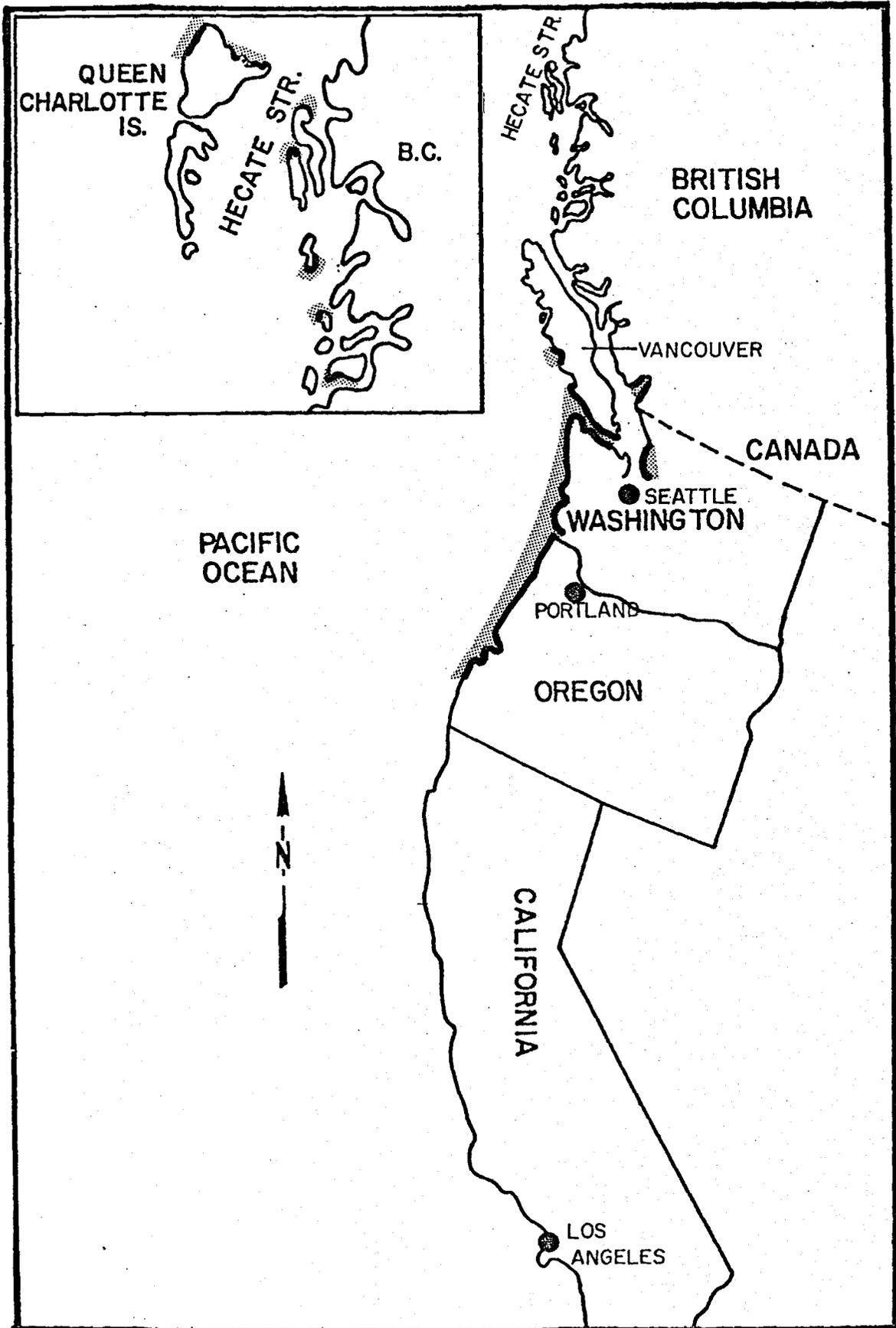


Figure 7. Distribution of Eohaustorius estuarius along North American-Pacific Coast. Hatching indicates that their distribution is only in estuaries.

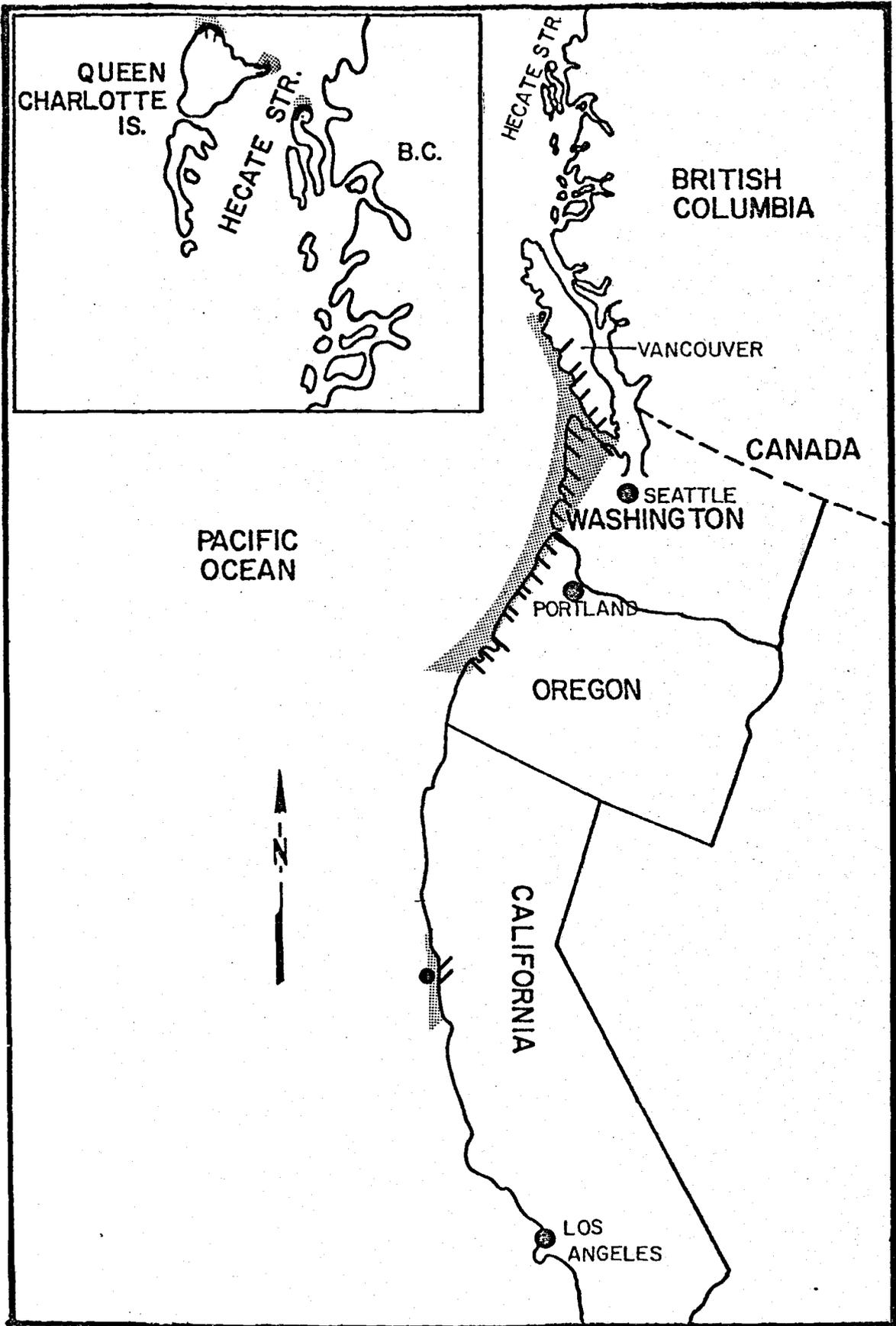


Figure 8. Distribution of Eohaustorius sawyeri along North American-Pacific Coast.

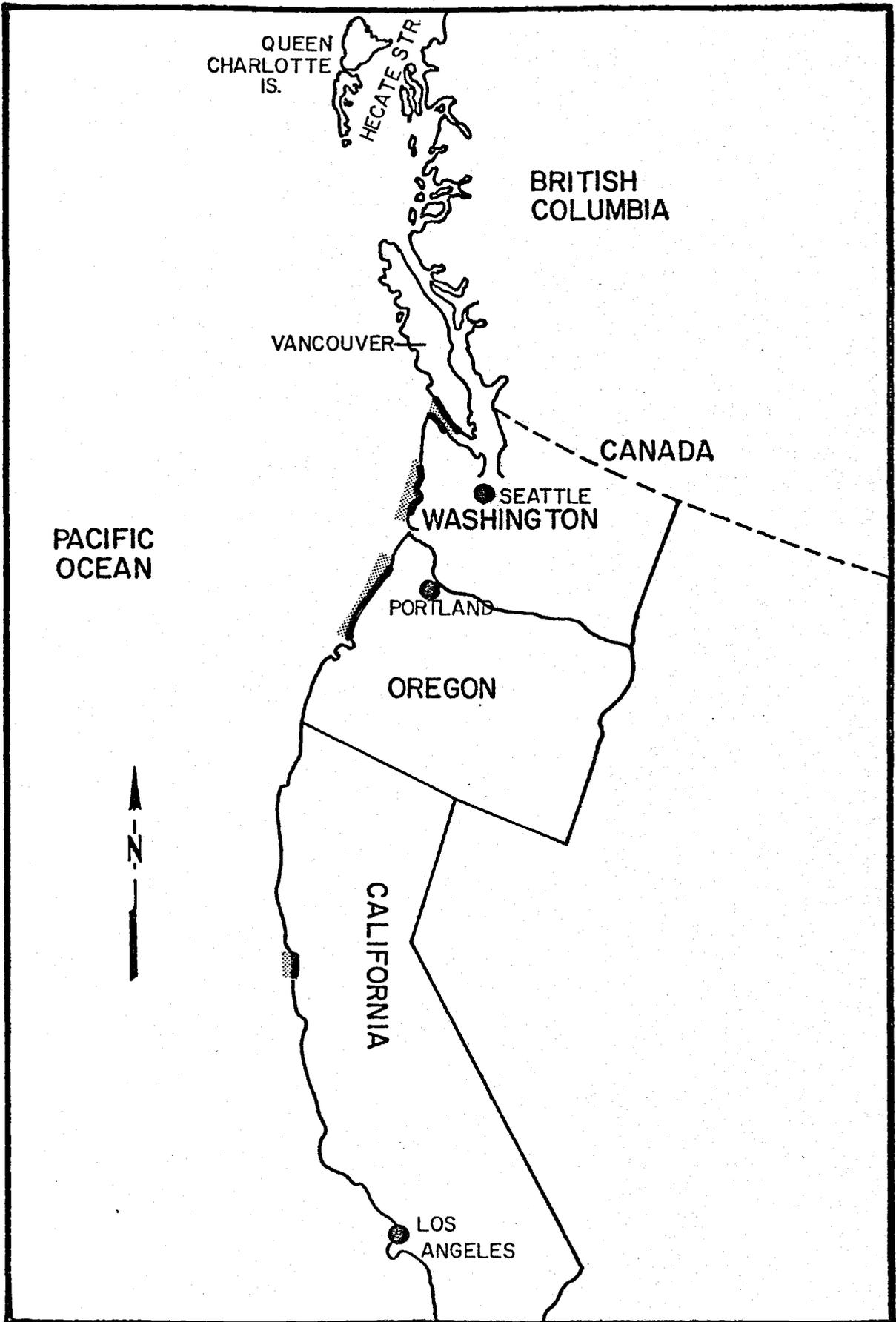


Figure 9. Distribution of Eohaustorius brevicuspis and E. estuarius in the vicinity of Beaver Creek, Lincoln County, Oregon.

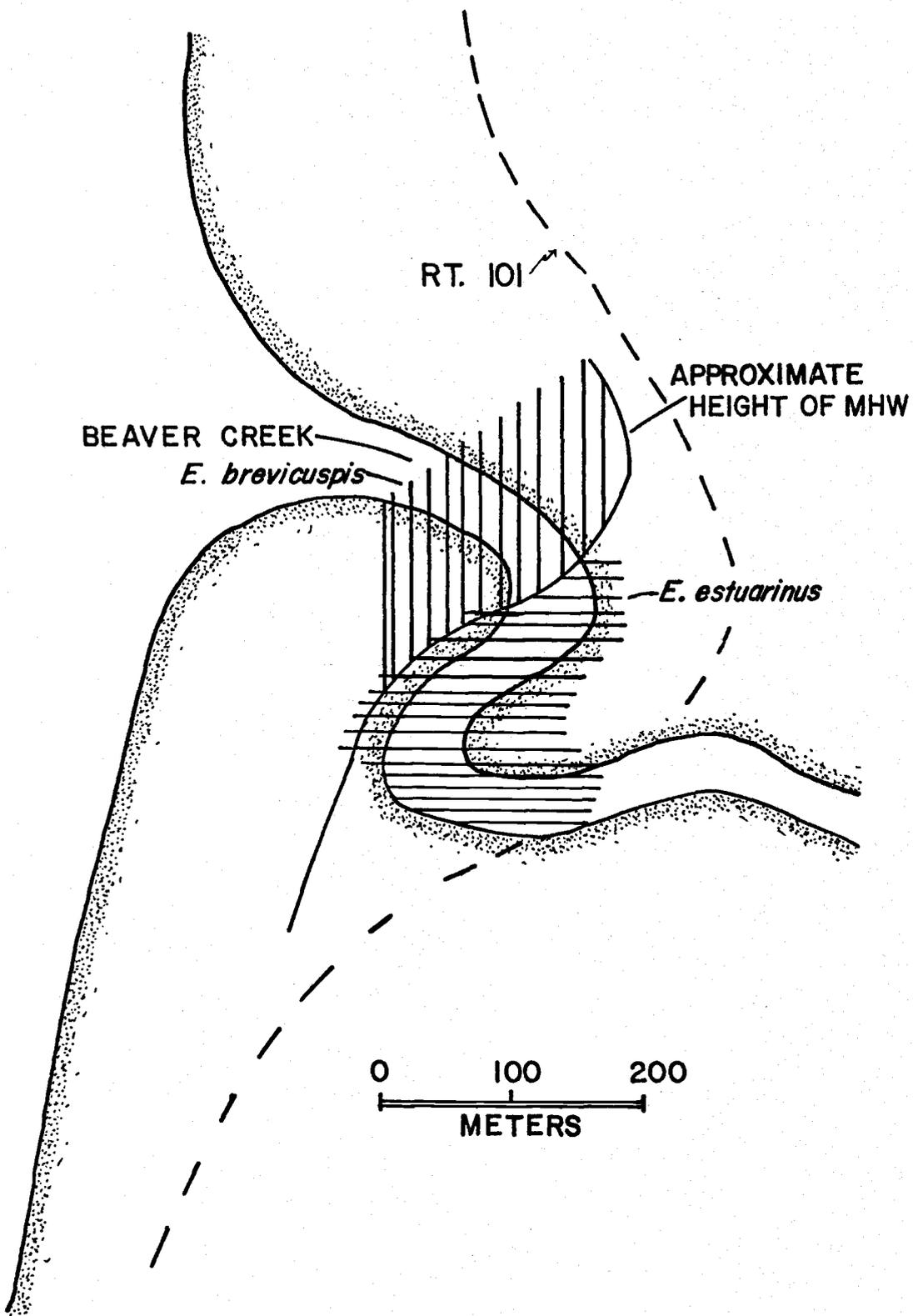


Figure 10. Size-frequency distribution of Eohaustorius estuarius at various Oregon sampling locations in February 1972 (shaded area = gravid female).

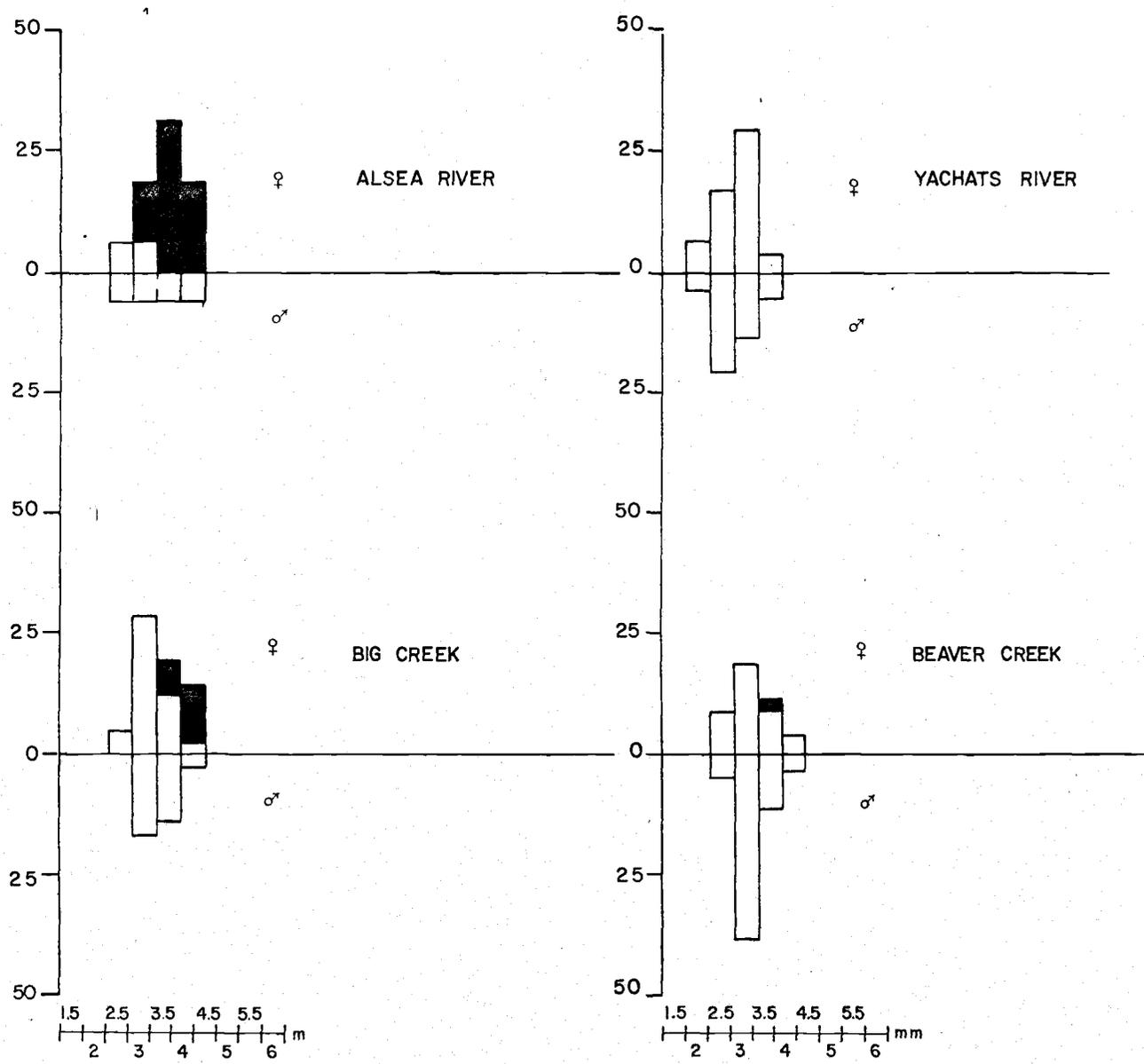


Figure 11. Size-frequency distribution of Eohaustorius brevicuspis at Lost Creek Beach, February 1971 - February 1972 (shaded areas = gravid females).

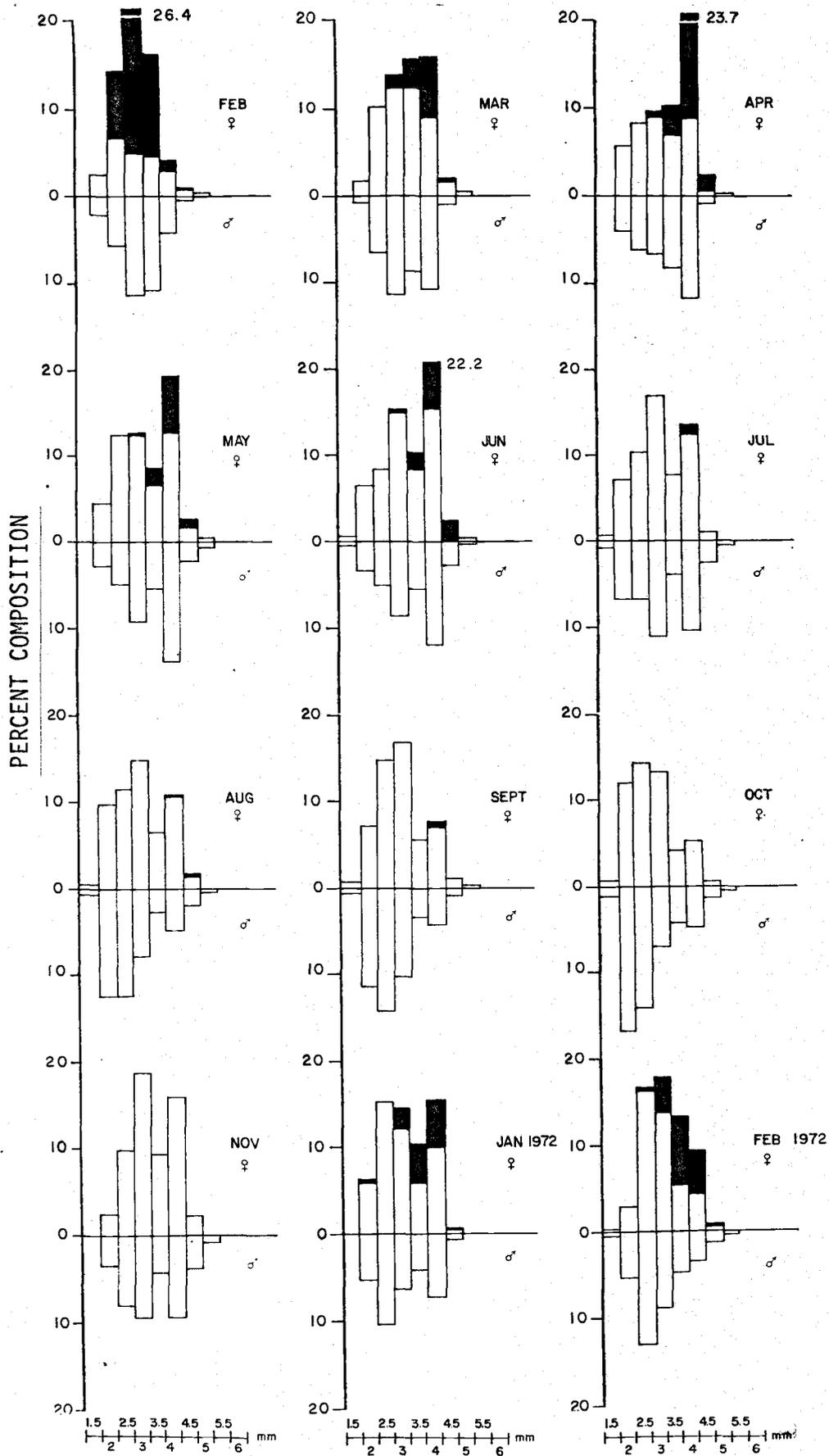


Figure 12. Size-frequency distribution of Eohaustorius
washingtonianus at Lost Creek Beach, February
1971 - February 1972 (shaded areas = gravid
females).

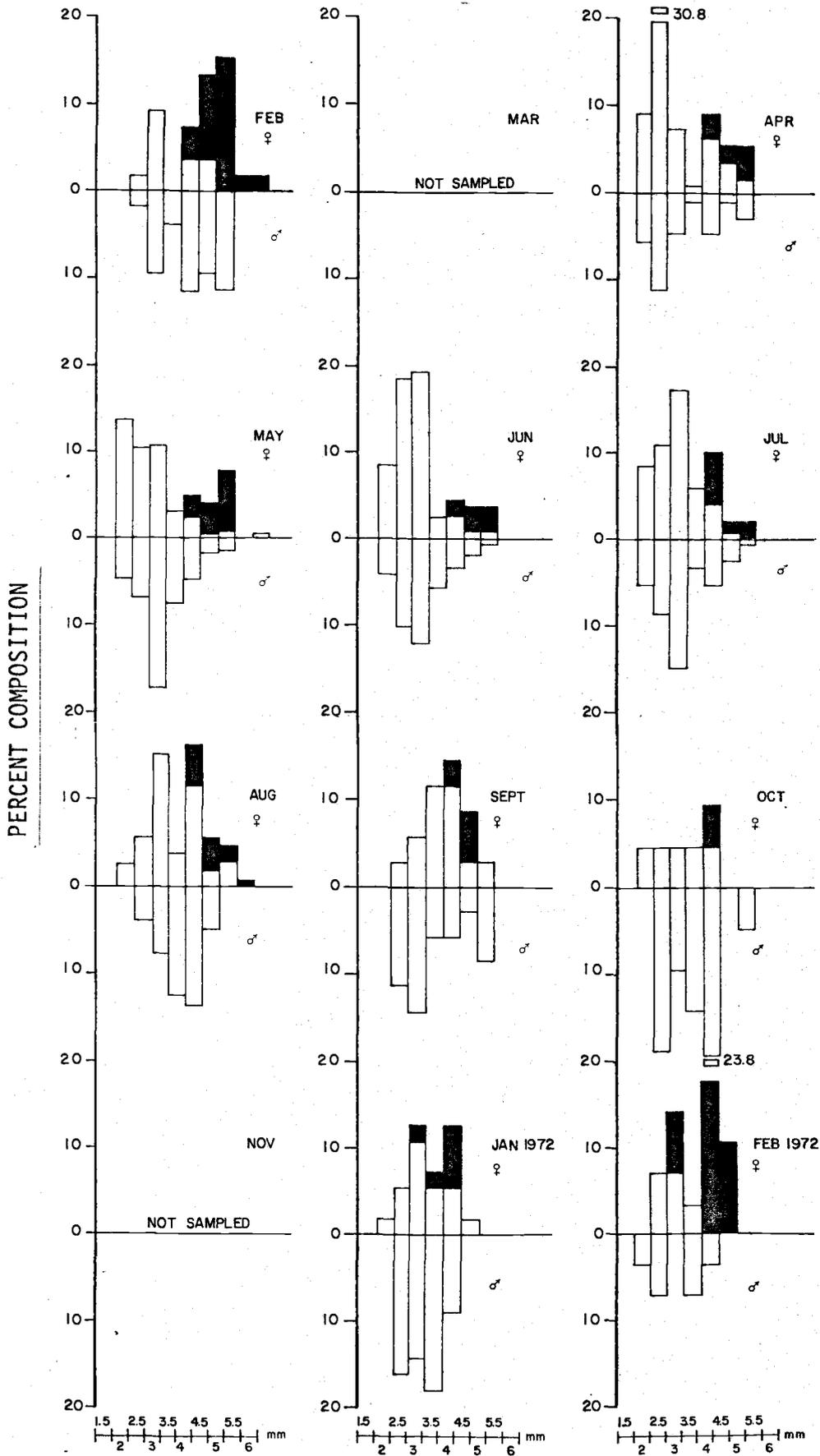


Figure 13. Size-frequency distribution of Eohaustorius
estuarius at Yaquina Bay, February 1971 -
February 1972 (shaded areas = gravid females).

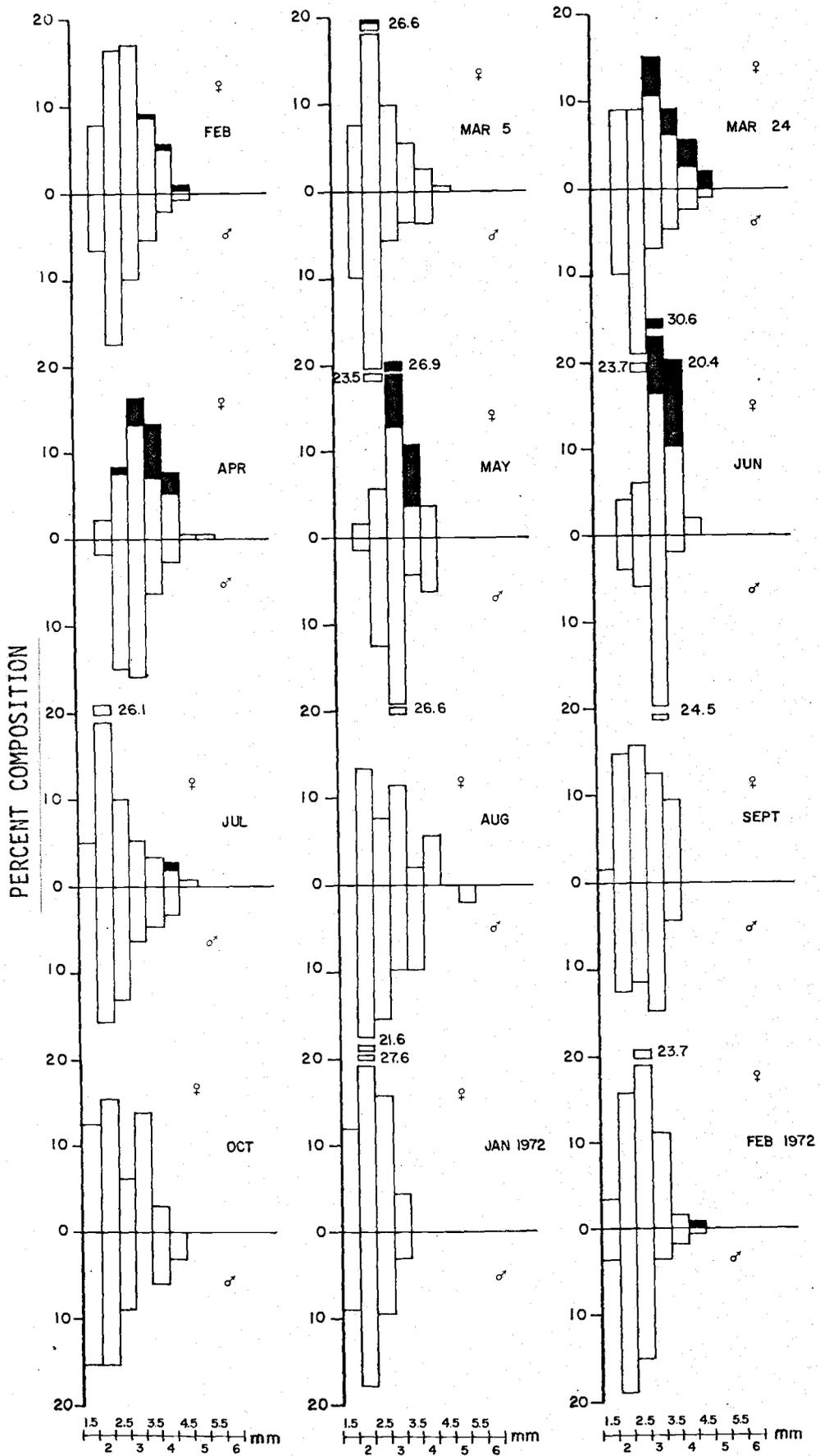


Figure 14. Total fecundity per square meter for Eohaustorius brevicuspis and E. washingtonianus at Lost Creek Beach, February 1971 - February 1972. (Dotted lines are assumed distribution.)

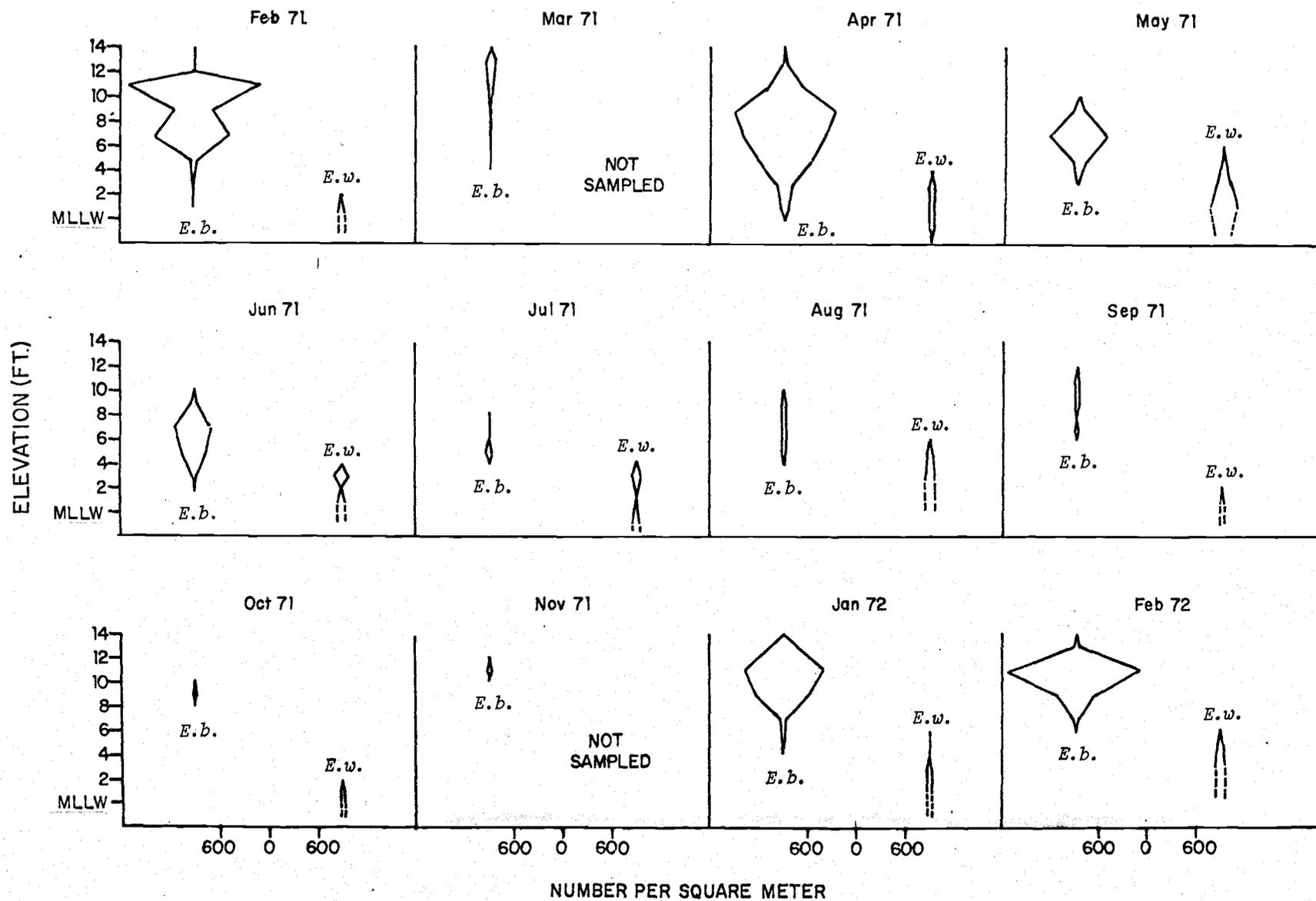


Figure 15. Zonation of mature Eohaustorius brevicuspis and E. washingtonianus at Lost Creek Beach, February 1971 - February 1972.

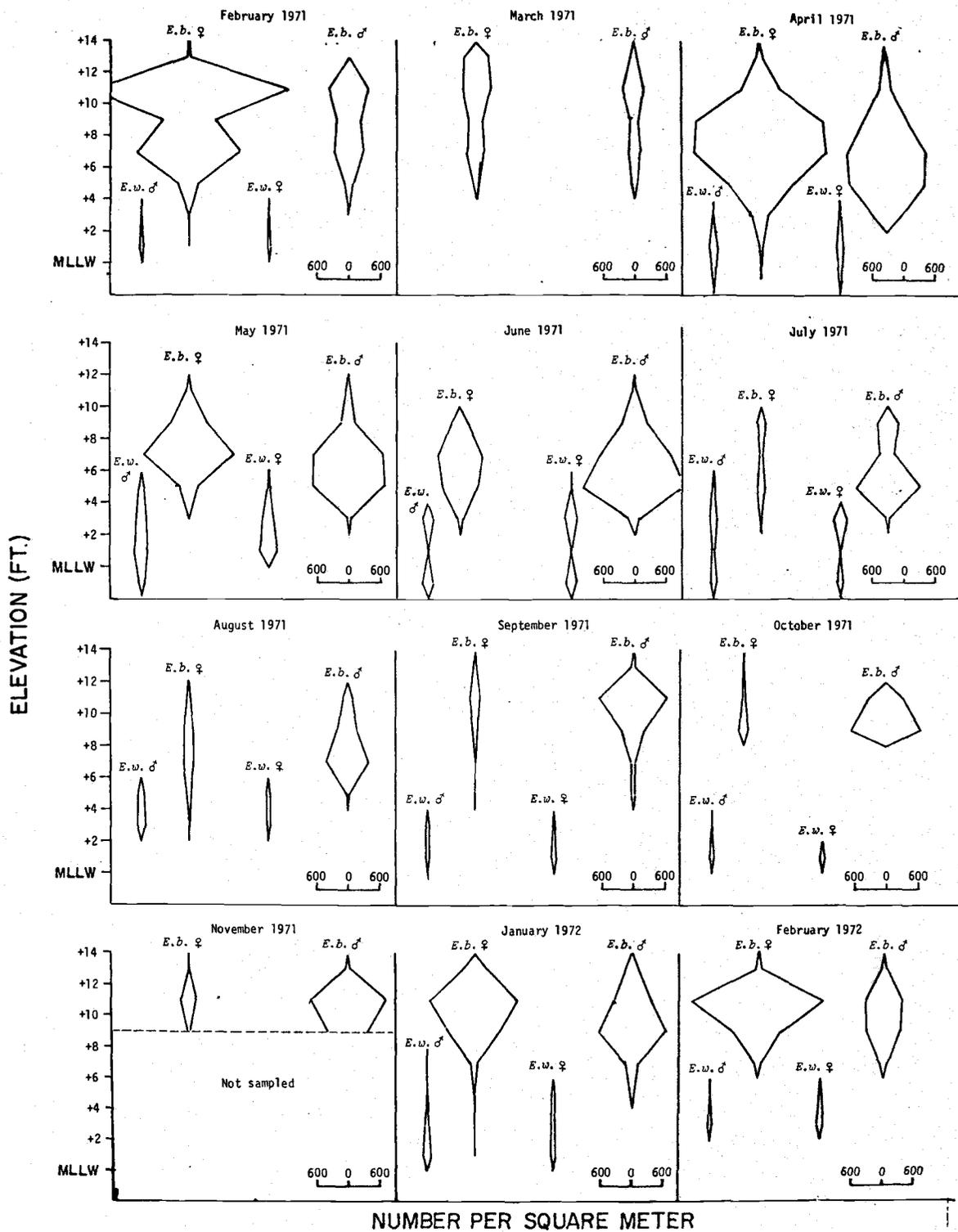


Figure 16. Survival of Eohaustorius brevicuspis at various salinities in preliminary salinity tolerance test.

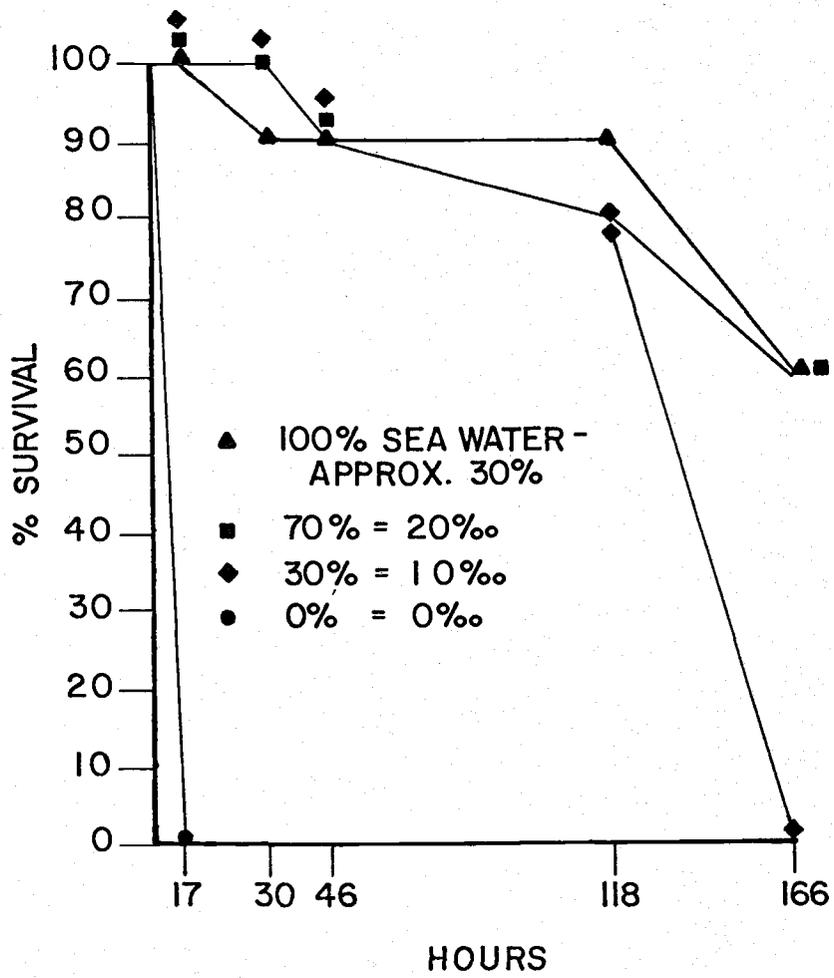


Figure 17. Percentage survival of E. brevicuspis at different temperature and salinity combinations.

- = 28 ‰
- = 23 ‰
- ▲ = 14 ‰
- ◆ = 6 ‰
- = 0 ‰

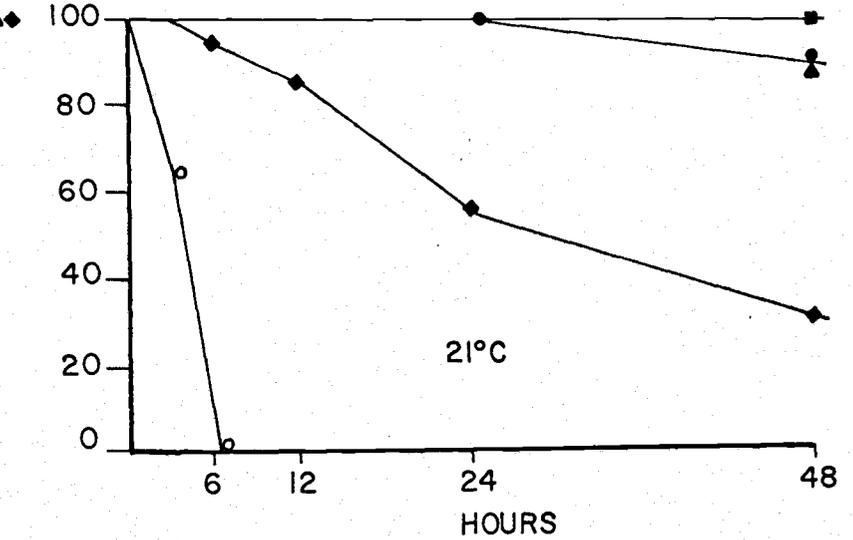
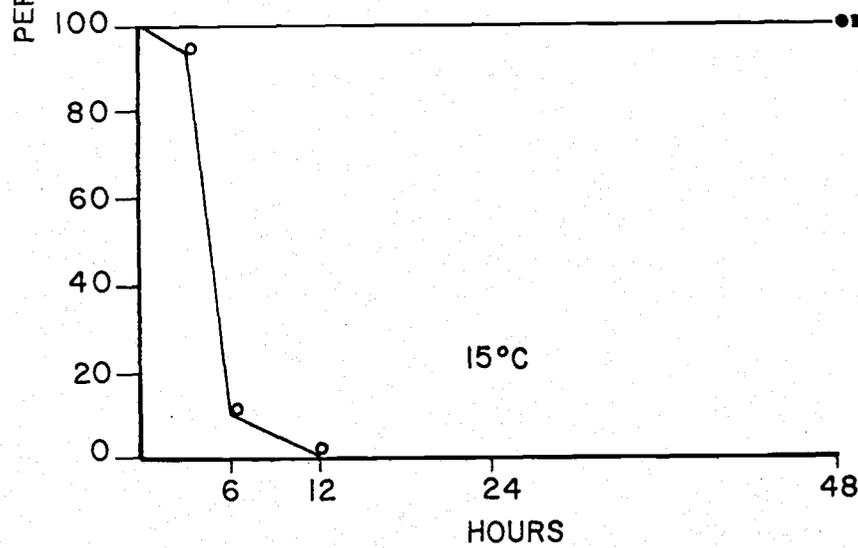
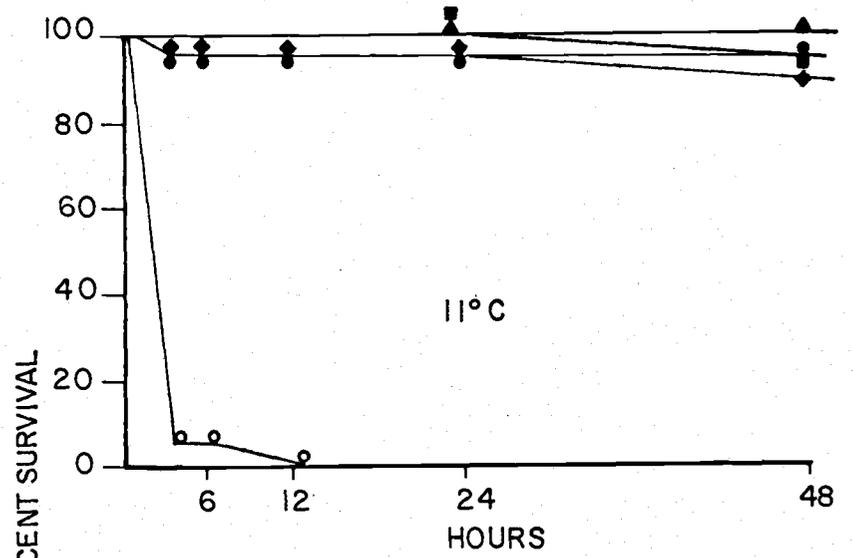
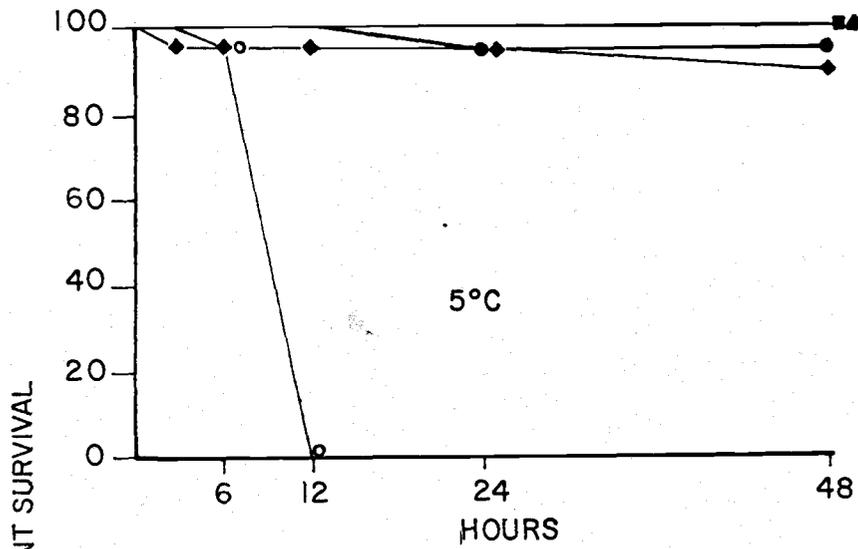


Figure 18. Surface response curves for E brevicuspis for various temperature salinity combinations. (Dashed lines delineate limits of data points).

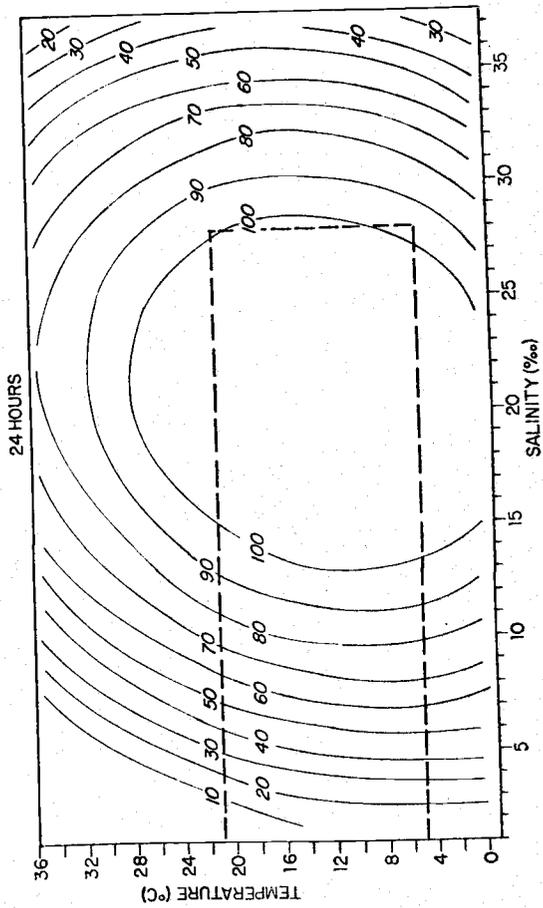
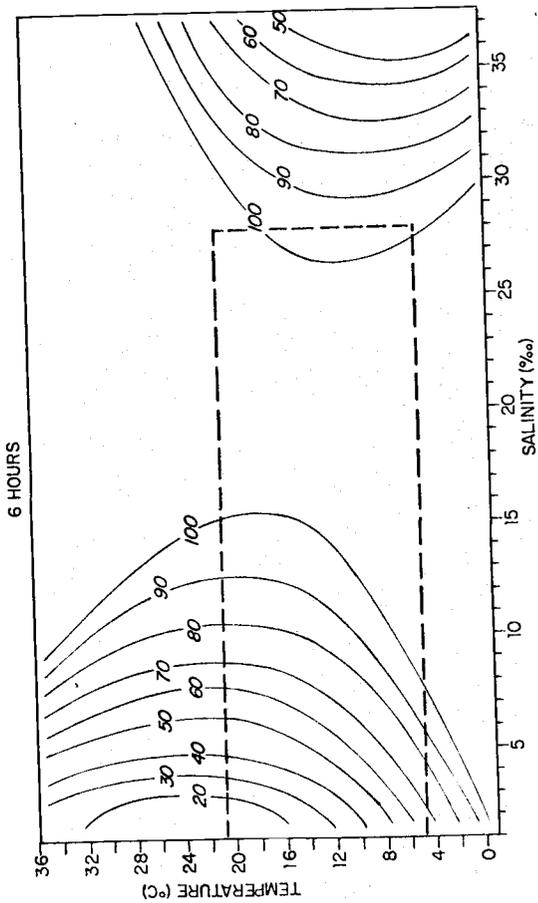
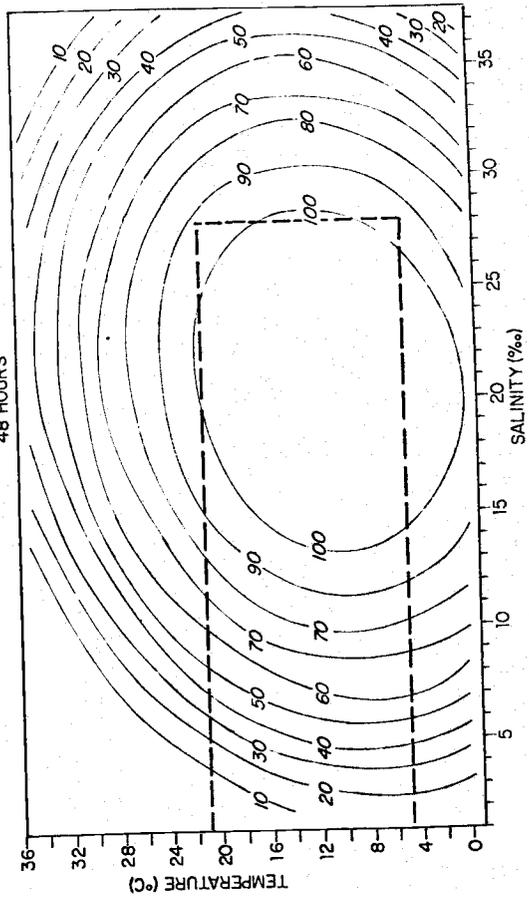
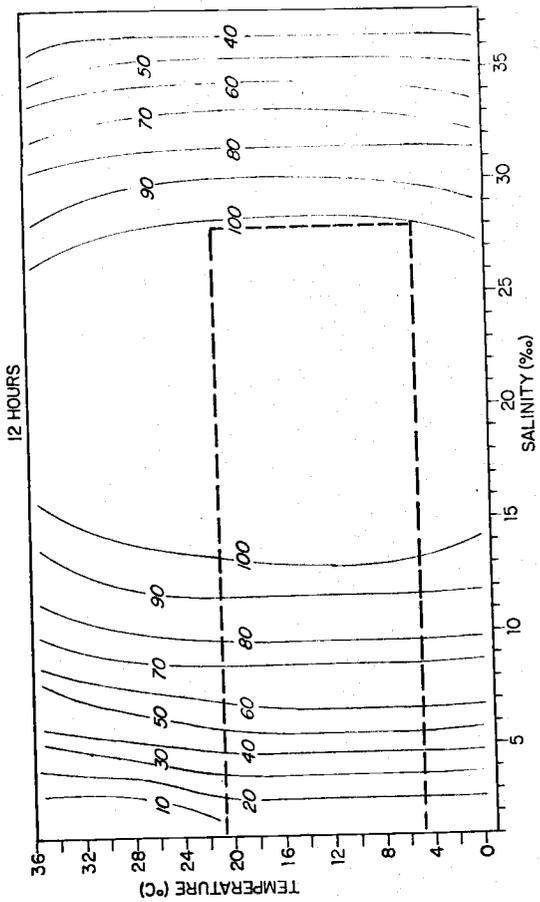
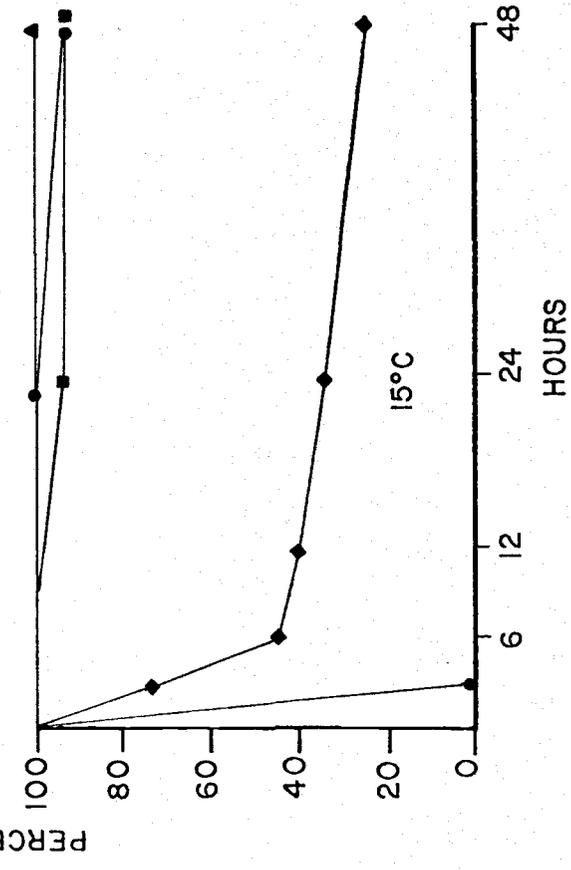
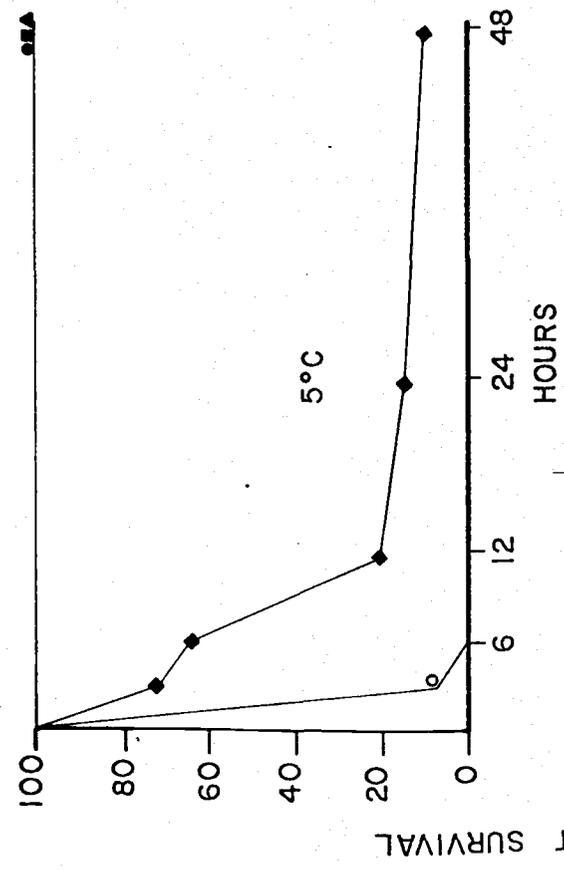
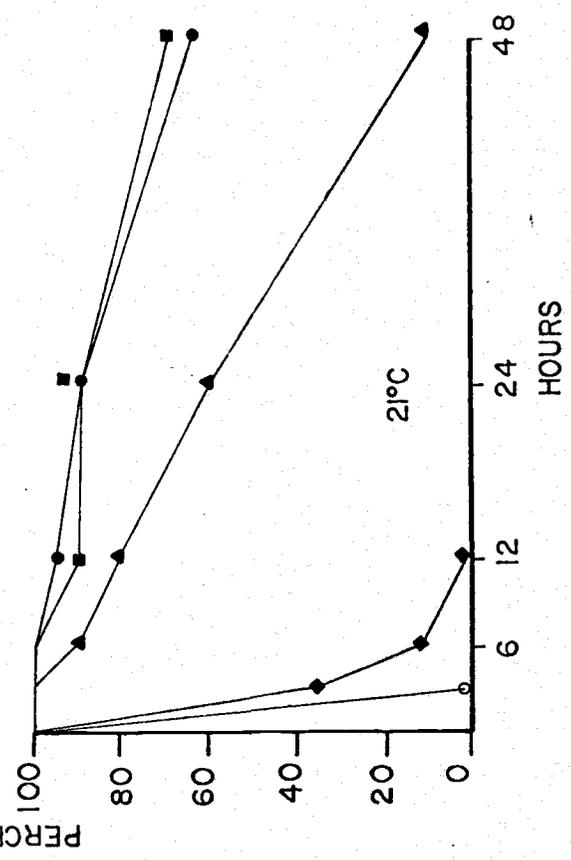
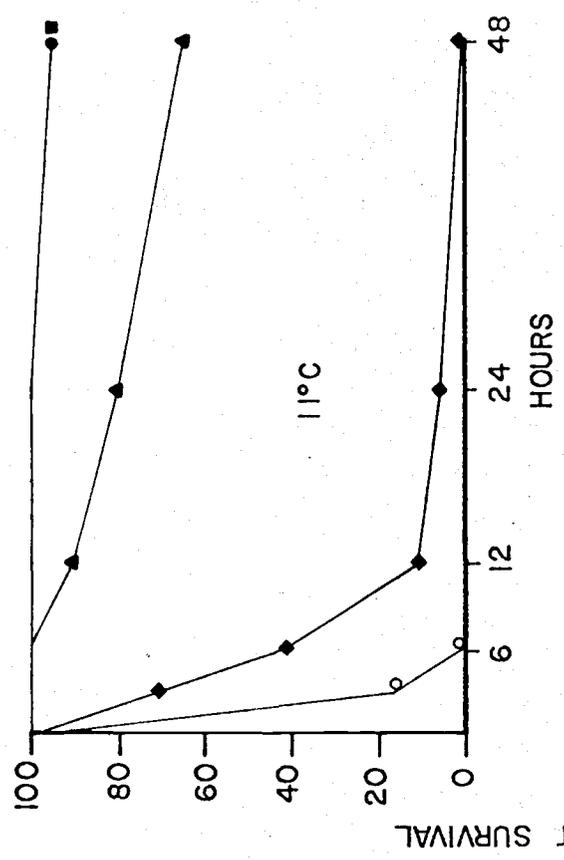


Figure 19. Percentage survival of E. washingtonianus at different temperature and salinity combinations.

- = 28 ‰
- = 23 ‰
- ▲ = 14 ‰
- ◆ = 6 ‰
- = 0 ‰



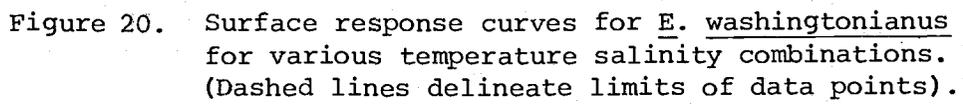


Figure 20. Surface response curves for E. washingtonianus for various temperature salinity combinations. (Dashed lines delineate limits of data points).

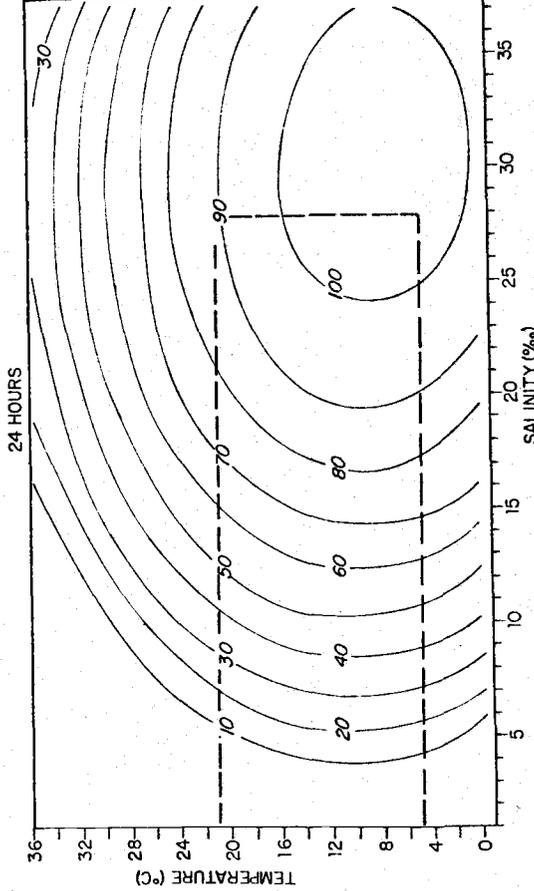
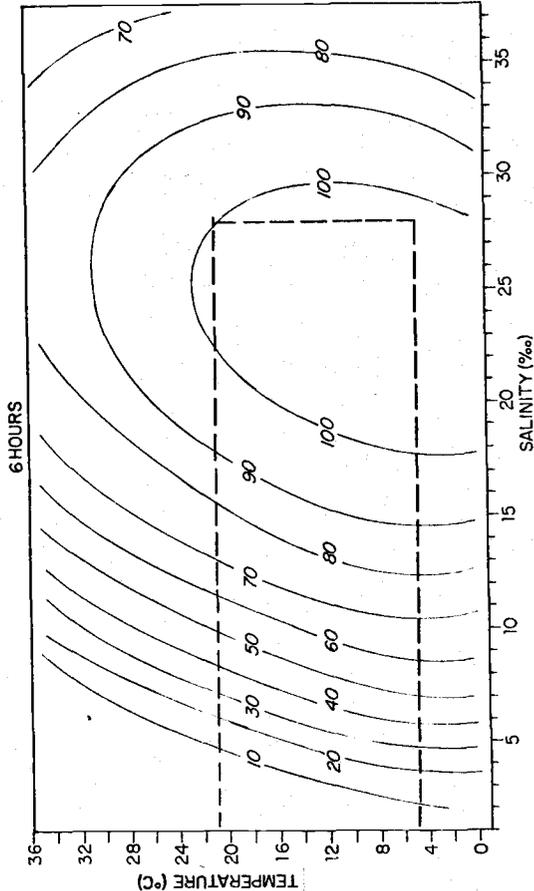
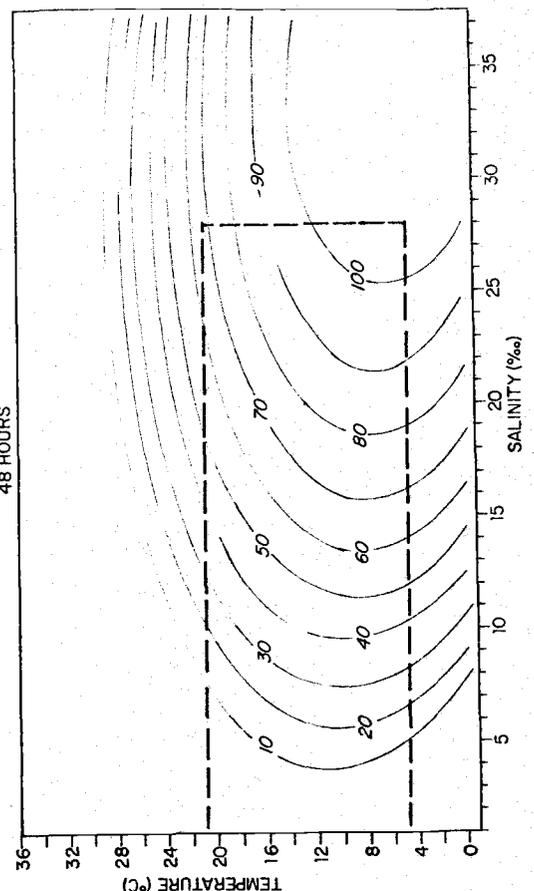
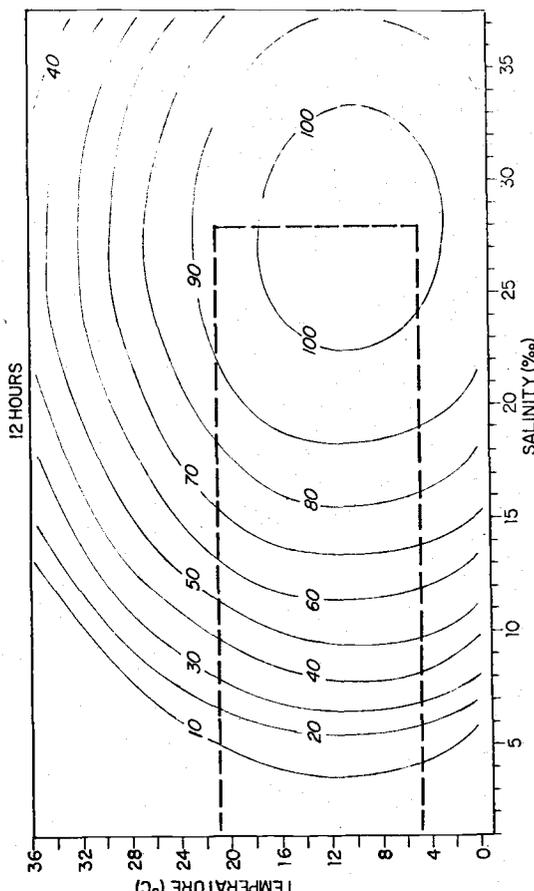
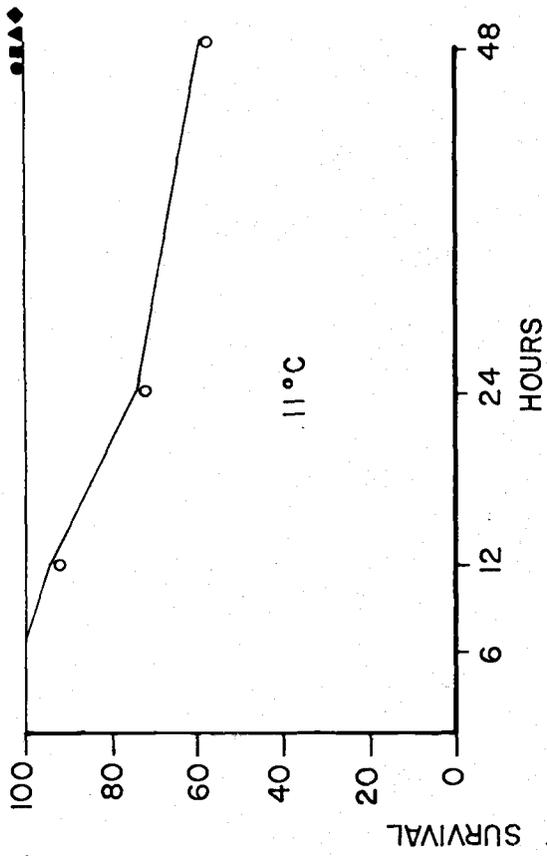
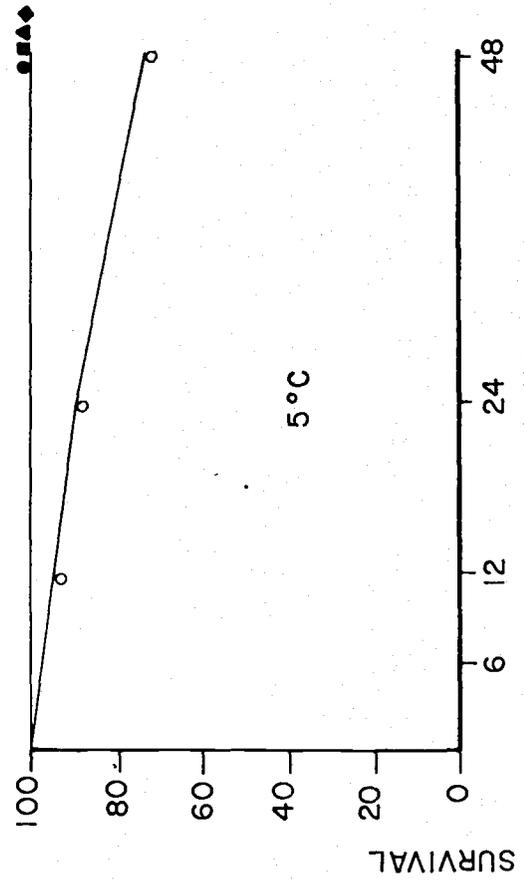
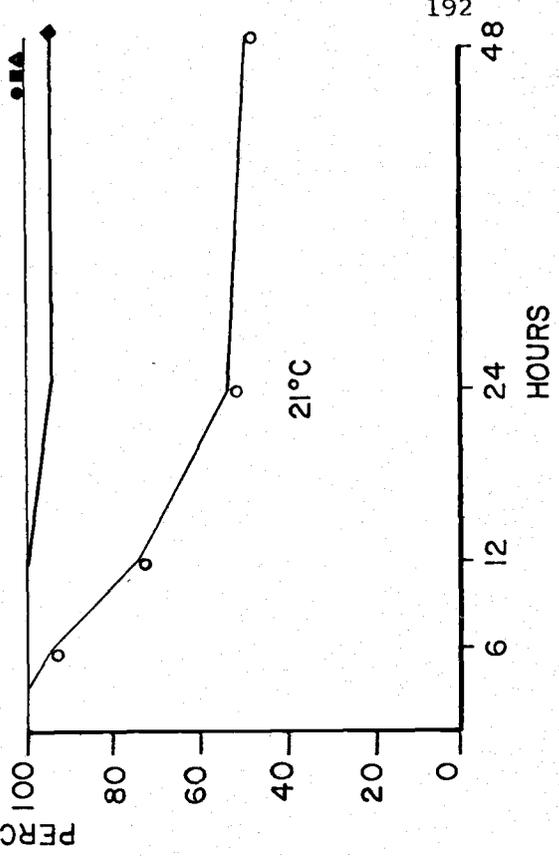
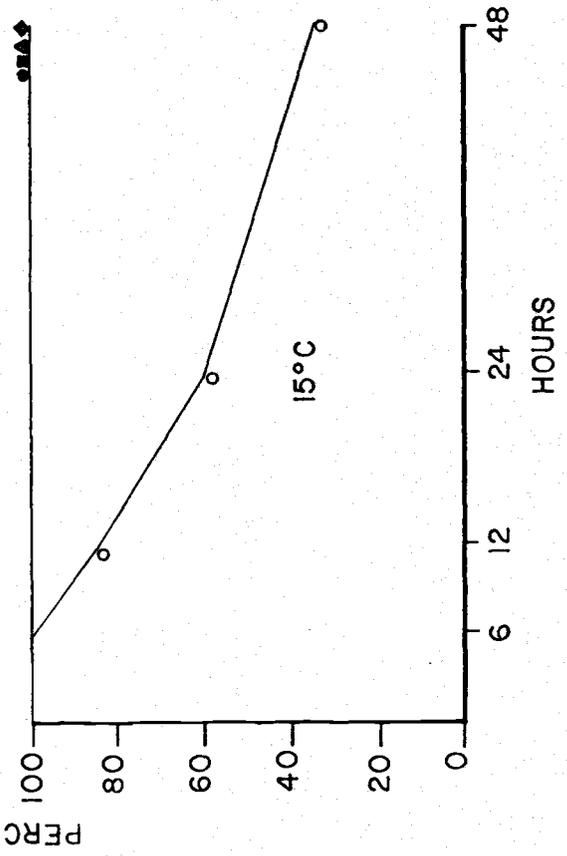


Figure 21. Percentage survival of E. estuarius at different temperature and salinity combinations.

- = 28 ‰
- = 23 ‰
- ▲ = 14 ‰
- ◆ = 6 ‰
- = 0 ‰



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Figure 22. Surface response curves for E. estuarius
for various temperature salinity combinations.
(Dashed lines delineate limits of data points).

