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POPULATION DYNAMICS AND DISTRIBUTION OF *NEOMYSIS MERCEDIS* AND *ALIENACANTHOMYSIS MACROPSIS* (CRUSTACEA: MYSIDACEA) IN RELATION TO THE PARASITIC COPEPOD *HANSENULUS TREBAX* IN THE COLUMBIA RIVER ESTUARY

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ABSTRACT

Two species of Columbia River estuary mysids, *Neomysis mercedis* Holmes and *Alienacanthomysis macropsis* (Tattersall), were found with a parasitic nicothoid copepod infesting the marsupium of the female mysids. The relationships between the life histories and the spatial and seasonal distributions of the mysids and the ectoparasitic copepod are examined. The remarkably high incidence of parasitism remained stable throughout the year in spite of seasonal fluctuations in the two mysid populations. *Neomysis mercedis is* an important component in the diet of fishes in other estuaries along the Pacific coast; however, it does not appear to be as important a food resource in the Columbia River estuary. This may be due to the parasite which probably has a significant effect on the population of the mysid hosts.

Two species of mysids, *Neomysis mercedis* Holmes and *Alienacanthomysis macropsis* (Tattersall), collected in the Columbia River estuary in 1980 and 1981, had a remarkably high incidence of a previously unknown nicothoid copepod living ectoparasitically within the marsupium of the mature females. A description of the parasitic copepod, *Hansenulus trebax, is* given by Heron and Damkaer (1986).

Mysids are important constituents of food webs in many coastal and estuarine areas of North America (Hopkins, 1965; Heubach, 1969; Levings, 1981; Price, 1982). However, they are difficult to sample quantitatively due to their demersal habitat preferences and swarming behavior (Fulton, 1982; Omori and Hamner, 1982). As mysid abundances are likely to be underestimated, their relative importance in estuarine ecosystems may not be fully recognized. Mysid densities in the Columbia River estuary appear to be lower than those reported from other estuaries where mysids are known to be important dietary components (Hopkins, 1965; Northcote *et al.,* 1976; Siegfried *et al.,* 1979). Analysis of the diet of fishes demonstrates the relative importance of mysids as a prey species. *Neomysis mercedis* has been reported to be the primary prey of fishes and caridean shrimp in several Pacific coast estuaries (Levy and Levings, 1978; Northcote *et al.,* 1979; Siegfried *et al.,* 1979; Siegfried, 1982). However, mysids were not found to be a significant food for fish or shrimp in the Columbia River estuary (Haertel and Osterberg, 1967; Craddock *et al.,* 1976; Bottom *et al.,* 1984; Simenstad *et al.,* 1984).

In this paper, aspects of the life history and ecology of the two species of mysids are explored in an effort to understand the unusually high infestation of the parasitic copepod and the effect of the parasite on the mysid populations.

STUDY AREA

The Columbia River is one of the major rivers on the Pacific coast of North America. It is a highly energetic system characterized by large-volume river discharge and strong tidal exchanges, resulting in a turbulent, relatively fresh, sandy-bottomed estuary with high turbidity from suspended sediments.

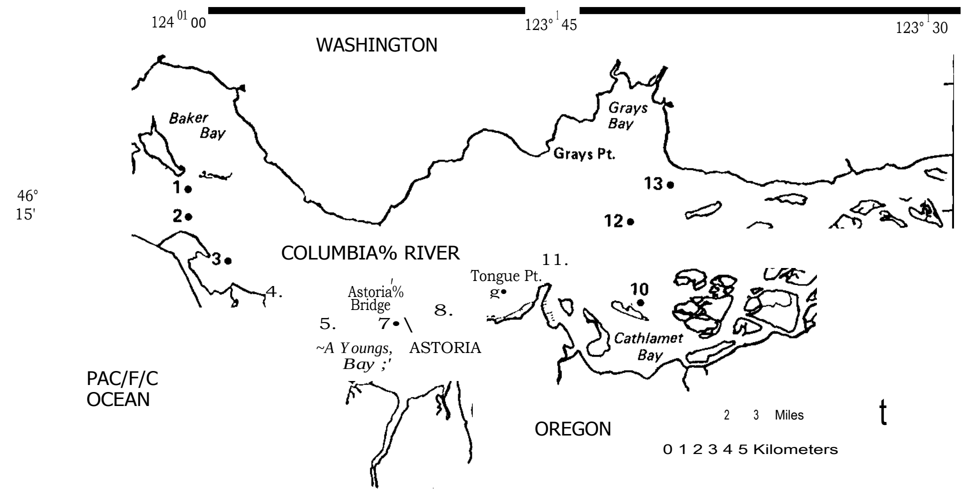


Fig. 1. Station locations in the Columbia River estuary.

The average riverflow is about 7,280 $m^3\ s^{-1}$, with a range from 4,200–17,000 $m^3\ s^{-1}$. The maximum salt intrusion is generally between 16 and 24 km from the mouth, but during extreme conditions of low riverflow and neap tides, the salt intrusion may penetrate as far as 50 km upriver. During high riverflow and ebb tides the estuary may be essentially fresh water (Simenstad *et al.,* 1984).

Thirteen sampling stations throughout the estuary extended from River Kilometer 8, near the mouth of the Columbia River, up to River Kilometer 37 (Fig. 1). Ten stations were located along the main navigational channel at 2-mile (3.2-km) intervals. Stations 1 and 6 were at the mouth and in the north channel, and Station 10 was in Cathlamet Bay. The first nine stations were in the estuarine channel region of the estuary which is delineated by brackish water and strong tidal and river currents. The entrapment or null zone is apparent as a turbidity maximum and is near the upriver boundary of the upstream bottom current where there is no net flow. High densities of zooplankton are often associated with this zone. During the high-flow season, its average position is near Station 4, and during low flow, it is between Stations 5 and 8.

Stations 11, 12, and 13 were in a mixed zone where fluvial processes dominate during high riverflow and estuarine mixing processes dominate during low riverflow. Cathlamet Bay (Station 10), a large protected bay off the main river channel, is characterized by low velocity currents and shallow channels and marshes. This bay is at or just above the edge of the saline intrusion except during low-flow/neap-tide conditions.

MATERIALS AND METHODS

Sampling Methods

Samples were taken semimonthly from April 1980 to April 1981 during 27 cruises. Zooplankton were collected in daylight at depths ranging from 9–25 m. A side-by-side double-net epibenthic sled was towed for 5 min in an oblique haul from the surface to the bottom and back to the surface again. Net mesh-sizes were 253 µm and 335 µm; each net had a round mouth area of 0.2 m^2. Flowmeters in the net mouths estimated the water filtered. Samples were preserved in buffered 4% formaldehyde. At each station, temperature and salinity measurements were obtained at 1-m intervals, using a portable induction salinometer.

Data Analysis

A Folsom plankton splitter was used to obtain a subsample of at least 100 mysids of the dominant species. Each individual mysid was classified according to sexual maturity stage (Table 1), measured, and examined for parasites. Length is given as the distance between the anterior margin of the carapace and the apex of the telson, measured to the nearest millimeter. Brood size for nonparasitized females was determined by counting mysid eggs from only the marsupia of brooding females that retained egg sacs totally intact, to minimize erroneous counts due to damaged or lost broods. Brood size was also

Table 1. The sexual maturity stages for *Neomysis mercedis* and *Alienacanthomysis macropsis,* classified after Beck (1977) and Mauchline (1971a).

Stage	Characterized by
Juveniles	Secondary sexual characteristics not developed
Immature females (9 I)	Oostegites present as 4 separate lamellae (anterior and posterior pair) not meeting midventrally
Mature females	
Nonbrooding females (4 II)	Oostegites larger and fringed with setae, posterior pair of lamellae tightly overlapping anterior pair to form compact pouch; no eggs or larvae visible
Brooding females (9 III)	Eggs or larvae present in brood pouch
Spawned females (9 IV)	Brood pouch empty, young emerged, overlapping lamellae slack, not contracted into compact form

counted for eggs in parasitized females and for larvae in nonparasitized and parasitized female N. *mercedis.*

Mean abundances were determined by species for each month and for each station at three hydrologic seasons: spring high flow (April–June), summer-fall low flow (July–October), and winter fluctuating flow (November–March). The effects of salinity on the distribution of the mysids and the parasite were examined. A weighted mean salinity *(S‰)* was calculated to account for the fact that the mysids (m) were not equally distributed at all salinity (s) levels, using the equation:

$$S\% \_ \; m,s, + m_z s_2 + \ldots m,,s,, \qquad ms$$
$$m,+m2+\ldots m„ \qquad m$$

RESULTS

Four species of mysids, *Neomysis mercedis, Alienacanthomysis macropsis, Proneomysis wailesi* Tattersall, and *Xenacanthomysis pseudomacropsis* (Tattersall) have been found parasitized by *Hansenulus trebax* (see Heron and Damkaer, 1986). The first two species occur in the Columbia River estuary. Two other mysid species from the Columbia River estuary, *Archaeomysis grebnitzkii* Czerniaysky and *Neomysis kadiakensis* Ortmann, were not found with the parasitic copepod.

Brooding female mysids carry their eggs and larvae in a marsupium or brood pouch. The "eggs" contain developing embryos but retain an egglike appearance. After a certain incubation time within the marsupium of the brooding female, the young mysids are released as juveniles. Within hours, the female mysid molts, is refertilized, and extrudes a new batch of eggs into the brood pouch. This process continues for a number of broods until the female dies.

The ectoparasitic copepod *Hansenulus trebax* cannot infest female mysids until the marsupial oostegites develop and form a secure pouch. Therefore, these parasites are associated only with mature female mysids (Q II, III, IV). The parasites are easily overlooked. The copepod ovisacs, and even the female copepods, until they become quite large, resemble mysid eggs in size, color, and shape (Fig. 2).

Neomysis mercedis

Life History and Abundance. — It is apparent, from the nearly continuous presence of juvenile mysids 2—3 mm in length, that *Neomysis mercedis* in the Columbia River estuary breeds during most of the year. Brooding females were found in all months except December and January. However, the intensive brooding period was during the warmest months, from May to November.

Of the total annual population of *N. mercedis,* juveniles comprised 71%, females

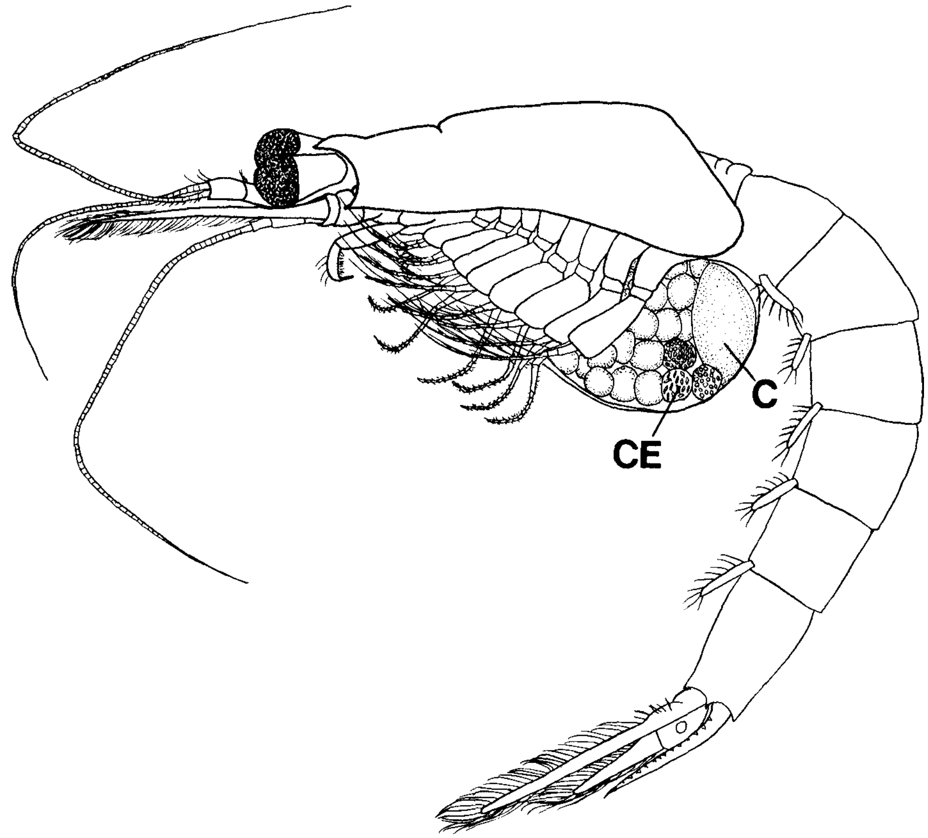


Fig. 2. A large female parasitic copepod (C), *Hansenulus trebax,* and several copepod ovisacs (CE) in various stages of development, among mysid eggs in the marsupium of a mature female mysid, *Neomysis mercedis.*

15%, and males 14%. Juveniles, though in greater numbers than mature females, had a similar seasonal occurrence. The monthly ratio of male to female mysids ranged from 0.3 in April to 2.3 in January. Females slightly outnumbered males during most of the main brooding season (May to November). The annual ratio of mean abundances of male to female mysids was 0.96.

Eight per cent of the total population of *N. mercedis* were mature females (2 II, III, and IV). Nonbrooding females (2 II) were found during all months except February, with a peak abundance in April 1980, a second peak in July, and a third peak in September (Fig. 3). Brooding females (9 III) were most abundant from May to November with a peak in July that corresponded to a subsequent August peak in juvenile abundance. A second peak in 9 III was seen in September. A direct relationship existed between the level of parasite infestation and the abundance of female mysids (Fig. 4). Generally, early in the season only the larger female mysids were parasitized, but by fall all sizes of mature females were infested. Large-sized 2 II were always parasitized. Many of the infested 9 II were found with marsupia completely filled with parasites, including a female and several male copepods, and between 2 and 23 copepod ovisacs. Spawned females (9 IV) were rarely collected because mysids are usually in this stage for only a

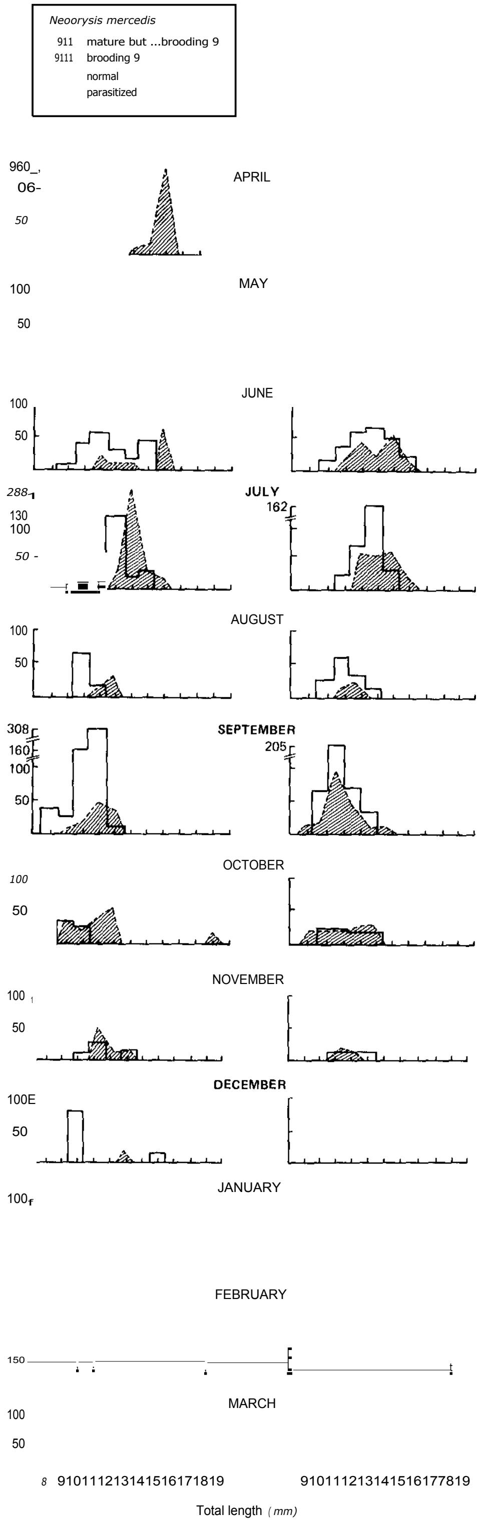


Fig. 3. Monthly length-frequency histograms of normal and parasitized nonbrooding (9 II) and brooding (9 III) mature female *Neomysis mercedis;* data for April are averages of 2 years.

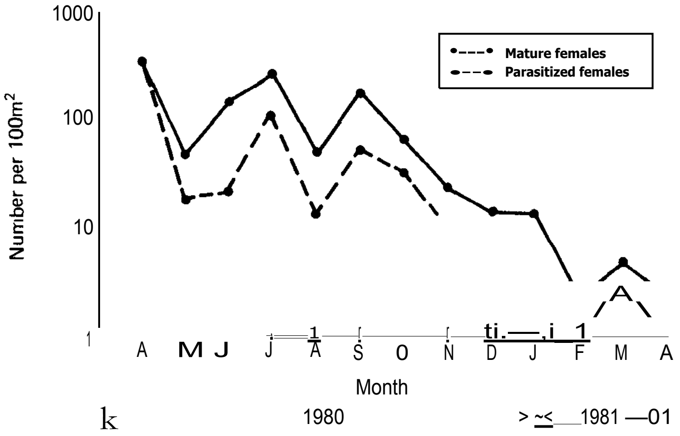


Fig. 4. Monthly mean abundance of all mature female and parasitized mature female *Neomysis mercedis* in the Columbia River estuary.

short time; however, 2 IV were found during the main spawning season and some of them were infested by the copepod. An average of 52% of all mature females *of N. mercedis* were parasitized.

Neomysis mercedis produces at least two generations a year (Fig. 3). The overwintering population matures and reproduces in spring. The spring generation matures rapidly and in June may produce a summer generation. The overwintering 4 III disappear from the population between June and July. Late summer populations produce a fall generation. Some individuals from the summer population, along with the fall generation, form the overwintering population. Parasites were found among the overwintering population *of* 4 II and 4 III and among the first overwintering females to mature.

The parasitic copepods directly reduce the fecundity *of* the mysid hosts by feeding on the developing embryos and larvae in the marsupium. In *N. mercedis,* 36% *of* the brooding females (4 III) carried *H. trebax* among their own eggs and larvae. *Of* these, 40% *of* the parasitized egg-bearing mysids showed eggs with evidence *of* damage caused by copepods; 35% *of* the parasitized larvae-bearing mysids had some larvae partially eaten by the parasites. Therefore, to understand the effect *of* this parasite on mysid populations, it is necessary to consider the mysid recruitment potential.

Forty-three broods *of* eggs produced during the spring, summer, and fall were counted for nonparasitized females of *N. mercedis.* Mysid eggs are initially extruded through the oviducts into two thin, mucilaginous saclike membranes which lie next to each other in the marsupium. Each egg sac contained approximately half of the total brood of eggs. The brooding females were 9–15 mm in length with a mean length of 11.8 mm (±0.4; 95% CI). The number of eggs ranged from 4–48 per brood with a mean of 28 mm (± 3.0; 95% CI) eggs per brood. The average egg diameter was 0.5 mm. Regression analysis did not correlate individual brood sizes to female body length due to the large variation in brood sizes between seasons and size classes. Overwintering females that first spawn in the spring are generally the largest, 13–16 mm (Fig. 3). The spring population matures and starts to reproduce at 10–12 mm. The summer population, with a faster growth rate in the warmer water, matures and reproduces at an even smaller size, 9 mm, by early fall. A positive correlation between a seasonal egg number and body length relationship has been established by other investigators (Heubach, 1969; Mauchline, 1971b). In this study, there was an insufficient number of brooding females with egg sacs intact, and therefore the seasonal relationship between the number of eggs and body length could not be determined. However, mean brood size (S) was positively correlated with female body length (L) by the regression equation:

$$S = 2.53L - 2.44 \qquad (N = 7,\ r = 0.98;\ P < 0.01).$$

Brood-size of larvae was also determined for nonparasitized *N. mercedis.* The number of larvae ranged from 14—42 per brood, with a mean of 25 mm (±2.6; 95% CI, N = 29) larvae per brood.

Brood sizes were determined for parasitized brooding females. The number of eggs ranged from 1—48 per brood, with a mean of 23 mm (±5.6; 95% CI, N = 31) eggs per brood. The number of larvae ranged from 1—42 per brood, with a mean of 12 mm (±5.1; 95% CI, N = 25) larvae per brood. The mean *egg* brood-size of nonparasitized female *N. mercedis* was not significantly different (P = 0.05) from the mean brood size of parasitized *N. mercedis* (Cochran's application of Student's t-test for unequal variances; Snedecor and Cochran, 1967). However, the difference between the means of nonparasitized and parasitized brood-size of larvae was significant ($P < 0.001$). Parasitized broods of mysid eggs that were not damaged by feeding copepods generally had only a single juvenile or a very small female copepod inside the marsupium, and were probably recently infested. Broods that showed evidence of feeding copepods had an average of 37% of the eggs damaged, and the marsupium generally contained a larger female and one or two juvenile copepods. When the mysid marsupium contained a large female copepod with ovisacs, no mysid eggs or larvae were observed.

Distribution within the Estuary. —A number of physical factors are important in the distribution of estuarine zooplankton populations, including riverflow, tidal cycle, vertical mixing, sediment size and structure, turbidity, temperature, and salinity. Because an estuary is such a complex system, usually a combination of these factors influences the abundance and distribution of mysids, rather than any one variable.

The distributions of juvenile, mature female, and parasitized female *N. mercedis* within the estuary were investigated for each hydrologic season (Fig. 5) to determine if mysid ecology influenced the frequency of parasitism, or if the parasite itself was habitat-limited. Parasites were found in animals at all stations and hydrologic seasons; however, the incidence of parasitism is generally greater in mysids occupying the lower to midestuarine zones.

Salinity is often the single most important physical factor affecting population distributions in an estuary, with the range of tolerable salinities being more important than an average salinity. Our study found *N. mercedis* at all stations in salinities ranging from 0—31‰. However, the highest annual densities for all mysid stages were found at Station 10 in salinities varying from 0—4‰. Nonparasitized female *N. mercedis* were most commonly found in waters with a weighted mean salinity of 3.9‰. Parasitized female *N. mercedis* were found in salinities from 0—27‰, but were most commonly found in water with a weighted mean salinity of 12.1‰.

To document further the correlation between salinity and the incidence of parasitism, cumulative percentage curves were calculated for normal and parasitized mysids (Fig. 6). A Kolmogorov-Smirnov two-sample test (Tate and Clelland, 1957) found that the differences between the distributions of normal and

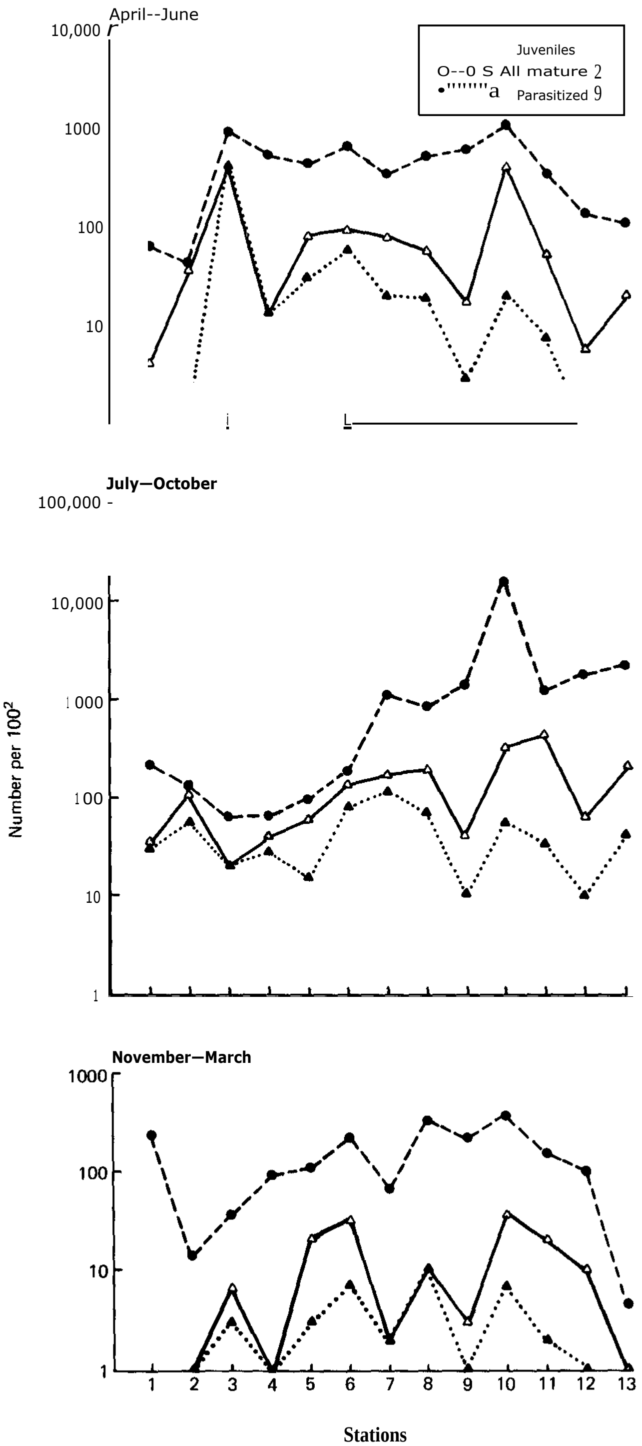


Fig. 5. Distributions of mean abundance of juvenile, all mature female, parasitized female, and brooding female *Neomysis mercedis* for three hydrologic seasons in the Columbia River estuary.

Fig. 6. Cumulative percentage-abundance of normal and parasitized mature female *Neomysis mercedis* with increasing salinity in the Columbia River estuary.

parasitized females in relation to salinity were significant at the 1% level for salinities less than 23%o. However, there is an apparent rapid decrease in abundance of parasitized mysids below about 16%o salinity. The distribution of *N. mercedis* can be related to its salinity tolerance, although salinity alone probably did not determine the distribution. However, low salinities apparently restricted the upstream distribution of *H. trebax.*

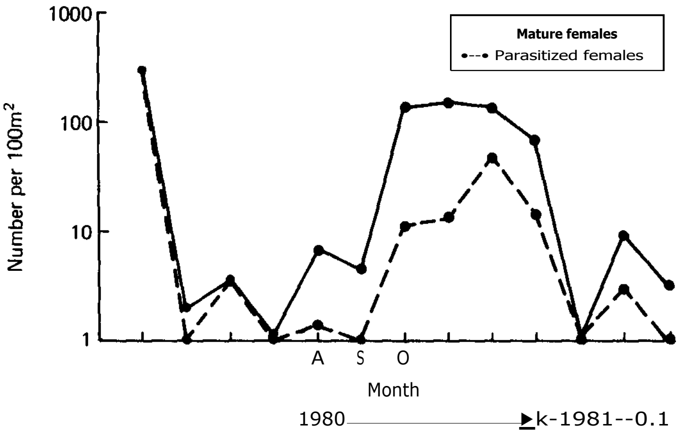
Cathlamet Bay (Station 10), less turbulent and with conditions of low salinity to fresh water, consistently maintained the greatest concentrations of mature female and juvenile *N. mercedis* during all three hydrologic seasons. The high densities of juveniles were indicative of the importance of this peripheral bay to the recruitment potential of the population of *N. mercedis.* The bay may also provide a refuge from the parasite. In the main river channels, where mysid densities were variable in time and space, riverflow was an important factor in mysid abundances. During the spring high flow season, *N. mercedis,* especially juveniles and 9 II, were concentrated farther downstream than during low flow conditions when the population shifted back upriver. The downriver extent of 9 III was always several stations upstream from the downriver limit of the other mysid stages. Circulatory processes may have influenced the consistently low mysid densities at Stations 4 and 9.

Alienacanthomysis macropsis

Life History and Abundance. — Like *N. mercedis, Alienacanthomysis macropsis* breeds throughout the year; but its major reproductive effort is between September and February. Recently released juveniles, 2—3 mm in length, were collected during all months except May and July, and their seasonal occurrence was similar to that of mature female mysids (Fig. 7). Brooding females were also present during most months.

Juveniles comprised 70% of the total annual population of *A. macropsis,* with a peak abundance from October to January. Females comprised 17% of the population, and males 12%. The monthly ratio of males to females varied from 0.4 in April to 4.8 in May. There were slightly more females than males during the main brooding period. The annual ratio of mean abundances of males to females was 0.75.

The mature females (9 II, III, IV) that were available to the parasite constituted



7. Monthly mean abundance of all mature female and parasitized mature female *Alienacanthomysis macropsis* in the Columbia River estuary.

8.5% of the population. Length frequency histograms suggest that *A. macropsis* produces only one generation annually (Fig. 8). Nonbrooding females (9 II) were most abundant from August through January, with peak abundances in December and January. Brooding females (4 III) were found during all months except July and February, with a maximum abundance in October. The earliest 4 III to mature begin producing young in August. By October the majority of females are spawning and continue to spawn into spring. Parasites were found in 9 III outside of the main brooding period, but the frequency of infestation dramatically increased during November and December. Large *A. macropsis* were more often found with parasites than smaller specimens until November and December. Spawned females (9IV) were found in April, and July through December. The proportion of parasitized females in the monthly mean abundances of mature female *A. macropsis* (Fig. 7) illustrates the increase in parasitism with the increase in breeding activity, as was found with *N. mercedis.* All mature females of *A. macropsis* had an average infestation level of 50%. In *A. macropsis,* 27% of the brooding females carried *H. trebax* among their eggs and larvae.

Thirty-six broods of eggs were counted from nonparasitized females 10—13 mm in length and with a mean body length of 11.9 mm (± 0.3; 95% CI). The number of eggs ranged between 9 and 29 eggs per brood, with a mean number of 14.0 (±1.5; 95% CI) eggs. The average egg diameter was 0.6 mm. The smallest individuals to mature and reproduce were 10 mm in length in September and October (Fig. 8). Regression analysis positively correlated mean brood size (S) to female body length (L) with the equation:

$$S = 2.83L - 19.93 \qquad (N = 4,\ r = 0.97;\ P < 0.05).$$

Distribution within the Estuary. —The distribution of juvenile, mature female, and parasitized female *A. macropsis* within the estuary (Fig. 9) had a very different pattern from that of *N. mercedis. Alienacanthomysis macropsis is* a lower estuarine to midestuarine species that occurred primarily between Stations 1 and 9. While a few individuals were occasionally found as far upriver as Station 11, the maximum concentrations were generally found downstream from Station 7. Juvenile abundances were higher in the lower estuary, particularly during the main brooding season. From the sites sampled, there was no evidence of a reproductive reservoir

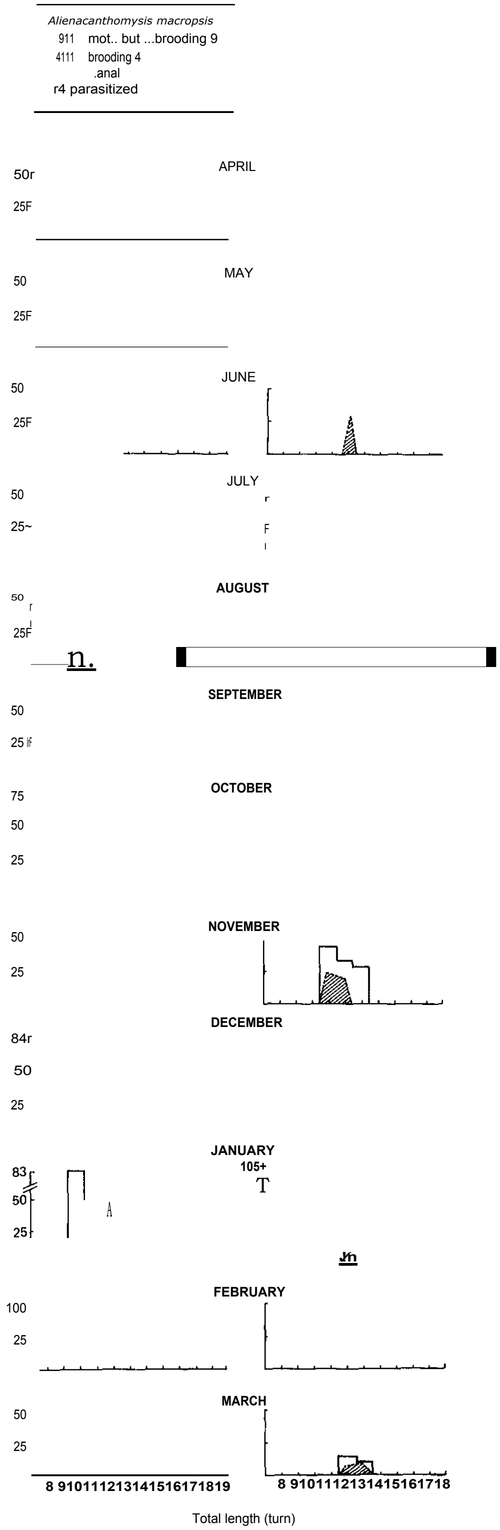


Fig. 8. Monthly length-frequency histograms of normal and parasitized nonbrooding (9 II) and brooding (9 III) mature female *Alienacanthomysis macropsis;* data for April are averages of 2 years.

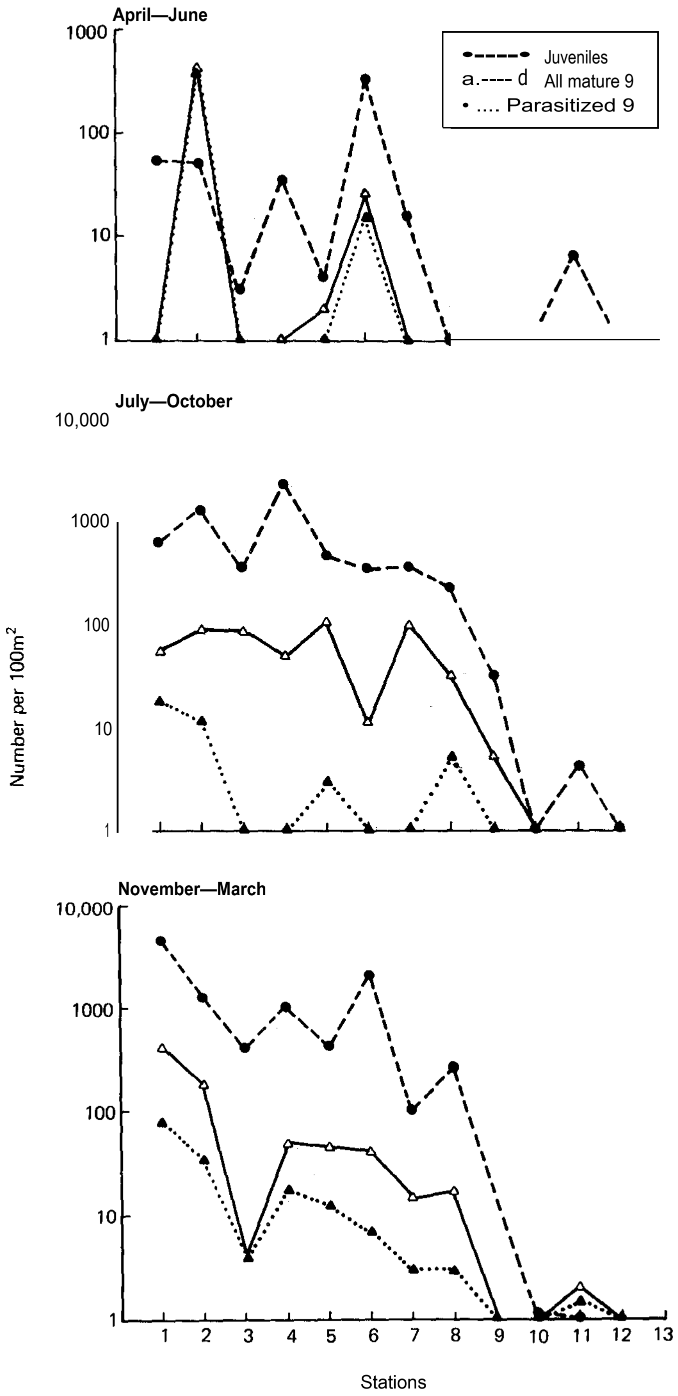


Fig. 9. Distributions of mean abundance of juvenile, all mature female, parasitized female, and brooding female *Alienacanthomysis macropsis* for three hydrologic seasons in the Columbia River estuary.

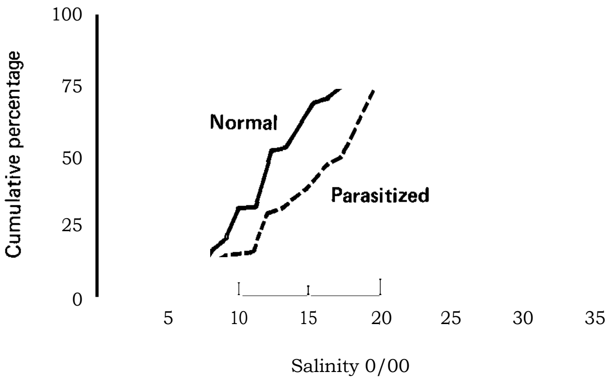


Fig. 10. Cumulative percentage-abundance of normal and parasitized mature female *Alienacanthomysis macropsis* with increasing salinity in the Columbia River estuary.

for *A. macropsis* similar to that of *N. mercedis* in Cathlamet Bay. Unlike *N. mercedis,* the distribution of brooding female *A. macropsis* very closely reflected that of the other mature females. Like *N. mercedis,* the density maxima of *A. macropsis* did show a similar shift upriver from the high flow season to the low flow season.

Parasitic copepods were found in some *A. macropsis* from all stations and hydrologic seasons, but the spatial trend again appeared to be a decrease in the incidence of parasitism from the lower to the upper estuary. *A. macropsis* was collected from water with salinities from 4-30%o. The weighted mean salinities for normal and for parasitized females were 11.4%o and 17%o. Cumulative percentage curves (Fig. 10) also demonstrated that normal and parasitized females had a more similar distribution in relation to salinity than did females of N. *mercedis.* However, a Kolmogorov-Smirnov two-sample test found that the distributions were significantly different at the 1% level for salinities less than 20%o.

DISCUSSION

This is the first study to report a parasitic copepod infesting mysids in North American waters, in spite of a number of mysid surveys along the east, west, and gulf coasts (Wigley and Burns, 1971; Williams, 1972; Williams *et al.,* 1974; Allen, 1978; Siegfried *et al.,* 1979; Price, 1982). All previous records of nicothoid copepods parasitic on mysids are from the European coast of the northeast Atlantic (Hansen, 1897; Tattersall and Tattersall, 1951; Mauchline, 1969).

The four mysid species parasitized by *Hansenulus trebax* occupy a wide geographic area potentially extending the range of the parasite from the Sea of Japan and the Arctic Ocean to southern California. Geographical distributions for these mysids are summarized by Daly and Holmquist (1986). *Neomysis mercedis* has been recorded along the North American Pacific coast from Prince William Sound, Alaska, to Point Conception, California. It is commonly found near shore, in areas influenced by fresh water, as well as in fresh-water lakes. *Alienacanthomysis macropsis* has been found from southern Alaska to southern California and is fairly common in shallow water. *Proneomysis wailesi* Tattersall ranges from southern Alaska to Washington in shallow to moderate depths. It is commonly found around the San Juan Islands and is rarely reported elsewhere. *Xenacanthomysis pseudomacropsis* (Tattersall) can be abundant in coastal open water of the Sea of Japan, the Arctic Ocean, and coastal waters between Alaska and Washington.

This species has not been recorded south of Puget Sound. The two other mysid species from the Columbia River estuary, *Archaeomysis grebnitzkii* and *Neomysis kadiakensis,* were not found with the parasitic copepod because usually only the juvenile and immature stages were collected. With improved sampling, perhaps more mature females could be collected and examined for parasites.

The success of *H. trebax* in the Columbia River estuary is undoubtedly influenced by the behavior, distribution, and morphology of *N. mercedis* and *A. macropsis.* Host-parasite relationships may be density-dependent, with host availability an important factor in determining the incidence of parasite infestation. The average infestation level of about 50% for both mysid species is remarkable. Social behavior is important to mysid community structure (Clutter, 1969; Mauchline, 1971b). Concentrated aggregations of individuals, or swarms, may benefit mysid populations by reducing predation, increasing reproductive contact, and helping to maintain their distribution within their habitat. Swarming may also increase host-parasite contact.

The success of *H. trebax* may be due especially to a host-parasite reproductive synchrony beneficial to the parasite. The main reproductive effort of *N. mercedis* is between spring and early fall, and that of *A. macropsis,* midfall to early spring, so that there is always a mature female mysid host available to the parasite (Figs. 4, 7).

Mysids generally have irregular distributions with high-density aggregations occurring in specific habitats. The populations of *N. mercedis* and *A. macropsis* had overlapping distributions in the central region of the Columbia River estuary (Figs. 5, 9). *Neomysis mercedis* was predominantly at the upstream end of the salt intrusion and into fresh water, whereas *A. macropsis* primarily occupied the lower estuarine to midestuarine mixed zone. Habitat and temporal partitioning can be important mechanisms allowing competing species to coexist. *Hansenulus trebax* has successfully exploited these mechanisms by utilizing the alternating reproductive cycles of the overlapping mysid populations to sustain its own population at a year-round high level.

Salinity is probably not a direct controlling factor in the distribution of N. *mercedis* within the Columbia River estuary. *Neomysis mercedis is* a euryhaline species, but is more commonly found in brackish to fresh-water habitats. Williams (1983), during an epibenthic survey of the Columbia River, found that the largest concentrations of *N. mercedis* occurred in August 1980 just upriver from our Station 13, in the riverine part of the estuary. Salinity probably limited the upstream distribution of *A. macropsis.* That salinity might also restrict the distribution of *H. trebax* was suggested in frequent lower proportions of parasitized *N. mercedis* in decreasing salinity (Fig. 6). However, as expected in such a physically dynamic region as the Columbia River estuary, there were exceptions to this trend. That *H. trebax* cannot adapt to fresh water is suggested by their apparent absence in *N. mercedis* from Lake Washington, a large fresh-water lake near Puget Sound.

Nicothoids are not known to cause the death of their hosts. However, some of these copepods are reported to inhibit ovulation, prevent maturation (or reduce to an immature stage), or affect the host's growth rate (Hansen, 1897; Bowman and Kornicker, 1967; Ritchie, 1975; Sheader, 1977).

The effect of the parasite *H. trebax* on its mysid hosts is poorly understood. However, mysid fecundity was reduced due to parasites feeding on mysid eggs and larvae. The magnitude of this reduction is difficult to quantify because of the sampling limits of this field study. Some mysid eggs and larvae are typically lost from brood pouches during the incubation period. Brood mortality during mar-

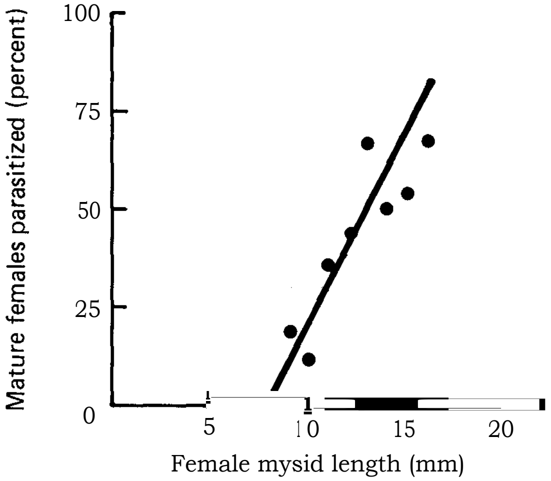


Fig. 11. Relationship between body length of mature female *Neomysis mercedis* and percentage parasitized by *Hansenulus trebax* in the Columbia River estuary.

supial development has been reported to be about 10% (Mauchline, 1973; Allen 1978). Some loss also can occur during the sampling process. For nonparasitized *N. mercedis,* the mean brood-size of larvae is about 10% less than the mean number of eggs per brood. The mean brood-size of larvae of parasitized *N. mercedis* is less than what would be expected even considering a 10% natural loss plus a 37% loss due to feeding copepods. Therefore, the 37% loss may be a minimum level.

The percentage of parasitized *N. mercedis* increased with host body-length (Fig. 11), suggesting that *H. trebax* was retained in the marsupium through host ecdysis until the mysid died. Mature female *N. mercedis* were most frequently 11 mm in length. Newly established juvenile copepods were found only in previously uninfested mature female *N. mercedis* 10–14 mm in length, with the highest frequency of occurrence at 11 mm. Maturing female copepods were found most often in 12-mm female *N. mercedis,* and ovigerous female copepods, sometimes with recently released pupal or juvenile copepods, were found in 10- to 16-mm female mysids, with a maximum occurrence at 13 mm. There is typically only one female copepod to a marsupium; only about 5% of the examined infested mysids carried more than one female copepod. Parasite maturity increased with host age; since larger female mysids generally had larger broods, the greatest impact of the parasite was on the host with the greatest recruitment potential.

Parasitized female *N. mercedis* generally were the same size as unparasitized females. Therefore, *H. trebax* did not appear to influence the female mysid growth rate. However, the parasite may have prevented maturation or delayed mysid brooding by inhibiting ovulation. The larger, parasitized 9 II may normally have matured to 9 III had they not been infested. This was especially evident in mysids, including the larger 9 II, where the marsupium contained a large female copepod and copepod ovisacs, but never mysid eggs.. or larvae.

The decrease in mysid abundances observed during May was perhaps related to the May 1980 eruption of Mount St. Helens. The volcano is about 90 km upriver from the estuary which became extremely turbid within days after the eruption. Phytoplankton productivity was reduced by 75% and did not return to a normal level for 2 months (Frey *et al.,* 1984). McCabe *et al.* (1981) noted that demersal fish populations were greatly reduced until August 1980; they also attributed a reduced feeding rate and decreased diversity in fish diet to a lower abundance and diversity of food.

Diminished mysid populations would decrease the potential of mysids as a predator and as a food resource. Simenstad *et al.* (1984) found *N. mercedis* to be an opportunistic feeder in the Columbia River estuary, with diet varying by location and by season. Small invertebrates such as rotifers (37%), copepods (21%), and cladocerans (20%) were important during the high-flow season. They also found that harpacticoid copepods comprised 90% of the year-round diet of *N. mercedis* in Youngs Bay.

The diet of fish in an estuary generally reflects the abundance and distribution of the dominant pelagic and epipelagic invertebrates. McCabe *et al.* (1983) and Bottom *et al.* (1984) described the food of Columbia River fishes. *Archaeomysis grebnitzkii* was the only mysid to be a dominant prey item, constituting more than 75% of the diet of two species of fishes. *Neomysis mercedis* was an important component in the diet of a number of fish, but it never comprised more than 25% of the diet of any fish. *Neomysis mercedis* also was eaten by juvenile Dungeness crab *(Cancer magister)* but only infrequently appeared in the diet of a shrimp *(Crangon franciscorum)* (Simenstad *et al.,* 1984) that was a major predator of *N. mercedis* in the Sacramento-San Joaquin estuary (Siegfried, 1982). *Neomysis mercedis* may not be as important a prey resource in the Columbia River estuary as it is in other estuaries due to the parasitic infestation affecting the mysid's potential abundance.

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