

AN ABSTRACT OF THE THESIS OF

Exequiel Gonzalez for the degree of Master of Science in
Oceanography presented on August 17, 1983

Title: Tidal Exchange of Decapod Larvae and Small Benthic Peracarids
Between the Ocean and the Salmon River Estuary, Oregon.

Signature redacted for privacy.

Abstract approved:

J. J. Gonor 

Zooplankton samples taken during daylight periods in a fast flushing estuary on the Central Oregon coast were analyzed for Brachyuran and Anomuran larvae and also for benthic gammaridean amphipods and Myscridacea. Several larval stages of Pinnixa littoralis, Hemigrapsus oregonensis, Pachycheles spp., Cancer oregonensis and Pagurus granosimanus were sufficiently abundant for quantitative analysis. Adults and juveniles of the amphipods Atylus tridens, Eogammarus confervicolus, Corophium brevis and the mysid Neomysis mercedis were present in both flood and ebb samples in numbers sufficient for analysis.

All these species showed extensive tidal exchange. Larval stages of decapod crustaceans are exported from the estuary and an important input from the nearshore ocean also takes place. Larval recruits to the adult population of the Salmon River must include larvae flushed from other estuaries all along the coast.

Adult benthic peracarid crustacean were abundant in samples taken at all tidal states indicating that their presence in the plankton is a normal occurrence. These benthic forms would not a

priori be considered as extensively involved in tidal exchange, but according to our data they are.

Tidal exchange of planktonic larvae and adults of small benthic species is clearly related to dispersal mechanisms of the species involved and contributes to maintaining the genetic variability of geographically separated populations.

TIDAL EXCHANGE OF DECAPOD LARVAE AND SMALL BENTHIC
PERACARIDS BETWEEN THE OCEAN AND THE SALMON RIVER
ESTUARY, OREGON

by

Exequiel B. Gonzalez

A THESIS

submitted to


Oregon State University

in partial fulfillment of
the requirements for the
degree of


Master of Science

Completed August 17, 1983
Commencement June 1984

APPROVED:



Signature redacted for privacy. —

Professor of Oceanography in charge of major


Signature redacted for privacy.

Dean of College of Oceanography

Signature redacted for privacy.

Dean of Graduate School 

Date thesis is presented August 17, 1983

Typed by Rebecca Simpkins for Exequiel B. Gonzalez

ACKNOWLEDGMENTS

This has been a long and difficult project to bring to conclusion. I would especially like to thank the work, patience, and encouragement provided by my major professor, Dr. Jefferson J. Gonor. Without his help this work had not been completed. Drs. Andrew Carey, Bruce Menge, and Charles Warren reviewed the manuscript, their suggestions are greatly appreciated.

Dr. J. Gonor and Gary Johnson provided the samples in which this work is based - to them I am deeply grateful.

Many fellow graduate students in Oceanography have contributed many hours of discussion about graduate studies, their advice is appreciated. I owe thanks to other Chilean students at OSU, Eduardo Salgado, Luis Cid, Ricardo Espinoza, Fernando Acuna and many others who gave advice and encouragement during the time I was a student.

My graduate studies were financially supported in part by the Organization of American States and Universidad del Norte, Antofagasta, Chile. I owe thanks to Dr. Victor Neal for his constant support, encouragement, and help.

My especial thanks to my wife Francisca, my daughters M. Francisca and M. Fernanda and my mother who always understands me and believed in what I was doing.

To my wife Francisca and my
daughters Maria Francisca
and Maria Fernanda

TABLE OF CONTENTS

I.	INTRODUCTION	1
II.	METHODS	6
III.	HYDROGRAPHY OF THE SALMON RIVER	10
IV.	LARVAL DYNAMIC AND ABUNDANCES	14
	1. Introduction	14
	2. Abundances	14
	a) <u>Pinnixa littoralis</u>	14
	b) <u>Hemigrapsus oregonensis</u>	16
	c) <u>Cancer oregonensis</u> , <u>Pachycheles</u> spp. and <u>Pagurus granosimanus</u>	17
	3. Ebb and Flood tide differences in density	21
	a) <u>Pinnixa littoralis</u>	21
	b) <u>Hemigrapsus oregonensis</u>	22
	c) <u>Cancer oregonensis</u> , <u>Pachycheles</u> spp. and <u>Pagurus granosimanus</u>	22
V.	PERACARID ACTIVITY AND ABUNDANCE	23
	1. Introduction	23
	2. Abundances and Ebb-Flood tide differences	23
	a) <u>Atylus tridens</u>	23
	b) <u>Eogammarus confervicolus</u>	25
	c) <u>Corophium brevis</u>	26
	d) <u>Neomysis mercedis</u>	27
VI.	DISCUSSION	29
VII.	BIBLIOGRAPHY	37
VIII.	APPENDIX	42

LIST OF FIGURES

<u>Figure</u>		<u>Page</u>
1	Salmon River estuary, Oregon showing location of sampling station A.	62
2	Tidal discharge through the mouth of the Salmon River estuary versus tidal position during the summer, 1979.	63
3	<u>Pinnixa littoralis</u> early zoea density versus tidal position. Samples are classified as ebb or flood flow.	64
4	<u>Pinnixa littoralis</u> late zoea density versus tidal position. Samples are classified as ebb or flood flow.	66
5	<u>Pinnixa littoralis</u> megalopa density versus tidal position. Samples are classified as ebb or flood flow.	68
6	<u>Hemigrapsus oregonensis</u> early zoea density versus tidal position. Samples are classified as ebb or flood flow.	70
7	<u>Hemigrapsus oregonensis</u> late zoea density versus tidal position. Samples are classified as ebb or flood flow.	72
8	<u>Cancer oregonensis</u> zoea I density versus tidal position. Samples are classified as ebb or flood flow.	74
9	<u>Pachycheles</u> spp. zoea I density versus tidal position. Samples are classified as ebb or flow.	76
10	<u>Pagurus granosimanus</u> megalopa density versus tidal position. Samples are classified as ebb or flow.	78
11	<u>Pinnixa littoralis</u> early zoea, flux through the mouth of the Salmon River Estuary versus tidal position during the summer 1979.	80
12	<u>Pinnixa littoralis</u> late zoea, flux through the mouth of the Salmon River Estuary versus tidal position during the summer 1979.	81

<u>Figure</u>		<u>Page</u>
13	<u>Pinnixa littoralis</u> megalopa, flux through the mouth of the Salmon River Estuary versus tidal position during the summer 1979.	82
14	<u>Hemigrapsus oregonensis</u> early zoea, flux through the mouth of the Salmon River Estuary versus tidal position during the summer 1979.	83
15	<u>Hemigrapsus oregonensis</u> late zoea, flux through the mouth of the Salmon River Estuary versus tidal position during the summer 1979.	84
16	<u>Cancer oregonensis</u> zoea I, flux through the mouth of the Salmon River Estuary versus tidal position during the summer 1979.	85
17	<u>Pachycheles</u> spp. zoea I, flux through the mouth of the Salmon River Estuary versus tidal position during the summer 1979.	86
18	<u>Pagurus granosimanus</u> megalopa, flux through the mouth of the Salmon River Estuary versus tidal position during the summer 1979.	87
19	<u>Atylus tridens</u> density versus tidal position. Samples are classified as ebb or flood flow.	88
20	<u>Atylus tridens</u> , flux through the mouth of the Salmon River Estuary versus tidal position during the summer 1979.	90
21	<u>Eogammarus confervicolus</u> density versus tidal position. Samples are classified as ebb or flood flow.	91
22	<u>Eogammarus confervicolus</u> flux through the mouth of the Salmon River Estuary versus tidal position during the summer 1979.	93
23	<u>Corophium brevis</u> adult, flux through the mouth of the Salmon River Estuary versus tidal position during the summer 1979.	94
24	<u>Corophium brevis</u> juvenile, flux through the mouth of the Salmon River Estuary versus tidal position during the summer 1979.	95

<u>Figure</u>		<u>Page</u>
25	<u>Corophium brevis</u> adult density versus tidal position. Samples are classified as ebb or flood flow.	96
26	<u>Corophium brevis</u> juvenile density versus tidal position. Samples are classified as ebb or flood flow.	98
27	<u>Neomysis mercedis</u> juvenile density versus tidal position. Samples are classified as ebb or flood flow.	100
28	<u>Neomysis mercedis</u> juvenile, flux through the mouth of the Salmon River Estuary versus tidal position during the summer 1979.	102

LIST OF TABLES

<u>Table</u>		<u>Page</u>
1	Tidal Prism (10 cubic meters) for the Salmon River Estuary during the summer 1979 (Johnson and Gonor, 1982).	8
2	Decapod larvae.	46
3	<u>Pinnixa littoralis</u> early zoea. Estimates for ebb and flood tide, mean densities, total number, and estimated flux for a tidal cycle on each sampling date.	47
4	<u>Pinnixa littoralis</u> late zoea. Estimates for ebb and flood tide, mean densities, total number, and estimated flux for a tidal cycle on each sampling date.	48
5	<u>Pinnixa littoralis</u> megalopa. Estimates for ebb and flood tide, mean densities, total number, and estimated flux for a tidal cycle on each sampling date.	49
6	<u>Hemigrapsus oregonensis</u> early zoea. Estimates for egg and flood tide, mean densities, total number and estimated flux for a tidal cycle on each sampling date.	50
7	<u>Hemigrapsus oregonensis</u> late zoea. Estimates for ebb and flood tide, mean densities, total number, and estimated flux for a tidal cycle on each sampling date.	51
8	<u>Cancer oregonensis</u> zoea I. Estimates for ebb and flood tide, mean densities, total number, and estimated flux for a tidal cycle on each sampling date.	52
9	<u>Pachycheles</u> spp. zoea I. Estimates for ebb and flood tide, mean densities, total number and estimated flux for a tidal cycle on each sampling date.	53
10	<u>Pagurus granosimanus</u> megalopa. Estimates for ebb and flood tide, mean densities, total number, and estimated flux for a tidal cycle on each sampling date.	54

11	Peracaridean crustacea	24
12	<u>Atylus tridens</u> . Estimates for ebb and flood tide, mean densities, total number and estimated flux for a tidal cycle on each sampling date.	55
13	<u>Eogammarus confervicolus</u> . Estimates for ebb and flood tide, mean densities, total number, and estimated flux for a tidal cycle on each sampling date.	56
14	<u>Corophium brevis</u> adult. Estimates for ebb and flood tide, mean densities, total number and estimated flux for a tidal cycle on each sampling date.	57
15	<u>Corophium brevis</u> juvenile. Estimates for ebb and flood tide, mean densities, total number, and estimated flux for a tidal cycle on each sampling date.	58
16	<u>Neomysis mercedis</u> juvenile. Estimates for ebb and flood tide, mean densities, total number and estimated flux for a tidal cycle on each sampling date.	59
17	Wilcoxon test, significance table. Differences between densities in ebb and flood tides (* = $p < 0.05$)	60
18	Mean densities of decapod larvae in nearshore stations off the Oregon coast during June-August (mean 1969-1971). Numbers per 100 cubic meters (from Lough, 1975).	61
19	Ebb and flood mean densities of <u>Callinassa californiensis</u> in the Salmon River Estuary, June through August 1979. Number per cubic meters (from Johnson and Gonor, 1982).	61

TIDAL EXCHANGE OF DECAPOD LARVAE AND SMALL BENTHIC PERACARIDS
BETWEEN THE OCEAN AND THE SALMON RIVER ESTUARY, OREGON

I. INTRODUCTION

The meroplanktonic zooplankton in shallow marine waters and estuaries is composed mainly of small benthic organisms and larvae of benthic invertebrates. Among these, crustaceans are probably the most important in abundance and diversity. In small estuaries peracarid crustaceans form the bulk of the benthic invertebrates in the meroplankton, along with the larvae of decapod crustacea confined to estuaries as adults. The planktonic larvae of decapod crustacea in estuaries will be strongly affected by the tidal exchange of estuarine and near shore waters. This tidal exchange is critically important for the benthic decapoda living in the estuary, and it will have implications for the maintenance of the populations in estuaries (Johnson and Gonor, 1982).

The flushing rate will determine the kind of plankton population present, in terms of endemicity. It has been suggested that estuaries with high flushing rates should have no endemic populations, merely plankton resembling that of the ocean off-shore. Estuaries with slower flushing rates should have endemic populations (Miller, 1983). The main problem for these populations is to maintain recruitment. Either retention of larvae within the parent estuary and/or input from the near-shore ocean of mixed larvae previously exported from the parent estuary and adjacent estuaries will supply larvae for recruitment (Johnson, 1981). Recruitment from outside the estuary is from larvae, juveniles, and adults that enter with the flood tide

(Johnson and Gonor, 1982). One important consideration for this kind of contribution is that the planktonic life of the larvae must be longer than the estuarine flushing time.

Probably the best known mechanism for recruitment of larvae of estuarine benthic organisms is retention. The literature is filled with references to this phenomena in many animal taxa. Most of the work has been done in the east coast of the United States.

One of the most important observations in relation to this mechanism is the presence of larvae near the bottom, where, in a stratified estuary the net flux of the estuary is upstream. Several studies have been done in order to find some evidence for the occurrence of retention. Cronin (1982) studying Rhithropanopeus harrisii (Crustacea, Decapoda) in a North Carolina estuary found that larval retention is the prevailing mechanism for the recruitment of this species. The same results have been obtained by Lambert and Epifanio (1982), Dittel and Epifanio (1982) and Boicourt (1982). Sandifer (1973) observed that larvae of a number of common species were considerably more abundant in bottom collections than near the surface. He also pointed out in a later paper (Sandifer, 1975) that the animals which remain in the lower, upstream moving layer of the water column during a substantial portion of their larval development are much more likely to be retained within the estuary than are those which do not.

Several different behavioral and non-behavioral responses have been proposed as an explanation for retention mechanisms. Rogers

(1940) suggested that presence near the bottom may be achieved by diurnal vertical migration. Cronin (1982) also proposed vertical migration as mechanism. He found the vertical migration of larvae of Rhithropanopeus harrisii ranged above and below the depth of no-net flow. Cronin and Forward (1982) reported this migration to be a tidally timed behavior.

De Wolf (1973) disagreed with the contention in that retention was an active process. He claimed that retention could be explained as a passive process resulting from greater tidal current velocities on the flood than on the ebb tide. Boicourt (1982) observed that the classical two-layer estuarine circulation has been proposed as the most likely mechanism for retaining larvae, but that larval retention must be also explained in estuaries with low stratification. He suggested that water motion is the crucial determinant of larval transport regardless of the possible role of larval motility. Vertical migration only enhances the retention mechanisms.

The possibility of input of larval recruits from the near-shore ocean has been mentioned as a minor contribution to the recruitment of benthic invertebrates in estuaries (Johnson, 1981). However it has been found that the export of larvae from the parent estuary and the later input into other estuaries is a common mechanism for larvae of some benthic invertebrates in estuaries. Rogers (1940) agrees that the nearshore oceanic zone must be a source of recruits for species inhabiting fast flushing estuaries where the physical characteristics preclude retention. Several other authors have found

that export to the nearshore ocean is a very common mechanism in some species (Johnson and Gonor, 1982; Sulkin and Van Henkelen, 1982; Christy and Stancyk, 1982; Strathmann, 1982; Dittel and Epifanio, 1982, and Lambert and Epifanio, 1982).

The swimming activity of benthic Peracarida involves a complex array of rhythmic behaviors, which are mainly associated with particular phases of the diel light and/or tidal cycles (Davis, 1979).

The cyclic behavioral and physiological patterns displayed by benthic invertebrates are in many cases in synchrony with the tides in their habitat. The phase relationships of tidal rhythms are species specific (Palmer, 1976). Morgan (1965) studied the swimming activity of Corophium volutator in South Wales and found a relation with the tides. Increasing activity was mainly early in the ebb tide, decreasing toward the low slack. This behavior was related to effects of hydrostatic pressure, with a decrease in pressure triggering swimming. Morgan also found that there was no effect of the light cycle in the tidal activity of Corophium. Meadows and Reid (1966) found that the same species studied by Morgan (1965) tends to swim toward the light. Davis (1979), who reviewed swimming activity rhythms of benthic crustaceans, put much more emphasis on diel periodicities as an explanation for the frequent presence of peracarids in the water column. He did not find any relation to the tidal cycle in his data for Youngs Bay (Columbia River, Oregon). The problem of tidal exchange in peracarideans and other benthic invertebrates without pelagic larvae has been poorly studied, but it involves complex behavioral aspects and it is also an important factor to consider in dispersal mechanisms.

Johnson and Gonor (1982) investigated the hypothesis that larvae of Callinassa californiensis must be exported to the nearshore ocean if their planktonic life is longer than the estuarine flushing time and if there is no retention within the parent estuary. In this study, we used the same samples as Johnson (1981) and Johnson and Gonor (1982), to determine if a similar behavior was shown by other decapod larvae and small benthic peracarids present in the zooplankton samples. The samples were taken by Johnson at a station near the mouth of the Salmon River Estuary, Oregon during summer 1979.

Our aims were (1) to compare the densities of the different groups during the daylight ebb and flood tides and (2) to determine the extent of the tidal exchange between the ocean and the estuary.

Questions asked include:

1. Are there any losses of larvae of truly estuarine organisms to the nearshore ocean?
2. How do these species, and especially benthic peracarid crustacean maintain their populations in the estuary?
3. What happens to the marine planktonic larvae, juveniles, or adults that enter the estuary?
4. Why do we find them in the water column?
5. What are the adaptative advantages of this activity?

Many of these questions cannot be fully answered with the type of information we have available; however, it will provide a good approximation to the problem. Our results will be based on minimum figures because in most of the cases the samples do not coincide with the maximum larval release for the species studied and the samples were taken during the daylight hours only.

II. METHODS

The field work was carried out in the Salmon River estuary (45°N-124°W), located 137 Km south of the Columbia River (Figure 1). For a detailed description of the study site, refer to Johnson (1981) and Johnson and Gonor (1982). The samples used were obtained weekly from June 23 to August 9, 1979, at a permanent station 0.2 Km from the mouth of the estuary. The sampling design and the description of the physical parameters considered are described in detail by Johnson (1981). The samples were taken at a single station using a 0.5m diameter, 0.5mm mesh, conical Nitex net suspended from a skiff anchored in mid-channel. Samples were taken approximately hourly over one daylight tidal cycle. The volume filtered was determined by the use of a calibrated flowmeter mounted in the net mouth, 12.5 cm from the frame. An average of 227 cubic meters (s.d. 88 cubic meters) was filtered to obtain each sample.

In his analysis of these samples, Johnson (1981) separated out only the larvae of Callinassa californiensis. In the present study all other decapod larvae, gammaridean amphipods, and mysids were picked from all the samples. Four samples required subsampling for decapod larvae.

Temperature (TBAR) and salinity (SBAR) measurements were taken on every point of the tidal cycle sampled. All measurements were made at least 0.5 m depth interval using the same calibrated Beckman inductor salinometer. Longitudinal and horizontal temperature and salinity transects were sampled at or near high tide because of the

shallowness of the estuary. Also an experiment was performed on the ebb tide to follow the path of estuarine water into the nearshore ocean. Volumes of ebb and flood water were estimated using a model of the shape of the Salmon River Estuary (Johnson, 1981). One parameter that Johnson (1981) considered was tidal position (TPOS), which is the ratio of elapsed time between the time when the sample was taken and the time of the nearest low slack, to the total duration of a particular one half tidal cycle. This measure was designed to reflect the effect of the height changes on the physical, chemical, and biological characteristic of the water column passing through the mouth of the estuary. Values range from -1 (ebb flows) to +1 (flood flows). Tidal position values of -1 to +1 are obtained at high slack tides and zero values are at low slack. Tidal discharge (TDIS) (Cubic meters per second) is another variable involved in the estimation of fluxes. The mean discharge during the time each sample was being taken was estimated as the product of the mean current velocity during that time and the cross-sectional area of the mouth at the midpoint of the sampling period (Johnson and Gonor, 1982). Other environmental variables considered were Bakun's upwelling index (Bakun, 1980) (UPWG); this variable is specific to each sampling date. Temperature, salinity, tidal position, and tidal discharge are sample specific variables.

In the estimation of net flux for the different species or stages we used basically two methods for comparing the twenty five pairs of ebb and flood flows. The first method (Johnson and Gonor, 1982)

considers the differences in densities between the total number estimated for each flow, i.e., the total number of organisms passing through the mouth of the estuary during a given flow. This was estimated as the mean of the raw larval density (number per cubic meters) for that flow multiplied by an estimate of the total volume ebbled or flooded (Table 1). However, Johnson and Gonor (1982) stated that according to Boon (1979) and Kjerfve (1975) this method has the disadvantage of producing serious errors, if discharge and larval concentration are correlated through time, specially in an estuary such as the Salmon River with a large tidal range to depth ratio. The second method used takes this possibility into account. This method (Johnson and Gonor, 1982) modified from those of Kjerfve and McKellar (198) and Boon (1979) estimates the larval flux (number per second) for each sample by taking the product of larval concentration (number per cubic meters) and tidal discharge (TDIS) (cubic meters per second) for the sampling interval.

Table 1. Tidal Prism (10^5 cubic meters) for the Salmon River Estuary during the summer 1979 (Johnson and Gonor, 1982).

	<u>6/23</u>	<u>6/30</u>	<u>7/08</u>	<u>7/15</u>	<u>7/22</u>	<u>7/30</u>	<u>8/09</u>
Flood	9.02	8.38	8.80	11.22	8.60	8.59	12.86
Ebb	6.10	7.70	5.76	8.52	5.51	6.27	11.04

The sample larval flux estimated was used for comparing the differences in larval presence in the flows. We also used the summed sample larval flux (ebb, negative; flood, positive) for each sampling date, to obtain a total flux estimate for that particular tidal cycle.

These three sets of results were analyzed statistically using a two tailed Wilcoxon matched-pairs signed rank test with $\alpha = 0.05$ (Siegel, 1956; Daniel, 1978). The test used the densities found for ebb and flood fluxes. In the case of the first method, seven samples, one pair per sample in the second twenty five for the sample larval flux estimate and seven for the total (summed) flux estimate for a tidal cycle were used.

The sets of pairs were used to test the significance of the null hypothesis, that during daylight tidal cycles the number of organisms (larvae or peracarids) leaving the estuary was the same as that entering.

III. HYDROGRAPHY OF THE SALMON RIVER ESTUARY

A detailed description of the hydrographic characteristics of the Salmon River estuary is given by Johnson (1981) and Johnson and Gonor (1982), for the same time the samples were taken and also by Askren, et.al. (1976) for a different period. We include here a summary of their observations. During summer the estuarine water column is well mixed, with respect to temperature and salinity, on the seaward side of the salt wedge. The region of marine influence extends approximately 3 km upstream from the mouth. The upper reaches are partly stratified and the salt wedge penetrates at least as far as the Highway 101 bridge, 5 km from the mouth.

The water column passing the sampling station in the mouth was well mixed throughout the tidal cycle so all vertical measurements of temperature and salinity were averaged. Low salinity, high temperature water passing the mouth late in the ebb originates at least three kilometers up the estuary. Temperature and salinity of the flood tide reaches a stable structure within two hours after low slack. This indicates that undiluted nearshore water is entering the estuary during most of the flood flow and that almost all of the ebb water is lost to the nearshore region. Johnson (1981) estimated that nearly 100% of the ebb water is lost to the nearshore region.

The fact that during the summer the alongshore current runs southward is also evidence indicating a nearly complete exchange in the estuary. The current is parallel to the coast and runs at velocities ranging from 8.6 to 26 km day⁻¹ (Huyer et.al., 1975). In

his drift card experiments, Johnson (1981) found that the average path of the cards released in the estuary mouth was first southward parallel to the shore, and then westward into the alongshore current and finally to the southwest. He concluded that in summer the ebb water does not remain behind Cascade Head but enters the nearshore current system and is swept southward, so most of the ebb water entering the nearshore current system is swept southward and does not return to the estuary.

Askren et.al. (1976) estimated a flushing time for the Salmon River of a few days, without taking into account the effect of upwelling. According to Duxbury (1979) upwelling effects may speed up flushing rates even though river discharge declines, so the flushing time might decrease. Johnson (1981) considered that the estimates of flushing times of a few days are reasonable for summer conditions.

During the sampling period, river discharge was low, decreasing from 2.2 to 1.1 m³ s⁻¹ according to Johnson and Gonor (1982). This small amount of variation could not have altered the circulation appreciably.

The sampling period was affected by seasonal upwelling; four of the samples analyzed were taken during relaxed upwelling and one was taken during a downwelling event (Bakun, 1980).

Both the extent to which ebb water returns to the estuary and the rate of discharge during the tidal cycle were estimated (Figure 2); the plot shows a pronounced asymmetry in tidal discharge. Generally, both ebb and flood peak discharges were reached nearer

high slack than low slack tide. It is clear that most of the ebbed volume emerges early in the ebb period (Johnson and Gonor, 1982). The spring, daylight tidal cycles sampled were from low-high to high-low and neap tidal cycles were sampled from low-high to low-low to high-high. Flows around high slack were sampled more intensively than flows around low slack (Johnson and Gonor, 1982). Temperatures ranged from 7.4 C to 18.2 C. Salinities ranged from 13.2‰ to 34.6‰, skewed to the higher salinities. After accounting for the effects of tidal position and upwelling (Johnson, 1981) on the relations between temperature and salinity and spring neap tide series, spring flood flows were cooler and more saline than neap flood flows. Neap flood flows had more variation in the values of salinity and temperature and they were less saline than spring ebb.

The changes in temperature and salinity in relation to the tidal cycle was the same for both spring and neap tide series. As flood progressed, temperature decreased (TPOS-TBAR $r = -.36$) and salinity increased (TPOS-SBAR $r = .59$; TBAR-SBAR $r = -.70$). As ebb tide progressed, temperature increased (TPOS-TBAR $r = .56$) and salinity decreased (TPOS-SBAR $r = -.84$; TBAR-SBAR $r = -.51$). The ebb patterns were more pronounced for neap tides series than for spring tide series.

Upwelling also has an effect on temperature and salinity. As the magnitude of the upwelling increased, temperature decreased and salinity increased for both ebb and flood flows, after accounting for the effects of tidal position and spring-neap tide series (Johnson, 1981). For ebb flows the relation between upwelling and

salinity is not clear, Johnson (1981) proposed a masked effect by the spring neap tide series.

The tidal discharge is closely related to TPOS for both flows (TPOS-TDIS, ebb $r = .79$ and for flood $r = .46$). It does not bear any correlation to upwelling. The relation with spring neap series is clearer in the ebb flows where on average the discharge is less for the neap tides.

IV. LARVAL DYNAMIC AND ABUNDANCES

1. Introduction

The samples gave us the opportunity to examine several kinds of meroplanktonic organisms which are present in the plankton of the Salmon River Estuary. Brachyuran and Anomuran larvae were chosen because of our better reliability in identifying these forms. Larvae of other crustaceans were also present, but were not considered due to identification difficulty.

Six Brachyuran and five Anomuran species were identified in the samples (Table 2). Some early larval stages, e.g. Pachycheles and Pugettia could not be identified to a specific level. However in these two genera megalopa stages were present and these could be identified to species.

The following sections will deal with some of the more abundant group of larvae. On the basis of abundance only five species of larvae were selected for further analysis. Those chosen were Pinnixa littoralis, Hemigrapsus oregonensis, Pachycheles spp., Pagurus granosimanus and Cancer oregonensis. Within these species only some larval stages were selected, on the basis of abundances, for statistical analysis. Other larval stages were sorted and counted, but not analyzed. Their densities are shown in the appendix.

2. Abundances

a) Pinnixa littoralis Holmes, 1894

This species was the main Pinnotherid present in our samples. Its known geographic distribution is from Sitka, Alaska to San Diego,

California (Schmitt, 1921). It is a common commensal in the bivalves Tresus capax and T. nutalli on the Californian coast and Saxidomus nutalli on the Washington coast (Morris et.al., 1980). In Yaquina Bay, Oregon it is commonly found in clams such as T. capax, T. nutalli and Mya arenaria (Lough, 1975).

Pearse (1966) found ovigerous females in late spring and summer and also in winter and early spring; the winter period is considered the more successful. Larvae of this species take 47 days to reach the megalopa stage in the laboratory. The presence of the larval stages of this species in Oregon coastal waters was studied by Lough (1975). During 1969 through 1971, he found that their occurrence is most frequently within five miles of shore and their presence throughout the year is very irregular with abundance peaks occurring almost every season. This variability in samples taken near Yaquina Bay are explained by Lough (1975) as an irregular influx of larvae in the coastal ocean from the Yaquina Bay plume. In the period of his study, Zoea I larvae first appeared in February and March with their subsequent stages overlapping a second major hatching in May and June. He estimated a larval life of 56 days (30 to 80 days).

In our Salmon River samples taken from late June through August, we found zoea I to V and Megalopa during all this period. The ebb and flood tide larval proportions were: zoea I 30%; zoea II 18%; zoea III 5%; zoea IV 2%; zoea V 7%; and megalopa 38%. Since the behavior of zoea I and zoea II was almost the same through all the sampling season, we have considered them as one group. The same is nearly true for zoeae III, IV, and V, so we also pooled them

into another category. The zoeae I-II group will be referred to as early zoeae and the zoeae III-V group as late zoeae.

Early zoeal stages were present during all the sampling season (Figure 3). Although late zoeal stages were found in every sample, the highest peaks were in early and late July (Figure 4). The first peak corresponds mainly to zoea 5 and the last mainly to zoea III and IV. The megalopa stage was more abundant in early July but its presence was observed in all samples decreasing toward the end of July and early August (Figure 5). The high density in July coincides with the downwelling period.

b) Hemigrapsus oregonensis (Dana, 1851)

The range of this shore crab along the Pacific coast is from Resurrection Bay, Alaska to Bahia de Todos los Santos, Baja California (Morris et.al., 1980). In estuaries it occurs on muddy bottoms (Batie, 1974) and it is mainly subtidal. Its intertidal abundance is limited by the availability of rocks, vegetation, or debris that may be used as a cover to escape from predation (Guin, 1978).

The reproductive season is from April through August (Batie, 1974). Hatching starts in May and continues into July. A second egg brood may be deposited in August and would hatch by late September. However, Batie (1974) found brooding females every month in his study of Yaquina Bay, Newport, Oregon population. Guin (1978) observed copulation in the field from January to September and she found the greatest number of brooding females early in Spring, but with some present throughout the year.

Larvae of H. oregonensis have been described by Hart (1935). There are five zoeal and one megalopa stage. The main difference among zoeal stages are size and number of swimming setae in the maxilliped exopodite, but in our samples we could not find any consistency in those characters for separating Zoea I from Zoea II. So we will consider them as one group, early zoeae.

Lough (1975) found larvae of H. oregonensis occurring sporadically in low numbers from May to December near the Oregon coast with peaks of abundance in June and September. Few megalopa were found beyond one mile of shore, but were numerous within Yaquina Bay, Newport, Oregon. The larval life for this species was estimated to last from 40 to 70 days (Lough, 1975) using field estimates and from 28 to 35 days by Hart (1935) in experimental conditions.

In our samples 95% of the Hemigrapsus larvae collected were early zoeae and the rest late zoea (zoea III, IV, V). Megalopae were found in very low densities only in July.

Early zoeae were present during all the sampling season with peaks in late June and mid to late July, with the highest densities late in July (Figure 6). This early zoeal high peak coincides with that of Pinnixa littoralis. Late zoea were present only in late July and August with no occurrences during the rest of the sampling period (Figure 7).

c) Cancer oregonensis, Pachycheles spp. and Pagurus granosimanus.

These species were present in low numbers and only a few zoeal stages were found. For Cancer oregonensis, only zoea I and megalopa

were represented in the sampling season. Pachycheles spp. were also represented by zoea I and megalopa. It is very difficult to distinguish between the larvae of two species of this genus, Pachycheles rudis and Pachycheles pubescens. These have been studied by Knight (1966), McMillan (1972) and Gonor (1973). All of them gave detailed descriptions of zoeae and megalopa, but definite identification requires careful dissection of each specimen. Pagurus granosimanus was represented during all the sampling season mostly by megalopae, with zoea 1 through 4 present only rarely. Cancer oregonensis (Dana, 1852) is distributed from St. George Islands (Pribilof Islands, Alaska) to Palos Verdes (Los Angeles, California). It is abundant subtidally, occasionally found under rocks or wedged in crevices and holes in the low intertidal zone on rocky shores (Morris et.al., 1980). In Puget Sound, eggs are deposited in late November and are carried until February when hatching is completed (Knudsen, 1964). He has also indicated a possible second brood during April-June for some individuals. Lough (1975) found the first substantial appearance of C. oregonensis larvae in January along the Oregon coast. He estimated the hatching period from January to July, with probably two broods, one with a peak in February and the other in May-June, with a general decrease in densities with time. The entire larval period extended from January through September, and estimated larval life of 155 days (123-203). Although the densities of Zoea I were low in our samples, it is possible to distinguish a peak in abundance late in June, with very low densities the rest of the time (Figure 8). Megalopa stages were present in very low densities only late

in June and from mid to late July. The samples were probably a little late in the time for catching high numbers of Zoea I. Late Zoeae are probably carried offshore, especially during the upwelling season. In Cancer oregonensis transport by upwelling is probably much more effective due to the distribution of the adults down to 435 m depth. Lough (1975) found in some of the offshore stations high densities of early and late Zoeal stages. It is probable that Cancer oregonensis larvae are only occasionally driven into estuaries.

Pachycheles pubescens and P. rudis live at the same tide level, in the low intertidal zone on rocky shores in very similar environments (Morris et.al., 1980). Their larvae have been obtained from May through September in plankton tows within one mile of Yaquina Bay, Newport, Oregon (Gonor and Gonor, 1973). Lough (1975) identified all the Pachycheles larvae he found as P. pubescens and they appeared sporadically throughout the year in great abundances near the shore, within 3 miles of the coast. Peak abundances occurred in May-June, January-February and October-November, with low periods during the end of March through most of April and also at end of the summer in August.

From dissection of some of the Pachycheles larva in our samples we were able to identify them as P. pubescens, however a generalization is dangerous. We have found a peak of zoea I late in July and early August (Figure 9). Some megalopae were also present, all of them identified as P. rudis. The peak of abundance was early in July and they were absent from the rest of the sampling season. The larval life for these species is not very well known. Gonor

(1970) found for P. rudis that the time from hatching to megalopa was 44 days and for the same species Knight (1966) found 24 days, for the same larval period. Pachycheles pubescens from hatch to juvenile takes about 34 to 40 days (McMillan, 1972). All of these estimates are from laboratory experiments. There are no estimations from the field.

Pagurus granosimanus was the only pagurid found in our samples. The adult of this species is common in lower middle and low intertidal zones on protected rocky shores from the Aleutians Islands, Alaska to Bahia de Todos los Santos in Baja California (Morris et.al., 1980). There is not much information about the reproduction of this species; like all other species in the family it passes through four zoeal stages and one megalopa stage before becoming a juvenile. Its larval life has been estimated about 50 days with a range of 26 to 81 days (Lough, 1975).

In our sampling we observed the presence of the four zoeal stages and one megalopa stage. However the most abundant was the megalopa, which was the only one considered in the statistical analysis. Zoea I was present in very low densities sporadically in the sampling season, but increasing in late July and August (Appendix). Zoea II through IV were only present in August in moderate densities. The Megalopa stage had a peak early in July (Figure 10), again coinciding with the occurrence of downwelling.

3. Ebb and flood tide differences in density

a) Pinnixa littoralis

Wilcoxon matched-pairs signed-rank test applied to the larval flux estimate per sample in the early and late Zoeal stages resulted in no significant evidence for the rejection of the null hypothesis that the amount of larvae per second in the ebb flow equaled the larvae per second in the flooded flow at $\alpha = 0.05$ for a two tailed test (Figures 11, 12, and Table 17).

It is important to mention that for early zoeal stages, the sum of the sample larval fluxes for each sampling date (total larval flux estimate for a particular tidal cycle) was higher in the ebb flow for June and early July, with the inverse situation during the rest of the sampling period (Table 3). This is probably related to the release time of the larvae, whose second highest peak is May-June (Lough, 1975). The late zoeal stages during the dates of highest abundance had no difference in density between ebb and flood flows (Table 4). One of the peaks was early in July due to the weight of zoea V, while the other was late in July where zoea III and IV are more important and the densities in the flood tide were the highest. For the megalopa stage, using the same Wilcoxon test, the null hypothesis, stated in the same terms mentioned above, was rejected. The amount of megalopa was higher in the flood than in the ebb flow (Figure 13) ($\alpha = 0.002$). The total larval flux estimate for P. littoralis megalopae in a particular tidal cycle (Table 5 and 17) shows significant differences between flood and ebb tides. Also the

estimates of total number for each flow was significantly different for ebb and flood tides.

b) Hemigrapsus oregonensis (Figures 14 and 15)

The Wilcoxon matched-pairs signed-rank test for the flux estimate per sample for early zoeal stages present in the ebb and flood flows indicated no significant difference between the flows.

The Wilcoxon test applied separately to the total number estimates for each flow, or to the total flux for a tidal cycle (Tables 6, 7, and 17) showed that they were not significantly different.

c) Cancer oregonensis, Pachycheles spp. and Pagurus granosimanus

Cancer oregonensis Zoea 1 had the highest density during the ebb, late in June (Table 8). The megalopa stage was present only during the flood flows (Appendix). Zoea 1 of Pachycheles was more abundant during flood flows and on five occasions the total flux for a particular tidal cycle was higher in the flood than in the ebb. Also the highest densities of the zoeal stages were found during the flood (Table 9), while megalopa was more abundant during the ebb flow (Appendix). For the total flux estimate for a tidal cycle none of the species showed statistically significant differences ($\alpha = 0.05$) (Table 17). Using the flux for each sample the three species showed no significant difference between the flood and ebb tides (Figures 16, 17, and 18, and Table 17). The differences between total number of larvae in the flood and ebb tide was significant only for Pagurus

($\alpha = 0.05$, Wilcoxon test). In this case the flood tide flow contained the higher number of larvae (Table 10 and 17).

V. PERACARID ACTIVITY AND ABUNDANCE

1. Introduction

Peracarids were well represented in the samples. Within this group we chose gammaridean amphipods and Mysidacea for close study, because of their abundances. Other groups were also present such as Cumaceans and Hyperiid amphipods, among the Peracarideans. Other benthic crustacea like ostracods and copepods were also present but rarely and in very low frequencies and abundances.

Among the peracarids which were sorted out and counted (Table 11 and Appendix) we decided to consider for further analysis only four species, the gammaridean amphipods Eogammarus confervicolus, Atylus tridens, and Corophium brevis and the Mysid Neomysis mercedis. Juveniles stages of the last three species were clearly distinguishable. In A. tridens the differences in densities through time of adult and juveniles were not significant (t-test, $\alpha = .05$). The densities through time of adult and juvenile stages in C. brevis differed significantly (t-test, $\alpha = .05$). The adult stage of Neomysis mercedis was present only occasionally and was not considered for the analysis.

2. Abundances and ebb-flood tide differences

a) Atylus tridens (Alderman, 1936)

There are only a few records of this species in the literature. The original description was done with material collected near Moss

Table 11. Peracaridean crustacea

Neomysis mercedis Holmes, 1896
Archaeomysis grebnitzkii Czerniavsky, 1882
Acanthomysis sp.
Atylus tridens (Alderman, 1936)
Eogammarus confervicolus (Stimpson, 1856)
Corophium brevis Shoemaker, 1949
Corophium spinicorne Stimpson, 1857
Corophium salmonis Stimpson, 1857
Jassa falcata (Montagu, 1808)
 Calliopidae (2 spp.)
 Haustoridae (1 spp.)

Beach, San Mateo County, California. Mills (1961) extended its distribution to Vancouver Island and the Queen Charlotte Islands, British Columbia. It has been also reported for the Columbia River Estuary, Oregon (Higley and Holton, 1978).

Mills (1961) recognize two stages in A. tridens, a non-pelagic stage reaching breeding condition at about 12mm, and a pelagic stage, reaching breeding at 20mm. We were not able to observe that difference, because our animals never reached 20mm. Mills (1961) concluded from his samples that A. tridens appears to be a polyhaline to marine animal present in outer coast situations and sheltered high salinity areas, where some sand with eelgrass and rock is present.

In the Salmon River Estuary, A. tridens was present during all the sampling season with a peak late in June and another in mid-July. The June peak occurred during the ebb tide and the July, during the flood tide (Figure 19).

Atylus tridens flux through the mouth of the Salmon River Estuary (Figure 20) was equal for the ebb and flood flow ($\alpha = 0.05$, Wilcoxon test). The total number estimates for each flow and the total flux estimate for a tidal cycle (Tables 12 and 17) did not show any difference for the ebb and flood tides.

In general we can say, with the exception of August, that during the ebb tide A. tridens densities decreased toward the low slack and during the flood the densities increased slightly toward the high slack (Figure 19).

b) Eogammarus confervicolus (Stimpson, 1856)

This boreal species was formerly known as Anisogammarus confervicolus (for details see Bousfield, 1977, 1979, and Barnard and Karaman, 1980). According to Tzvetkova (1975) it widely distributed along the North-Pacific American coast ranging from the Alaskan peninsula to San Francisco Bay (California) where it is found mainly in estuaries. E. confervicolus is abundant in the Columbia River Estuary, including the fresh water reach (Higley and Holton, 1978; Davis, 1979). This amphipod is epibenthic and mainly associated with filamentous algae, such as Enteromorpha (Pomeroy and Levings, 1980). Barnard (1954) found it in a log

boom, in mud, in Cladophora glomerata and also in sandy beaches. The Salmon River Estuary seems to be a typical habitat for this amphipod. Numbers present in our daytime samples were not surprising, due to its mainly nocturnal activity (Davis, 1978 and Levings, 1976).

Levings (1976) observed that although frequently present in the water in the British Columbia estuaries at high tide, only a small proportion of the population leaves cover on each high tide.

Although in the Salmon River Estuary the presence of E. confervicolus was very consistent throughout the sampling season, its densities were low compared to some data reported for night samples in the literature. However in some cases densities were high in daylight samples like in early July (Figure 21). Highest densities were found during the ebb flow, but there was not a significant difference (Wilcoxon test $\alpha = 0.05$) between ebb and flood in the total number estimates for each flow, (Table 13), nor for the net flux estimate for each sample or for a tidal cycle (Table 13, Figure 22).

c) Corophium brevis Shoemaker, 1949

Defined by Davis (1979) as a marine species, C. brevis has been poorly studied. It was described by Shoemaker with material from Puget Sound, Washington and it has also been collected in both San Francisco Bay and Humboldt Bay, California; Clayoquot Sound, Vancouver Island; and Stephens Passage, Alaska. Barnard (1954) reported it from Oregon, living among algal debris, and also in Ulva. Davis (1979) cited it as a rare species in Youngs Bay, Columbia River

Estuary, Oregon. Higley and Holton (1978) found it in several places in the Columbia River Estuary.

Corophium brevis was the most abundant peracarid in our samples. Due to its density we considered the juveniles and adults forms separately. Their density differed significantly (t-test, $\alpha = 0.05$) through time. Although there are no significant difference between densities on ebb and flood flows, the tendency in juveniles is for slightly higher densities during the ebb tide and in adults for higher densities in the flood tide (Figures 23 and 24). In general, both forms tend to have an increase in density toward the low slack and a decrease toward the high slack (Figures 25 and 26). Highest densities occurred late in June and early in July. In the adult form all the highest densities were during the flood. The highest density of the juvenile form was observed in a flood flow sample but its density was frequently higher during the ebb flows (Table 15). The total number of C. brevis estimates for each flow and the net flux estimate for a tidal cycle (Tables 14 and 15) did not show any differences for the ebb and flood tides, using the Wilcoxon test.

c) Neomysis mercedis Holmes, 1896

The distribution of N. mercedis has been recorded from Prince William Sound on the south coast of Alaska to the San Francisco Bay area (Holmquist, 1973). The type locality is Lake Merced on the San Francisco Peninsula (Tattersal, 1951). It is typically an epibenthic species living in coastal areas, estuaries, lagoons, inlets, and bays.

This classifies it as a marine-brackish water organism, with a salinity range from fresh water to 30‰ and a temperature range from 7° to 27°C (Holmquist, 1973). Body size in the adult is generally from 9 to 19 mm (Mauchline and Murano, 1977). The food habits of N. mercedis have been studied by Kost and Knight (1975) who found that diatoms and detritus were the most abundant material in the guts. The proportion of both items varies according to the size of the animal, with the detritus proportion increasing as body size increases. Seasonally diatoms increase in relative amounts in the diet in summer and detritus increases in the winter months. In general N. mercedis is omnivorous.

The juvenile form of N. mercedis in the Salmon River Estuary was present throughout all the summer 1979. Peaks of density occurred mainly in late June and early July, although there was a peak also in late July (Figure 27). There were no significant differences between the densities in the ebb and flood tides (Table 16). The fluxes through the mouth of the Salmon River Estuary were not different (Table 16, Figure 28). The net flux estimated for each sample was slightly higher for the ebb tide with an average of 3.95 organisms per second and for the flood samples of 2.76 organisms per second.

VI. DISCUSSION

Estuaries are greatly influenced by the marine environment. Their communities are composed mainly of euryhaline organisms, and the endemic estuarine fauna has few species. The extent to which some species are dependent upon the physical environment is poorly known.

Benthic invertebrates in estuaries have to face the problem of maintaining their populations within determined habitat ranges. The pelagic larvae of some of them makes this more difficult. In response, they must evolve some adaptative strategies. In general, these fall in two categories: 1 - Retention of larvae in the estuary by several mechanisms widely discussed in the literature, such as permanent residence near the bottom for net upstream transport (Sandifer, 1973, 1975) together with shortening of the pelagic phase of the life cycle (Carriker, 1967); 2 - Recruitment of larvae, juveniles, and adults from the nearshore as a result of supply from the same or other estuaries. This strategy involves longer larval stages.

In the Salmon River Estuary, it has been proposed that the latter strategy is used by populations of Callianassa californiensis, due to the characteristics of the site (Johnson and Gonor, 1982). The flushing time is only of a few tidal cycles, and there are no other indications of physical mechanisms that could help in the retention of larvae in the estuary.

In this study our interest was to determine what happens with the larvae of other crustacea present in the estuary. Although the sampling period did not coincide with the time of maximum release,

some of the larvae were abundant, especially early zoea and megalopae of Pinnixa littoralis and zoeae of Hemigrapsus oregonensis. High densities are necessary in order to determine the extent of the tidal exchange and the main forms of recruitment in the estuary. For these two species, statistical analysis showed that the number of early zoeae ebb and flooded were not different. This indicates an exchange of these stages between the estuary and the ocean.

We recognize that samples taken at night as well as during the day would have more clearly indicated the nature of larval flux at the Salmon River.

The presence of Pinnixa megalopae in the samples is probably our strongest evidence for tidal influx of larvae. This stage was significantly more abundant in the flood tide, indicating recruitment from the nearshore ocean.

The density of H. oregonensis early zoeae was not different in the ebb and flood, also indicating an exchange. Unfortunately we did not find enough megalopae, so the evidence in this species for recruitment in the estuary is lacking.

Larvae of Cancer oregonensis, Pachycheles spp. and Pagurus granosimanus were present in low densities. Their presence was not significantly different in the tidal flows. In Pagurus megalopae, there was a slight tendency to higher densities during the flood tide.

Lough (1975) found all of these larvae in Oregon coastal waters (Table 18), distributed mainly near the coast. The densities Lough found were higher than the ones we found and also the time of the

highest values do not coincide with ours. In general Lough (1975) found the highest densities in June. In our data, at least for zoeal stages, the highest densities were found late in July; megalopa stages were abundant early in July. Because of this, it is hard to quantitatively compare our densities with Lough's (1975) data. He also found a great deal of variability between 1969 and 1971 making the use of averages (Table 18). for those years somewhat debatable.

However Lough's (1975) data demonstrate the presence of these larval species in the nearshore ocean at the same time of year as our samples were taken. From Gonor et.al. (1979) we know that the adults of these species are common in the estuaries of the Oregon coast. The findings of tidal exchange of their larvae therefore is not surprising.

The data from Lough (1975) and Johnson and Gonor (1982) (Table 19) show that our results are representative of typical larval numbers and some conclusions may be drawn from them, at least in the case of Pinnixa and Hemigrapsus. For the rest of the species, the conclusions are more speculative.

Cancer oregonensis, due to its distribution on the outer Oregon coast, was not as important as the other high density larval stages. Its presence is minor, resulting in very low densities in the samples. Pachycheles species are not estuarine. The density of their larvae have the tendency to be higher in the flood (Figure 17), although this was not statistically significant. The few megalopa stages found for this group were present during the ebb. This could indicate

a low preference for metamorphosis in estuarine habitats, and that the ones which enter occasionally leave the estuary as megalopa or juveniles. Since there were relatively low densities during the ebb the survival rate of megalopa may be low inside the estuary.

Pagurus granosimanus was present mainly as megalopae. Densities were higher during the flood, indicating net input from the nearshore ocean.

Although almost all the early larval stages have higher densities in the flood flow, something may be said in relation to the main tendencies in both flows. The general trend in the densities was an increase toward the high slack and a decrease toward the low slack (Figures 3, 6, 8, and 9), this favors high densities near the high slack point when the possibilities of being flushed out are the best. However, the early stages also return to the estuary (Figures 11, 14, 16, and 17). This might mean that reinvasion is not necessarily confined to megalopa or juveniles. Dittel and Epifanio (1982) and Lambert and Epifanio (1982) have suggested that the principal source of recruits of benthic decapod crustacea in estuaries are megalopas and juveniles, probably this is not true in the Salmon River estuary.

Some studies have discussed the possibilities of better survival rates for larvae either in the estuary or in the ocean (Strathmann, 1982). We do not have any information on tolerances to physical parameters or behavioral mechanisms that permits us to suggest any advantages in the survival rates either in the estuary or the ocean.

The fact that early stages are relatively more abundant in flood flows could mean that there is more mortality in the estuary, so that slightly more come in than go out, but not statistically significant numbers.

The results support the idea that tidal exchange is a very important dispersal mechanism in estuaries, and also it provides evidence of an active input of organic material from the nearshore ocean in the form of planktonic larvae. It is well known that zooplankters are retained in coastal waters, (Peterson et.al., 1979) so the input to estuaries is not difficult to visualize. Johnson and Gonor (1982) have used this same argument for the return of Callianassa larvae.

Peracarid crustaceans were abundant in the samples. They would not a priori be considered as extensively involved in tidal exchange, but according to our data they are. They represent an important source of evidence on the problem of tidal exchange in estuaries. Their characteristics of direct development, and their condition as mainly infauna or epifauna makes them very interesting when considering the exchange of material in estuaries.

The four species considered did not show differences in abundance between the ebb and flood tides, reaffirming again the extent of the tidal exchange in the Salmon River Estuary. Although the differences were not significant, densities of adult Corophium brevis were higher during the flood tide. In A. tridens, E. confervicolus, N. mercedis,

and C. brevis juvenile, densities were similar in both flows. This is important especially in Corophium, because it could indicate a tendency to dispersal in the juvenile stages and a reinvasion as an adult. The average flux of Corophium adults, in the flood flow, was 8.04 per second and in the ebb was 2.90 per second.

From our data it is clear that both adult and juveniles of small benthic peracarid crustaceae are constantly being flushed out of the estuary and that there are also mechanisms for reinvasion from the nearshore ocean. The fact that infaunal or epibenthic peracarids have a behaviorally controlled activity which allows them to move large distances passively is important, not only as dispersal mechanisms at a small scale, such as the colonization of new space, especially the new open space resulting from human intervention (Swartz et al., 1980), but also on a larger scale including biogeographical distributions. Such regular movements into the water column may make these benthic species available to mid-water predators, linking benthic and mid-water production processes.

There is no strong evidence on what triggers the swimming activity of benthic invertebrates, which places them in the plankton where they can be transported by tidal exchange. The two most discussed explanations are light controlled mechanisms (Meadows and Reid, 1966) and tidally controlled mechanisms, through a process of pressure effects (Morgan, 1965, 1972).

For the species studied by us there are no reports in the literature of either of the proposed mechanisms Morgan (1972) found that in general increases in pressure in some organisms such

as Corophium inhibited swimming, but in Synchelidium or in some crabs, such as Macropipus, the pressure results in an increased activity. These responses however as species specific.

From our data we could say that Corophium brevis tends to increase its activity with a decrease in pressure while A. tridens tends to increase its activity with an increase in pressure. These types of responses are related to different strategies in dispersal mechanisms. A. tridens has a more active pelagic life and possibly being flushed from the estuary initiates the development of the much larger planktonic individuals found by Mills (1961) which are much more adapted morphologically to a pelagic existence. Corophium brevis is restricted to the lower portions of estuaries and to basically intertidal areas on the coast.

The adaptative advantages of tidal exchange and retention of larvae in estuaries has been discussed extensively in the literature (Sheltema, 1975; Strathman, 1982; Burton and Feldman, 1982, and Hedgecock, 1982). Two basic concepts stressed in these studies, although discussed in relation to larvae of decapod crustacea can also be applied to small adult benthic invertebrates: (1) natural selection reduces the variability within populations, and (2) gene flow introduces new genetic variability (Sheltema, 1975). A study of larval dispersal in estuaries should consider several aspects: larvae retained within the estuary will be important in maintaining an endemic adult population; larvae flushed out of the estuary may be important not only in establishing gene flow with other populations

but also maintaining and extending the species range; and larvae entering the estuary and originating from some other region introduce new genetic variability and maintain genetic continuity with distant adult populations.

The last two statements are fully applicable to the Salmon River situation. The larvae flushed out are carried out of the estuary and do not return to the same estuary, due to the physical characteristics of the coast (Huyer, et.al., 1975) and according to the drift card experiment of Johnson (1980). The larvae that enter during the flood must be from coastal locations and the several estuaries north of the Salmon River and bring new genetic material to the estuary.

In the case of Peracarids there could be behaviorally controlled mechanisms, mainly related to pressure, but our data do not show a very strong evidence in this sense.

The fact that tidal exchange favors input and output in the Salmon River Estuary helps to maintain the population in the estuary and probably to keep a genetic homogeneity among the Oregon populations.

Dispersal from our point of view is a key point in the tidal exchange in estuaries and further analysis of the problem in the Salmon River or other estuaries in the Oregon coast could help in understanding better the mechanisms and dynamics of exchange of organic material in estuaries.

BIBLIOGRAPHY

- Askren, D., R. Hansen, B. Higgins, S. Noble, and R. Pratt, 1976. A Physical description of the Salmon River Estuary. Marine/Estuarine Water Quality Dynamics, ce572. Ocean Engineering Programs, Oregon State University, 67pp.
- Bakun, A. 1980. Coastal upwelling indices, daily and weekly means for 1979. Unpublished data from NOAA/NMFS Pacific Environmental Group, Monterrey, California, (not seen).
- Barnard, J. L., 1954. Marine Amphipoda of Oregon. Oregon State Monogs., Studies in Zool., 8: 1-103, pls. 1-33, 1 fig.
- Barnard, J. L., and G. S. Karaman, 1980. Classification of Gammarid amphipoda. Crustaceana, Suppl. 6: 5-16.
- Batie, R. E. 1974. Population structure of the intertidal shore crab Hemigrapsus oregonensis (Brachyura, Grapsidae) in Yaquina Bay, a central Oregon coast estuary. Doctoral thesis. Corvallis, Oregon State University. 128 numb. leaves.
- Boicourt, W.C., 1982. Estuarine larval Retention mechanisms on two scales. In Estuarine Comparisons. (Kennedy, U.S., ed.). Academic Press, New York. 445-458 pp.
- Boon, J. D., 1979. Suspended solids transport in a salt marsh creek - an analysis of errors. In Estuarine Transport Processes (Kjerfve, B., ed.). University of North Carolina Press, Chapel Hill. 147-159 pp.
- Bousfield, E. L., 1977. A new look at the systematic of gammaridean amphipods of the world. Crustaceana, suppl. 4:282-316.
- Burton, R. S. and M. W. Feldman, 1982. Population genetics of coastal estuarine invertebrates: does larval behavior influence population structure. In Estuarine Comparisons (Kennedy, V.S., ed.). Academic Press, New York. 537-552 pp.
- Carriker, M. R., 1967. Ecology of estuarine benthic invertebrates: a perspective. In Estuaries (Lauff, G., ed.). Pub.No.83 AAAS, Washington, D.C. 442-487 pp.
- Christy, J. H. and S. E. Stancyk, 1982. Timing of larval production and flux of invertebrate larval in a well mixed estuary. In Estuarine Comparisons (Kennedy, V.S., ed.) Academic Press, New York. 489-504 pp.

- Cronin, T. W., 1982. Estuarine retention of larvae of the crab Rhithropanopeus harrisi. Est. Coastal Shelf Sci. 15:207-220.
- Cronin, T. W. and R. B. Forward, 1982. Tidally timed behavior: effects on larval distribution in estuaries. In Estuarine Comparisons (Kennedy, V.S., ed.). Academic Press, New York. 505-520 pp.
- Daniel, W. W., 1978. Applied Nonparametric Statistics. Houghton Mifflin Co., Boston. 510. pp.
- Davis, J. S. 1979. Diel Activity of benthic crustaceans in the Columbia River estuary. M.S. Thesis, Corvallis, Oregon State University. 170 numb. leaves.
- De Wolf, P. 1973. Ecological observations on the mechanisms of dispersal of barnacle larvae during planktonic life and settling. Neth. J. Sea Res. 6:1-129.
- Dittel, A. I. and C. E. Epifanio, 1982. Seasonal Abundance and Vertical migration of Crab larvae in Delaware Bay. Estuaries, 5(3):197-202.
- Duxbury, A. C., 1979. Upwelling and estuary flushing. Limnol. Oceanogr., 24(4):627-633.
- Gonor, S. L., 1970. The larval histories of four porcellanid anomurans (Crustacea, Decapoda) from Oregon. M.S. Thesis. Corvallis, Oregon State University. 106 numb. leaves
- Gonor, S. L. and J. J. Gonor, 1973. Descriptions of the larvae of four north Pacific Porcellanidae (Crustacea:Anomura). Fish. Bull., 71(1):189-223.
- Gonor, J.J., D. R. Strehlow, and G.E. Johnson. 1979. Ecological assessments at the North Bend airport extension site. A report submitted to the Dept. of Land Conservation and Development, State of Oregon, July, 1979. 163pp.
- Guin, M.P., 1978. The role of stridulation in the behavior of the shore crab Hemigrapsus oregonensis. M.S. Thesis, Corvallis, Oregon State University. 53 numb. leaves.
- Hart, J. F. L., 1935. The larval development of British Columbia brachyura. I. Xanthidae, Pinnotheridae (in part) and Grapsidae. Can. J. Res., 12(4):411-432.
- Hedgecock, D. 1982. Genetic consequences of larval retention. Theoretical and morphological aspects. In Estuarine Comparisons (Kennedy, U.S., ed) Academic Press, New York. 553-570 pp.

- Higley, D. L. and R. L. Holton, 1978. A Grab. sample study of the benthic invertebrates of the Columbia River estuary. Supplemental Data Report. 1 November 1975 through 29 February 1976. School of Oceanography, Oregon State University - Supplement to Reference 76-3.
- Holmquist, C., 1973. Taxonomy, distribution, and ecology of the three species Neomysis intermedia (Czerniavsky), N. awatshensis (Brandt), and N. mercedis Holmes (Crustacea, Mysidacea). Zool. Jb. Syst. Bd., 100:197-222.
- Huyer, A., Pillsbury, R. D., and R. L. Smith. 1975. Seasonal variation of the alongshore velocity field over the continental shelf off Oregon. Limnol. Oceanogr. 20:90-95.
- Johnson, G. E., 1980. The tidal exchange of Callinassa californiensis larvae between the ocean and the Salmon River estuary, Oregon M.S. Thesis, Corvallis, Oregon State University. 51 numb. leaves.
- Johnson, G. E. and J. J. Gonor, 1982. The tidal exchange of Callinassa californiensis (Crustacea, Decapoda) larvae between the ocean and the Salmon River estuary, Oregon. Est. Coastal Shelf Sci. 14:501-516.
- Kjerfve, B., 1975. Velocity averaging in estuaries characterized by a large tidal range to depth ratio. Est. Coastal Mar. Sci. 3:311-323.
- Kjerfve, B. and H. N. McKellar, 1980. Time series measurements of estuarine material fluxes. In Estuarine Perspectives. Proceedings of the Fifth International Estuarine Research Conference (Kennedy V.S., ed.). Academic Press, New York. 341-357 pp.
- Knight, M. D., 1966. The larval development of Polyonyx quadriungulatus glassell and Pachycheles rudis Stimpson (Decapoda, Porcellanidae) cultured in the laboratory. Crustaceana 10:75-97.
- Knudsen, J. W., 1964. Observations of the reproductive cycles and ecology of common brachyura and crablike anomura of Puget Sound, Washington. Pac. Sci., 18(1):3-33.
- Kost, A. L. B. and A. W. Knight, 1975. The food of Neomysis mercedis Holmes in the Sacramento-San Joaquin estuary. Calif. Fish Game 61:35-46.
- Lambert, R. and C. E. Epifanio, 1982. A comparison of dispersal strategies in two genera of brachyuran crab in a secondary estuary. Estuaries, 5(3):182-188.
- Levings, C. D., 1976. Basket traps for surveys of a Gammarid Amphipod, Anisogammarus confervicolus (Stimpson), at two British Columbia Estuaries. J.Fish. Res. Bd. Can. 33:2066-2069.

- Lough, R. G., 1975. Dynamics of Crab larvae (*Anomura*, *Brachyura*) off the Central Oregon coast, 1969-1971. Doctoral thesis, Corvallis, Oregon State University. 299 numb. leaves.
- Mauchline, J. and M. Murano, 1977. World list of the Mysidacea, Crustacea. *J. Tokyo Univ. Fish.* 64(1):39-88.
- McMillan, F. E., 1972. The larval development of northern California Porcellanidae (Decapoda, Anomura). I. *Pachycheles pubescens* Holmes in comparison to *Pachycheles rudis* Stimpson. *Biol. Bull.* 142:57-70.
- Meadows, P. S., and A. Reid, 1966. The behavior of *Corophium volutator* (Crustacea:Amphipoda). *J. Zool. London*, 150:387-399.
- Miller, C. B., 1983. The zooplankton of Estuaries. In *Ecosystems of the World*, 26. *Estuaries and enclosed Seas*. (Ketchum, B. H., ed.). Elsevier, New York, 103-150. pp.
- Mills, E. L., Amphipod Crustaceans of the Pacific coast of Canada. I. Family Atylidae. *Bull. Nat. Mus. Canada*, 172:13-33.
- Morgan, E., 1965. The activity rhythm of the amphipod *Corophium volutator* (Pallas) and its possible relationship to changes in hydrostatic pressure associated with tides. *J. Anim. Ecol.*, 34:731-746.
- Morgan, E., 1972. The pressure sensitivity of marine invertebrates - a resume after 25 years. *Proc. R. S. E. (B)*, 73(29):287-299.
- Morris, R. H., D. P. Abbott, and E. C. Haderlie, 1980. *Intertidal Invertebrates of California*. Stanford Univ. Press, Stanford, California. 690 pp.
- Palmer, J. D., 1976. *An introduction to biological rhythms*. Academic Press, New York. 375 pp.
- Pearse, J. B. 1966. On *Pinnixa faba* and *Pinnixa littoralis* (Decapoda: Pinnotheridae) symbiotic with the clam, *Tressus capax* (Pelecypoda:Mactridae). In *Some contemporary studies in Marine Sciences* (Barnes, H., ed.) G. Allen and Unwin, London 565-589 pp.
- Peterson, W. T., C. B. Miller, and A. Hutchinson, 1979. Zonation and maintenance of copepod populations in the Oregon upwelling zone. *Deep Sea Res.* 26A:467-494.
- Pomeroy, W. M. and C. D. Levings, 1980. Association and feeding relationships between *Eogammarus confervicolus* (Amphipoda, Gammaridae) and benthic algae on Sturgeon and Roberts Bank Fraser River Estuary. *Can. J. Fish. Aquat. Sci.*, 37(1):1-10.

- Rogers, H. M., 1940. Occurrence and retention of plankton within the estuaries, *J. Fish. Res. Bd. Can.*, 5:164-171.
- Sandifer, P. A., 1973. Distribution and abundance of decapod crustacean larvae in the York River Estuary and adjacent lower Chesapeake Bay, Virginia, 1968-1969. *Chesapeake Sci.*, 14:235-257.
- Sandifer, P. A., 1975. The role of pelagic larvae in recruitment to populations of adult decapod crustaceans in the York River Estuary and adjacent lower Chesapeake Bay. *Est. Coastal Mar. Sci.*, 3:269-279.
- Scheltema, R. S., 1975. Relationship of larval dispersal, gene-flow and natural selection to geographic variation of benthic invertebrates in estuaries and along coastal regions. In Estuarine Research, Vol. I: Chemistry, Biology, and the Estuarine System. (Cronin, L.E., ed.). Academic Press, New York. 372-391 pp.
- Schmitt, W. L., 1921. The marine decapod Crustacea of California. *Univ. Calif. Pub. Zool.*, 23:1-470.
- Shoemaker, C.R., 1949. The amphipod genus Corophium on the west coast of America. *J. Wash. Acad. Sci.*, 39:66-82.
- Siegel, S., 1956. Nonparametric Statistics for the behavioral sciences. McGraw Hill, New York. 312 pp.
- Strathmann, R. R., 1982. Selection for retention or export on larval distributions. In Estuarine Comparisons. (Kennedy, V.S., ed.). Academic Press, New York. 521-536 pp.
- Sulkin, S. D., and W. Van Heukelen, 1982. Larval recruitment in the crab Callinectes sapidus Rathbun: An amendment to the concept of larval retention in estuaries. In Estuarine Comparisons. (Kennedy V. S., ed.). Academic Press, New York. 459-476 pp.
- Swartz, R. C., W. A. De Ben, F. A. Cole, and L. C. Bensten, 1980. Recovery of macrobenthos at a dredge site in Yaquina Bay, Oregon. In Contaminants and sediments. Vol. 2, Analysis chemistry, biology. Ann Arbor, Ann Arbor Sciences, 459-476 pp.
- Tattersal, W. M., 1951. A review of the Mysidacea of the United States *Natl. Mus. Bull. U.S.N.M.*, 201:1-292.
- Tzevtkova, N. L., 1975. Geographical distribution of species of the genus Anisogmarrus Derzhavin (Amphipoda, Gammaridae). *Crustaceana*, 28(2):191-199.

APPENDIX

APPENDIX

List of species appearing in Table A.

1. Hemigrapsus oregonensis, Megalopa
2. Pachycheles, Zoa 2
3. Pachycheles rudis, Megalopa
4. Pugettia, Zoa 1
5. Pugettia, Zoa 2
6. Pugettia, Megalopa
7. Xanthidae, Zoa 1
8. Cancer magister, Zoa 1
9. Cancer magister, Megalopa
10. Cancer oregonensis, Megalopa
11. Pagurus granosimanus, Zoa 1
12. Pagurus granosimanus, Zoa 2
13. Pagurus granosimanus, Zoa 3
14. Pagurus granosimanus, Zoa 4

List of species appearing in Table B.

1. Corophium salmonis
2. Corophium spinicorne
3. Neomysis mercedis, adult
4. Archaeomysis grebnitzkii, adult
5. Archaeomysis grebnitzkii, juvenile
6. Acanthomysis spp., adult
7. Acanthomysis spp., juvenile
8. Gammaridean amphipods (Calliopidae, Haustoridae, and Jassa falcata)

Table A. Decapod larvae, densities in 100 cubic meters
(see list of species)

	1	2	3	4	5	6	7	8	9	10
Jun. 23/1									1.69	
/2						1.99				
/3							1.66			
/4						1.10				
/5										
/6										
Jun. 30/1				0.40						
/2				0.77		0.39				
/3						0.54				
/4										
/5						2.23				
/6			0.30			1.64				0.33
/7						3.37				0.37
/8						5.06				
Jul. 8/1									3.06	
/2	0.72			0.36		0.36			1.44	0.36
/3				1.54			0.77		4.62	
/4									0.74	0.74
/5			11.3							
/6	0.40									
/7										
/8									0.65	
Jul. 15/1			3.83	1.43			0.96			
/2										
/3										
/4			7.47			2.04				
/5			0.41							
/6			2.97							
/7						0.58				
/8						2.43				
Jul. 22/1						0.38		0.38		
/2				0.37				0.75		
/3										2.22
/4				0.37		0.37				2.24
/5										
/6										
/7										
/8										
Jul. 30/1				1.61				0.40	0.37	
/2				1.06						
/3										
/4	1.18						0.79			
/5	0.95						3.78	1.58		0.63
/6	0.37						23.0	3.65		0.37

CONTINUED

Table B. Peracarids, densities in number per cubic meters (see list of species).

	1	2	3	4	5	6	7	8
Jun. 23/1								
/2								1.0
/3								
/4								2.2
/5					0.93			2.8
/6	1.94			0.97	2.90			2.9
Jun. 30/1					0.80			75.52
/2								47.64
/3								
/4					1.17			12.91
/5								
/6								
/7								17.59
/8								11.39
Jul. 8 /1	1.58		1.15			3.95	7.90	35.59
/2	1.80			2.16	7.90	1.54	2.31	
/3						0.74	2.22	53.93
/4							1.76	23.69
/5						1.61	1.62	
/6								11.30
/7	0.72	1.43					0.65	
/8		1.30				0.48		
Jul. 15/1								3.35
/2		4.82						2.14
/3								
/4		0.68			0.68		2.04	2.72
/5		0.41			0.40			9.8
/6		1.86			1.11			13.73
/7							0.29	10.99
/8					1.52			
Jul. 22/1					0.38		0.38	
/2							0.75	
/3							0.63	
/4			0.37		0.37			
/5							0.38	
/6							0.36	
/7								
/8								
Jul. 30/1					0.40		0.40	2.01
/2								1.59
/3				2.08	17.67			2.08
/4							0.39	1.18
/5								
/6							0.39	21.18
Aug. 9 /1								
/2								
/3								
/4								
/5		0.24						
/6		1.03			0.52			

Table 2. Decapod larvae.

Brachyura

<u>Pinnixa littoralis</u> Holmes, 1984	Zoea 1-5	Megalopa
<u>Hemigrapsus oregonensis</u> (Dana, 1851)	Zoea 1-5	Megalopa
<u>Pugettia</u> spp.	Zoea 1-2	
<u>Pugettia gracilis</u> Dana		Megalopa
<u>Cancer oregonensis</u> (Dana, 1852)	Zoea 1	Megalopa
<u>Cancer magister</u> Dana, 1852	Zoea 1	Megalopa
<u>Lophopanopeus bellus</u> (Stimpson, 1860)	Zoea 1	

Anomura

<u>Pachycheles</u> spp.	Zoea 1-2	
<u>Pachycheles rudis</u> Stimpson		Megalopa
<u>Pagurus granosimanus</u> (Stimpson, 1859)	Zoea 1-4	Megalopa
<u>Pagurus ochotensis</u> Brandt	Zoea 1	
<u>Oedignathus inermis</u> (Stimpson)		Megalopa

Table 3. Pinnixa littoralis early zoea. Estimates for ebb and flood tide, mean densities, total number and estimated flux for a tidal cycle on each sampling date.

Date	Flow	Mean density (#/100 cubic meters)	Total number ($\times 10^3$)	Total flux during sampling period (#/sec)
6/23	Flood	8.43	76.1	10.62
	Ebb	9.32	56.9	22.61
6/30	Flood	0.00	0.00	0.00
	Ebb	11.08	85.31	20.30
7/08	Flood	1.59	14.0	2.63
	Ebb	8.36	48.2	26.07
7/15	Flood	15.87	178.0	61.05
	Ebb	0.78	6.70	1.50
7/22	Flood	5.65	48.6	13.45
	Ebb	3.58	19.7	9.46
7/30	Flood	208.6	1792.0	404.41
	Ebb	25.96	162.80	47.96
8/09	Flood	23.14	297.6	66.02
	Ebb	11.07	122.2	32.56

Table 4. Pinnixa littoralis, late zoea. Estimates for ebb and flood tide, mean densities, total number and estimated flux for a tidal cycle on each sampling date.

Date	Flow	Mean density (#/100m)	Total number (x 10 ³)	Total flux per sampling period (#/sec)
6/23	Flood	2.55	23.00	3.71
	Ebb	1.10	6.71	3.00
6/30	Flood	0.00	0.00	0.00
	Ebb	0.10	750.8	0.24
7/08	Flood	16.30	143.40	34.69
	Ebb	15.36	88.4	40.59
7/15	Flood	1.51	16.90	5.90
	Ebb	0.00	0.00	0.00
7/22	Flood	1.23	10.60	2.95
	Ebb	1.80	9.90	5.18
7/30	Flood	46.00	395.10	86.86
	Ebb	2.19	13.70	3.25
8/09	Flood	4.02	51.70	11.13
	Ebb	1.58	17.40	5.02

Table 5. Pinnixa littoralis megalopa. Estimates for ebb and flood tide, mean densities, total number and estimated flux for a tidal cycle on each sampling date.

Date	Flow	Mean density (#/cubic meters)	Total number (x 10 ³)	Total flux during sampling (#/sec)
6/23	Flood	0.56	5.10	0.53
	Ebb	1.38	8.40	0.53
6/30	Flood	2.30	19.30	4.61
	Ebb	0.77	5.95	1.24
7/08	Flood	186.74	1643.34	400.90
	Ebb	8.21	47.28	21.01
7/15	Flood	4.77	53.52	17.67
	Ebb	0.92	7.84	1.02
7/22	Flood	0.73	6.26	1.58
	Ebb	0.00	0.00	0.00
7/30	Flood	0.33	2.86	0.55
	Ebb	0.13	0.83	0.21
8/09	Flood	2.20	28.33	6.58
	Ebb	0.36	3.94	1.14

Table 6. Hemigrapsus oregonensis early zoea. Estimates for ebb and flood tide, mean densities, total number and estimated flux for a tidal cycle on each sampling date.

Date	Flow	Mean density (#/cubic meters)	Total number (x 10 ³)	Total flux during sampling (#/sec.)
6/23	Flood	1.12	1.07	1.07
	Ebb	5.92	36.10	14.62
6/30	Flood	0.00	0.00	0.00
	Ebb	37.80	291.04	46.16
7/08	Flood	0.94	8.26	1.02
	Ebb	1.32	7.60	3.27
7/15	Flood	44.70	501.57	63.97
	Ebb	26.60	226.61	31.45
7/22	Flood	1.56	13.42	3.90
	Ebb	16.37	90.20	25.53
7/30	Flood	406.15	3488.89	780.30
	Ebb	54.08	339.10	64.38
8/09	Flood	36.45	468.79	103.50
	Ebb	23.61	260.65	69.37

Table 7. Hemigrapsus oregonensis late zoea. Estimates for ebb and flood tide, mean densities, total number and estimated flux for a tidal cycle on each sampling date.

Date	Flow	Mean density (#/cubic meters)	Total number (x 10 ³)	Total flux during sampling (#/sec.)
6/23	Flood	0.00	0.00	0.00
	Ebb	0.00	0.00	0.00
6/30	Flood	0.00	0.00	0.00
	Ebb	0.00	0.00	0.00
7/08	Flood	0.00	0.00	0.00
	Ebb	0.00	0.00	0.00
7/15	Flood	0.00	0.00	0.00
	Ebb	0.00	0.00	0.00
7/22	Flood	0.00	0.00	0.00
	Ebb	0.19	1.03	0.54
7/30	Flood	19.27	165.50	35.32
	Ebb	4.63	29.01	5.49
8/09	Flood	12.39	159.29	34.86
	Ebb	3.58	39.56	11.00

Table 8. Cancer oregonensis zoea I. Estimates for ebb and flood tide, mean densities, total number and estimated flux for a tidal cycle on each sampling date.

Date	Flow	Mean density (#/cubic meters)	Total number (x 10 ³)	Total flux during sampling (#/sec.)
6/23	Flood	2.32	20.95	3.70
	Ebb	9.63	58.74	24.95
6/30	Flood	0.20	1.63	0.27
	Ebb	3.21	24.68	6.28
7/08	Flood	0.46	4.05	0.70
	Ebb	0.20	1.17	0.64
7/15	Flood	0.17	1.88	0.51
	Ebb	0.82	6.97	1.35
7/22	Flood	0.38	3.23	0.86
	Ebb	0.00	0.00	0.00
7/30	Flood	1.53	13.17	3.00
	Ebb	0.00	0.00	0.00
8/09	Flood	1.19	15.26	3.25
	Ebb	1.05	11.63	3.15

Table 9. Pachycheles spp. zoea I. Estimates for ebb and flood tide, mean densities, total number and estimated flux for a tidal cycle on each sampling date.

Date	Flux	Mean density (#/cubic meters)	Total number ($\times 10^3$)	Total flux during sampling (#/sec.)
6/23	Flood	0.00	0.00	0.00
	Ebb	1.58	9.64	3.02
6/30	Flood	0.29	2.41	0.52
	Ebb	0.10	0.75	0.24
7/08	Flood	2.34	20.55	3.59
	Ebb	0.89	5.10	2.20
7/15	Flood	0.30	3.34	1.09
	Ebb	1.20	9.59	2.83
7/22	Flood	8.75	75.28	18.03
	Ebb	0.28	1.56	0.70
7/30	Flood	28.77	247.11	57.02
	Ebb	0.80	5.03	1.25
8/09	Flood	29.62	380.91	79.61
	Ebb	3.61	39.89	10.72

Table 10. Pagurus granosimanus megalopa. Estimates for ebb and flood tide, mean densities, total number and estimated flux for a tidal cycle on each sampling date.

Date	Flow	Mean density (#/cubic meters)	Total number ($\times 10^3$)	Total flux during sampling (#/sec.)
6/23	Flood	2.33	20.99	2.67
	Ebb	3.98	24.28	8.15
6/30	Flood	6.25	52.38	10.39
	Ebb	0.78	6.00	1.14
7/08	Flood	16.89	148.59	31.67
	Ebb	7.63	43.95	17.65
7/15	Flood	0.23	2.52	0.86
	Ebb	0.00	0.00	0.00
7/22	Flood	1.07	9.18	2.59
	Ebb	0.50	2.77	1.25
7/30	Flood	1.53	13.14	2.21
	Ebb	0.71	4.47	0.95
8/09	Flood	0.10	12.82	2.99
	Ebb	0.42	4.67	0.96

Table 12. Atylus tridens. Estimates for ebb and flood tide mean densities, total number and estimated flux for a tidal cycle on each sampling date.

Date	Flow	Mean density (#/cubic meters)	Total number (x 10 ³)	Total flux per sampling period (#/sec)
6/23	Flood	0.00	0.00	0.00
	Ebb	0.73	4.47	2.00
6/30	Flood	5.77	48.37	7.68
	Ebb	40.96	315.35	77.43
7/08	Flood	9.34	82.17	12.81
	Ebb	6.93	39.90	19.36
7/15	Flood	12.58	141.09	45.80
	Ebb	6.07	51.70	7.06
7/22	Flood	2.26	19.41	5.37
	Ebb	1.29	7.09	3.14
7/30	Flood	7.05	60.56	11.01
	Ebb	1.52	9.50	2.22
8/09	Flood	0.88	11.32	2.69
	Ebb	2.62	28.89	7.18

Table 13. Eogammarus confervicolus. Estimates for ebb and flood tide, mean densities, total number and estimated flux for a tidal cycle on each sampling date.

Date	Flow	Mean density (#/100m)	Total number (x 10 ³)	Total flux per sampling period (#/sec)
6/23	Flood	3.47	31.32	3.70
	Ebb	3.58	21.84	6.64
6/30	Flood	0.76	6.34	1.78
	Ebb	0.29	2.26	0.20
7/08	Flood	3.53	31.05	5.14
	Ebb	5.13	29.57	10.50
7/15	Flood	0.32	3.57	1.06
	Ebb	3.42	29.14	2.93
7/22	Flood	1.97	16.97	3.89
	Ebb	1.47	8.11	2.45
7/30	Flood	0.35	3.01	0.66
	Ebb	0.13	0.84	0.21
8/09	Flood	0.28	3.56	0.84
	Ebb	1.45	16.04	3.07

Table 14. Corophium brevis adult. Estimates for ebb and flood tide, mean densities, total number and estimated flux for a tidal cycle on each sampling date.

Date	Flow	Mean density (#/100 cu.meter)	Total number (x10 ³)	Total flux per sampling period (#/sec.)
6/23	Flood	75.10	6773.75	74.48
	Ebb	6.14	37.45	11.24
6/30	Flood	3.70	30.96	6.44
	Ebb	5.82	44.81	7.90
7/08	Flood	51.62	454.23	63.43
	Ebb	10.06	57.93	23.40
7/15	Flood	12.37	138.79	27.10
	Ebb	2.69	22.90	2.59
7/22	Flood	5.01	43.09	10.38
	Ebb	1.35	7.46	3.20
7/30	Flood	2.33	20.04	3.35
	Ebb	1.55	9.74	1.64
8/09	Flood	5.91	75.96	17.97
	Ebb	9.54	105.29	22.81

Table 18. Mean densities of decapod larvae in nearshore stations off the Oregon coast during June-August (mean 1969-1971). Numbers per 100 cubic meters (from Lough, 1975).

	June	July	August
<u>Pinnixa littoralis</u> , early zoea	224.0	1.0	10.8
<u>Pinnixa littoralis</u> , late zoea	225.0	11.0	21.3
<u>Pinnixa littoralis</u> , megalopa	0.0	0.0	0.2
<u>Hemigrapsus oregonensis</u>	91.0	0.6	0.8
<u>Pachycheles</u> spp., zoea 1	1137.0	23.0	50.6
<u>Cancer oregonensis</u> , zoea 1	95.0	0.5	17.2
<u>Pagurus granosimanus</u> , megalopa	0.5	0.9	3.1

Table 19. Ebb and flood mean densities of Callinassa californiensis in the Salmon River Estuary, June through August 1979 number per cubic meters (from Johnson and Gonor, 1982).

	June 23	June 30	July 8	July 15	July 22	July 30	August
Flood	5.2	0.5	3.6	2.1	8.7	28.7	250.2
Ebb	39.6	378.0	35.0	327.7	15.4	16.6	127.4

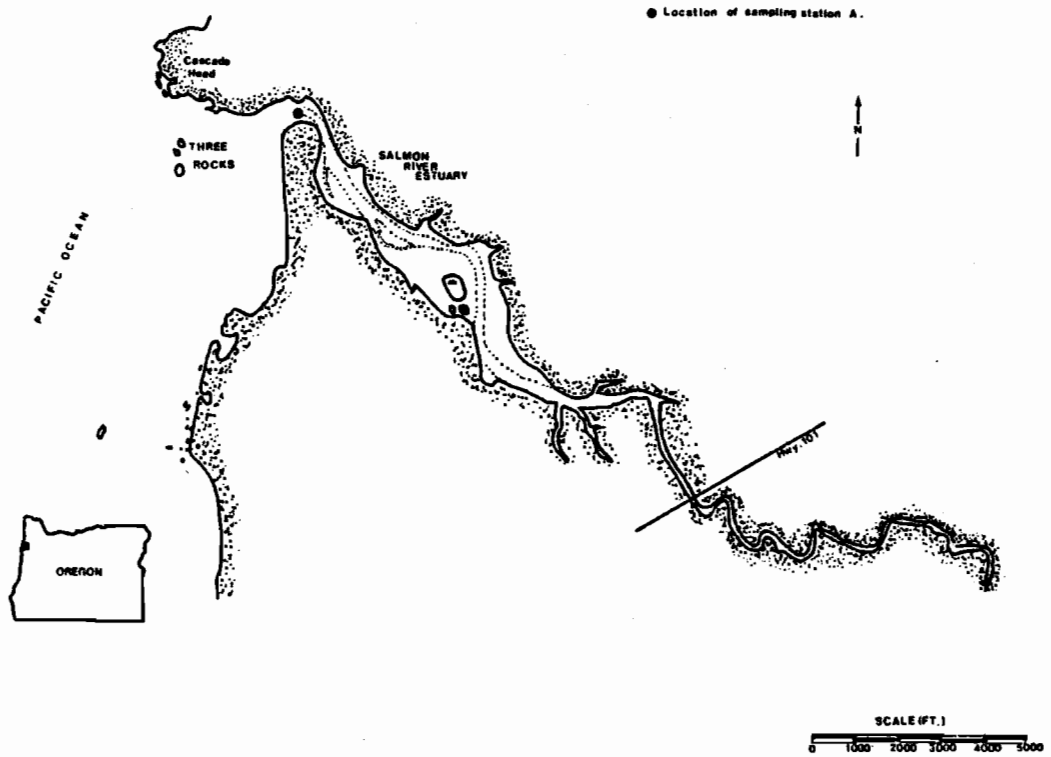


Figure 1. Salmon River Estuary, Oregon showing location of sampling station A.

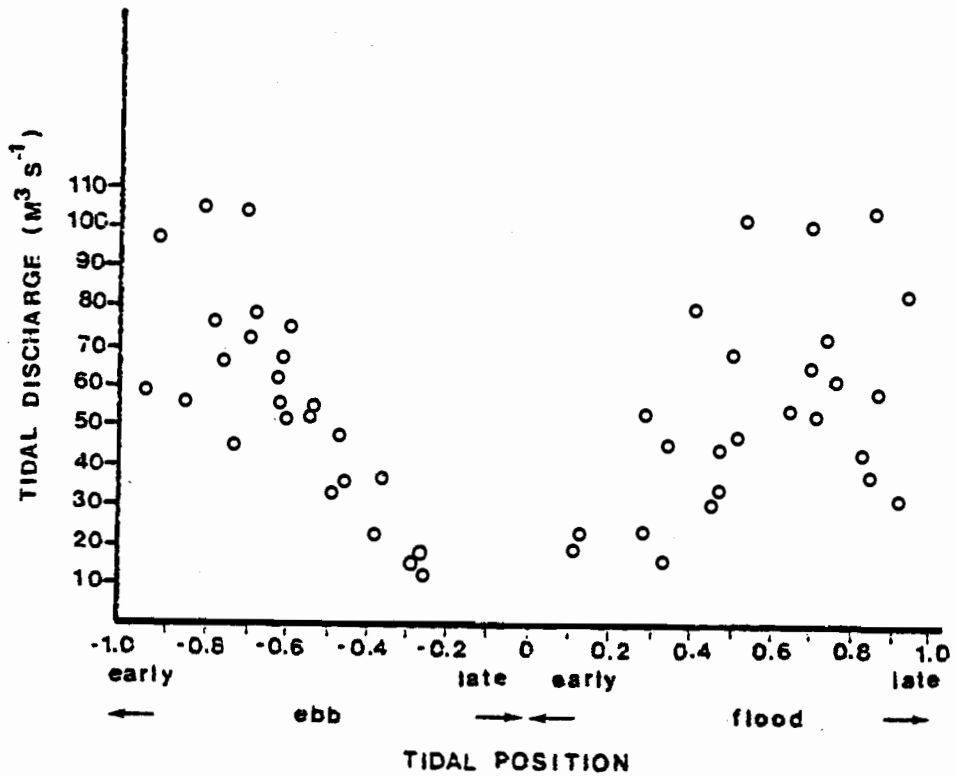


Figure 2. Tidal discharge through the mouth of the Salmon River Estuary versus tidal position during the summer 1979.

Figure 3. Pinnixa littoralis early zoea density versus tidal position. Samples are classified as ebb or flood flow.

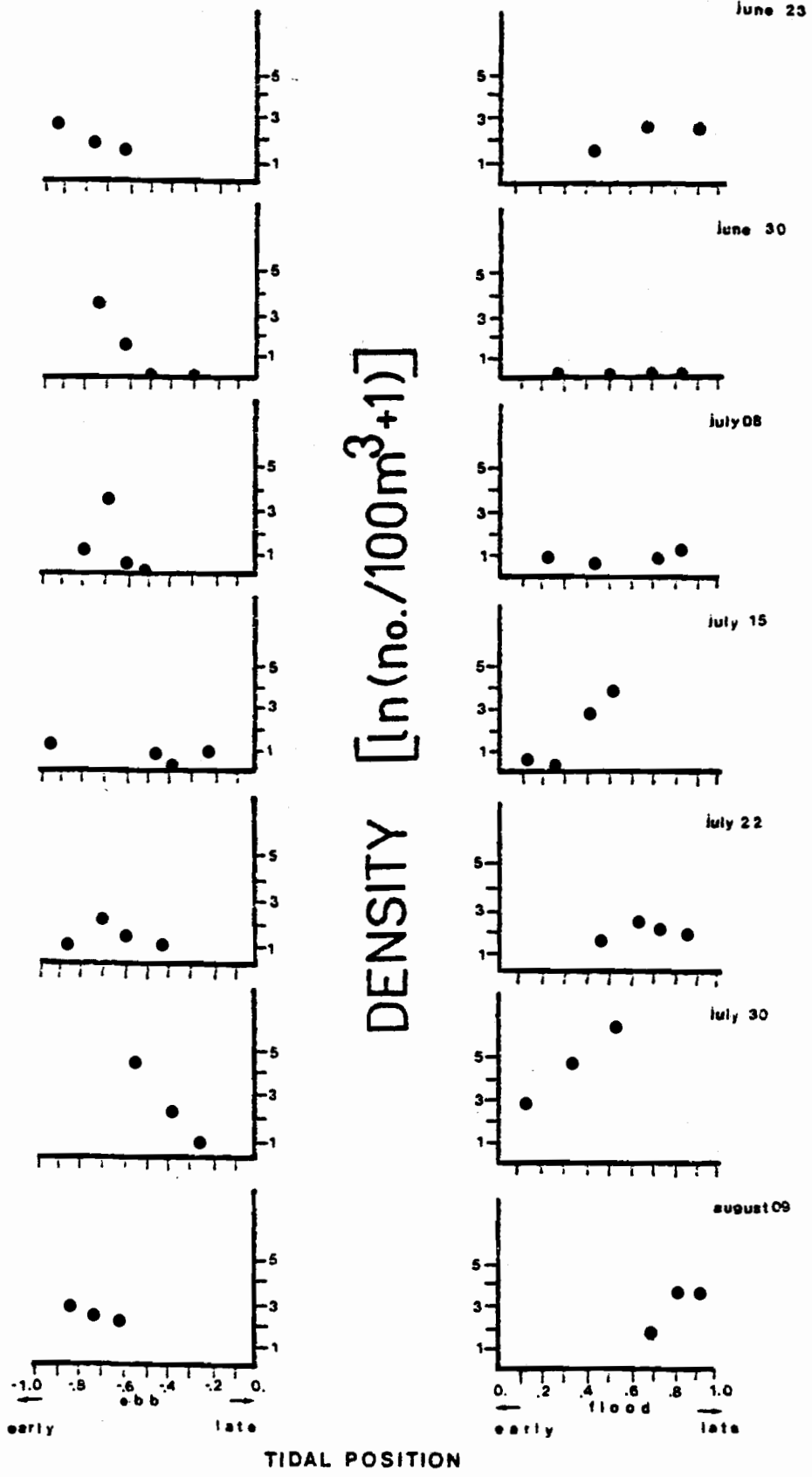


Figure 3.

Figure 4. Pinnixa littoralis late zoea density versus tidal position. Samples are classified as ebb or flood flow.

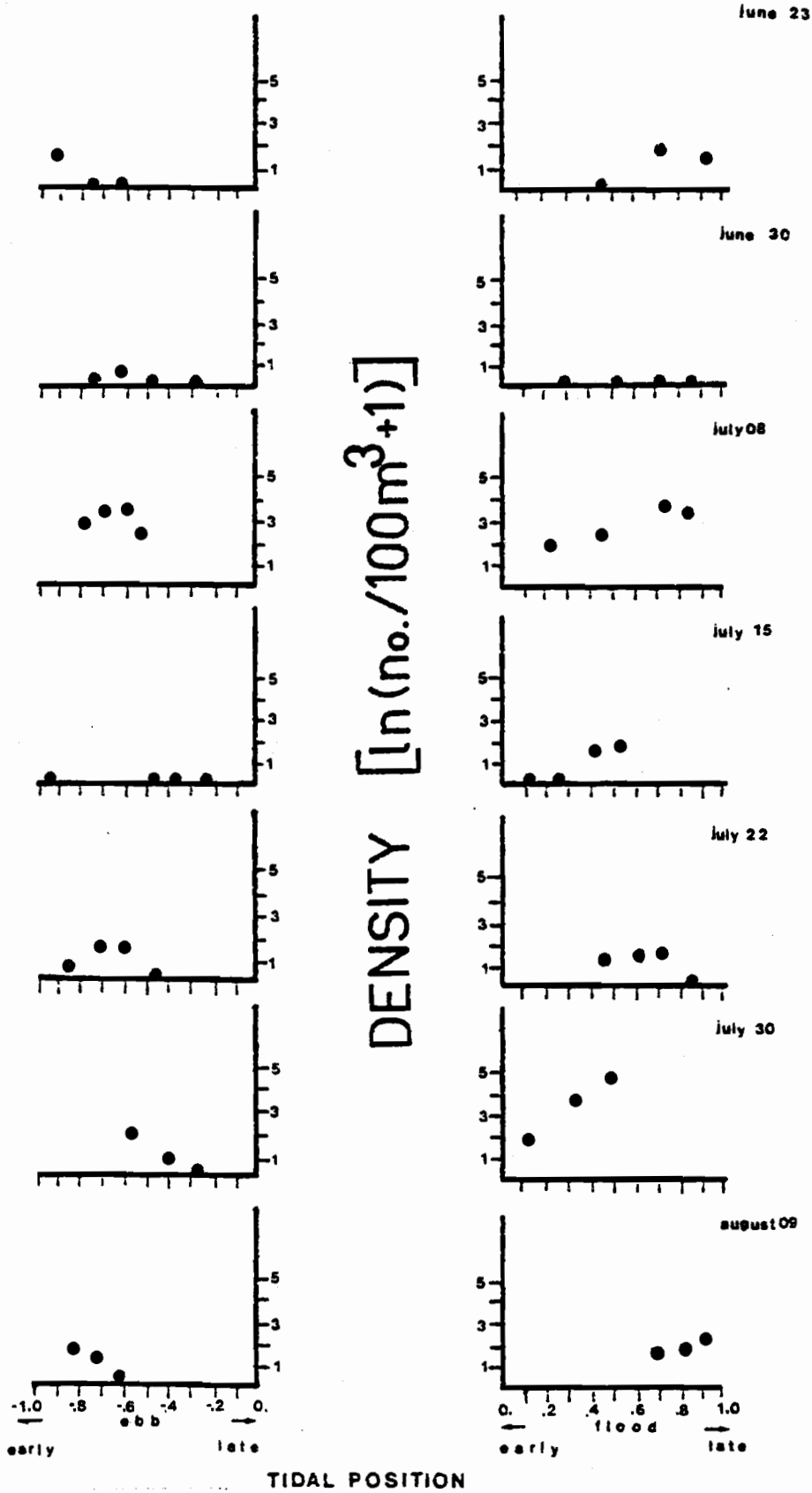


Figure 4.

Figure 5. Pinnixa littoralis megalopa density versus tidal position. Samples are classified as ebb or flood flow.

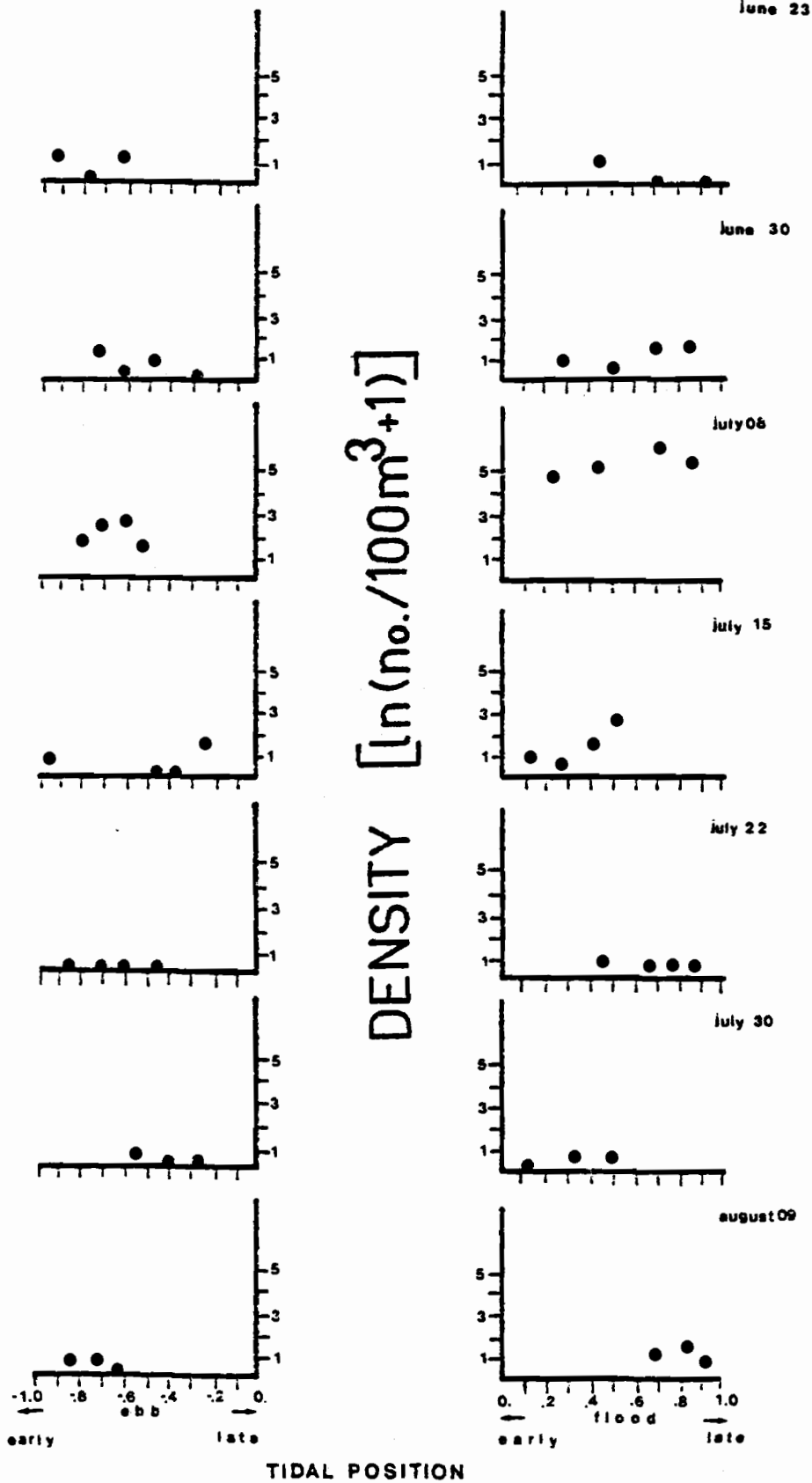


Figure 5.

Figure 6. Hemigrapsus oregonensis early zoea density versus tidal position. Samples are classified as ebb or flood flow.

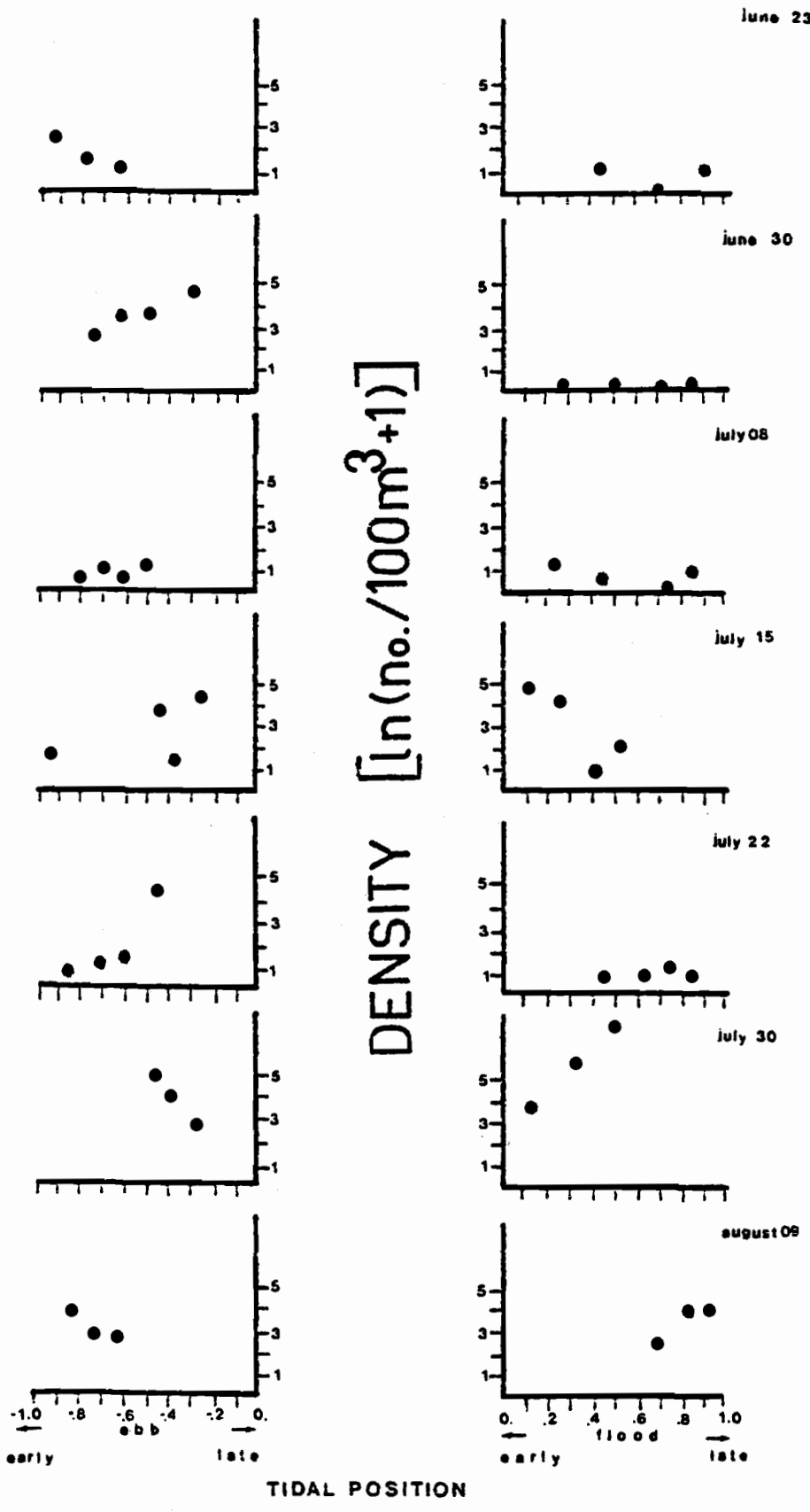


Figure 6.

Figure 7. Hemigrapsus oregonensis late zoea density versus tidal position. Samples are classified as ebb or flood flow.

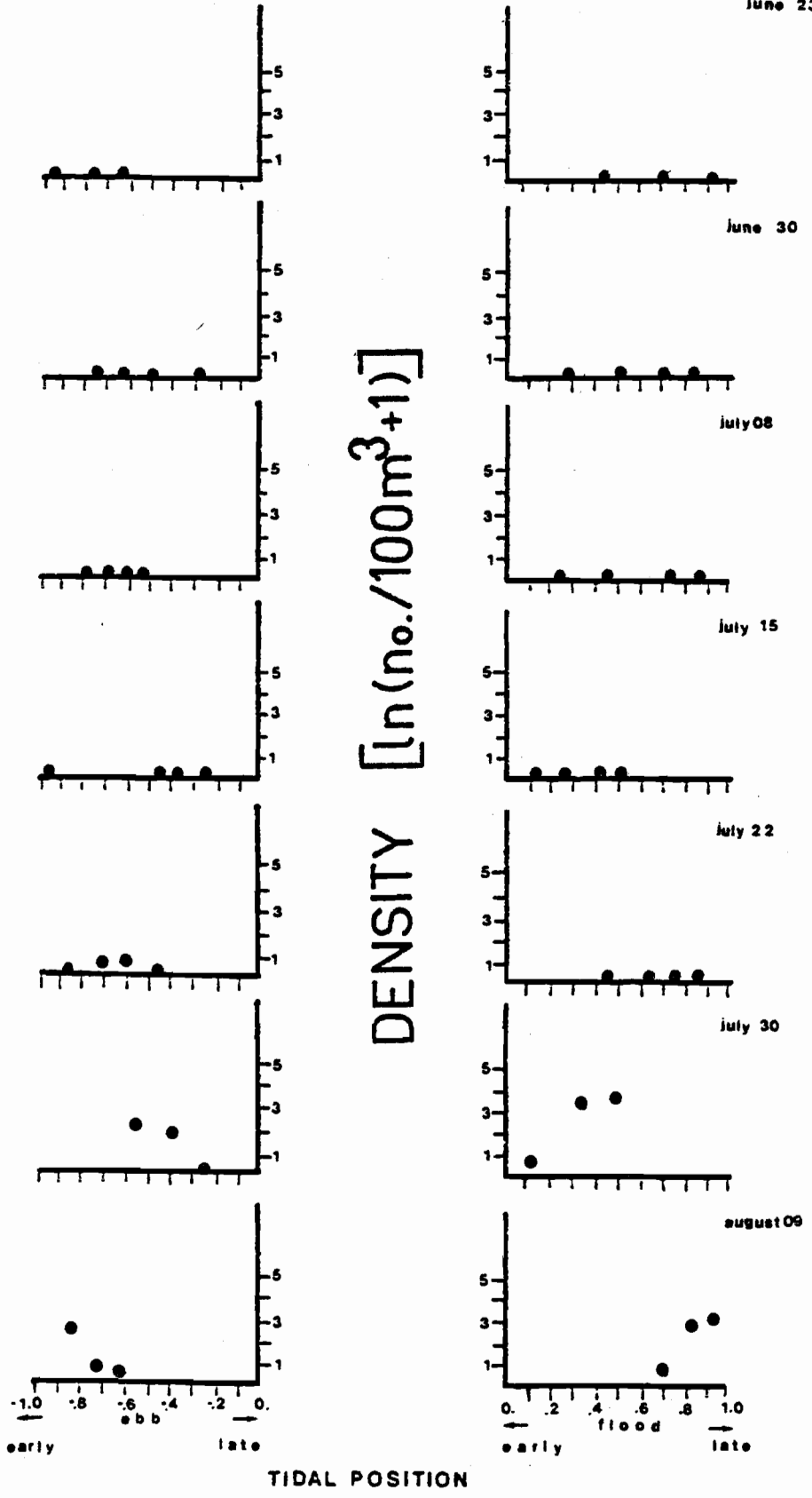


Figure 7.

Figure 8. Cancer oregonensis zoea I density versus tidal position. Samples are classified as ebb or flood flow.

Figure 9. Pachycheles spp. zoea I density versus tidal position. Samples are classified as ebb or flood flow.

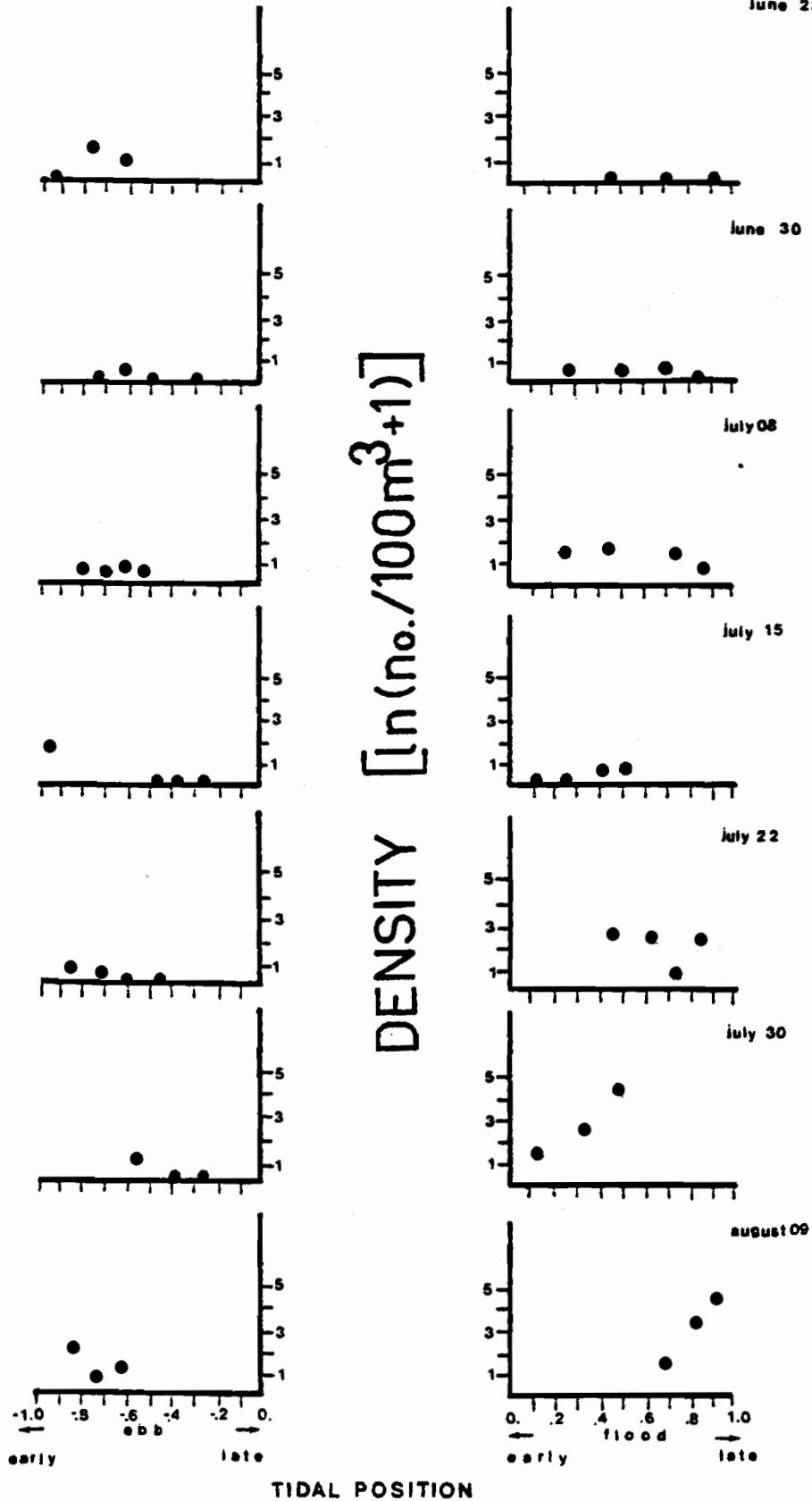


Figure 9.

Figure 10. Pagurus granosimanus megalopa density versus tidal position. Samples are classified as ebb or flood flow.

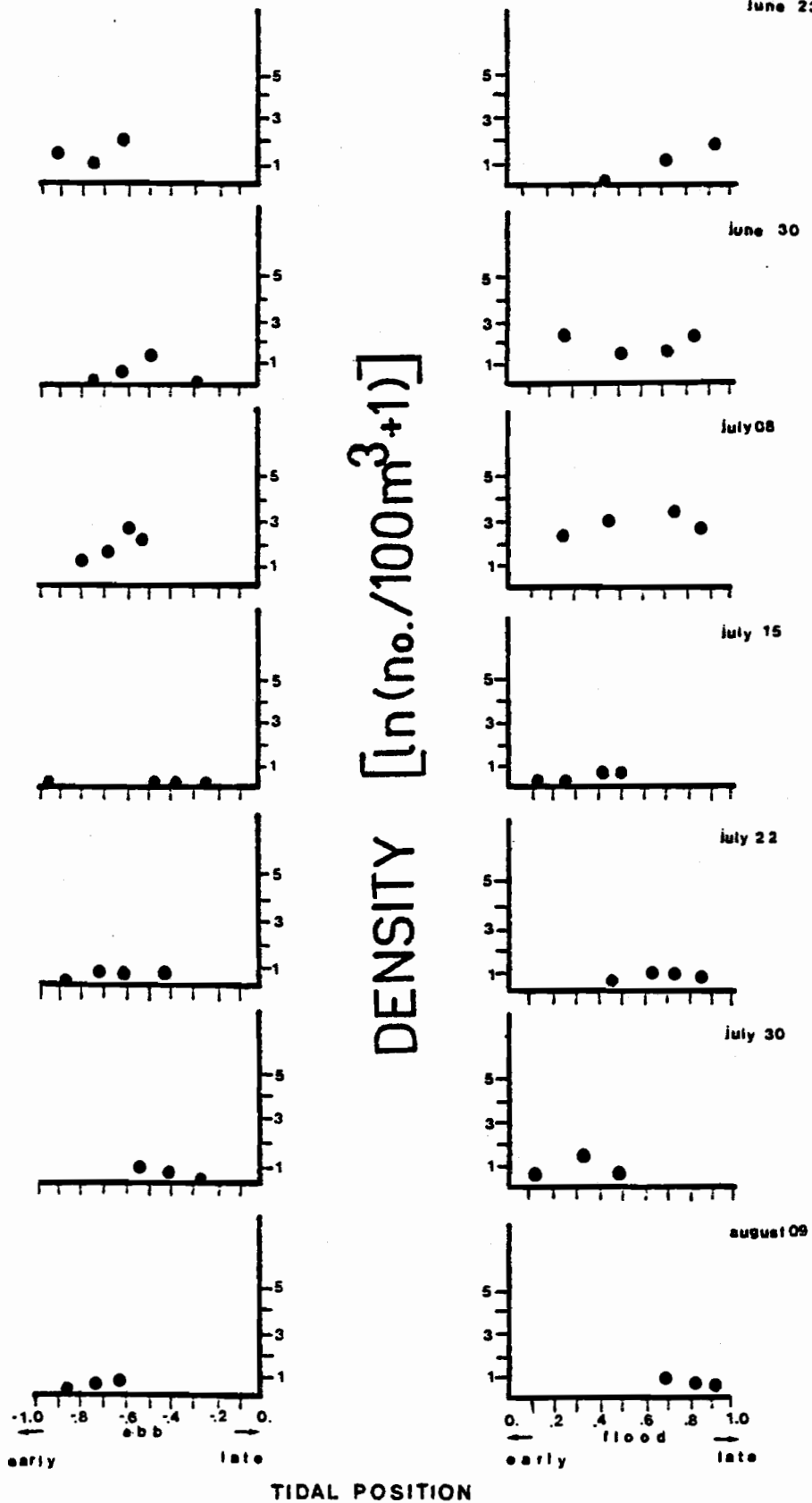


Figure 10.

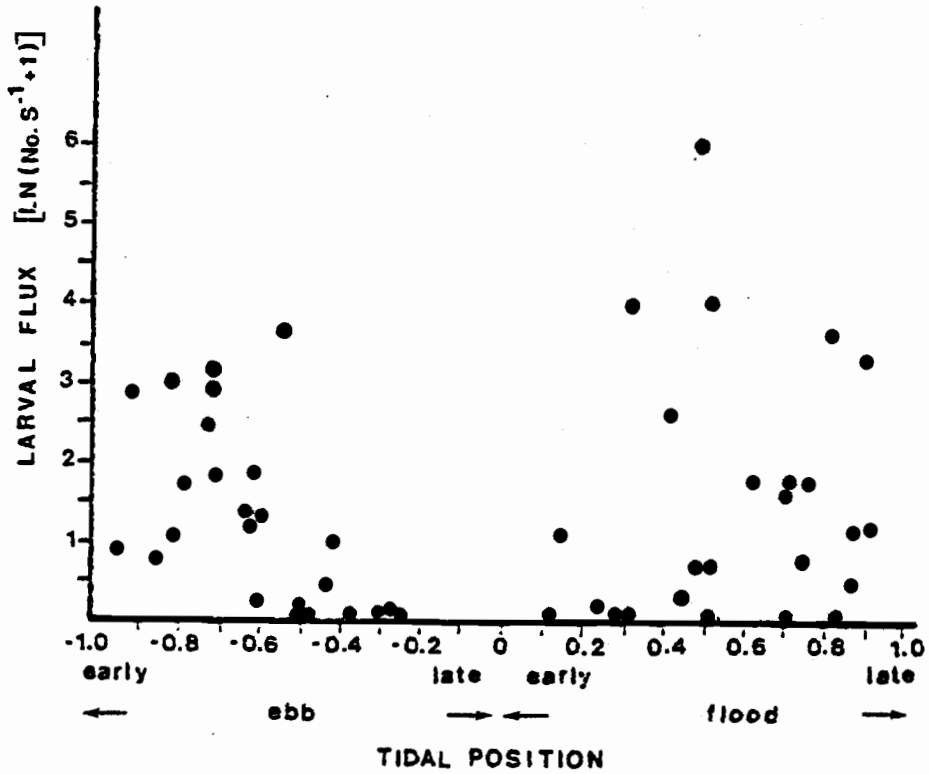


Figure 11. *Pinnixa littoralis* early zoea, flux through the mouth of the Salmon River Estuary versus tidal position during the summer 1979.

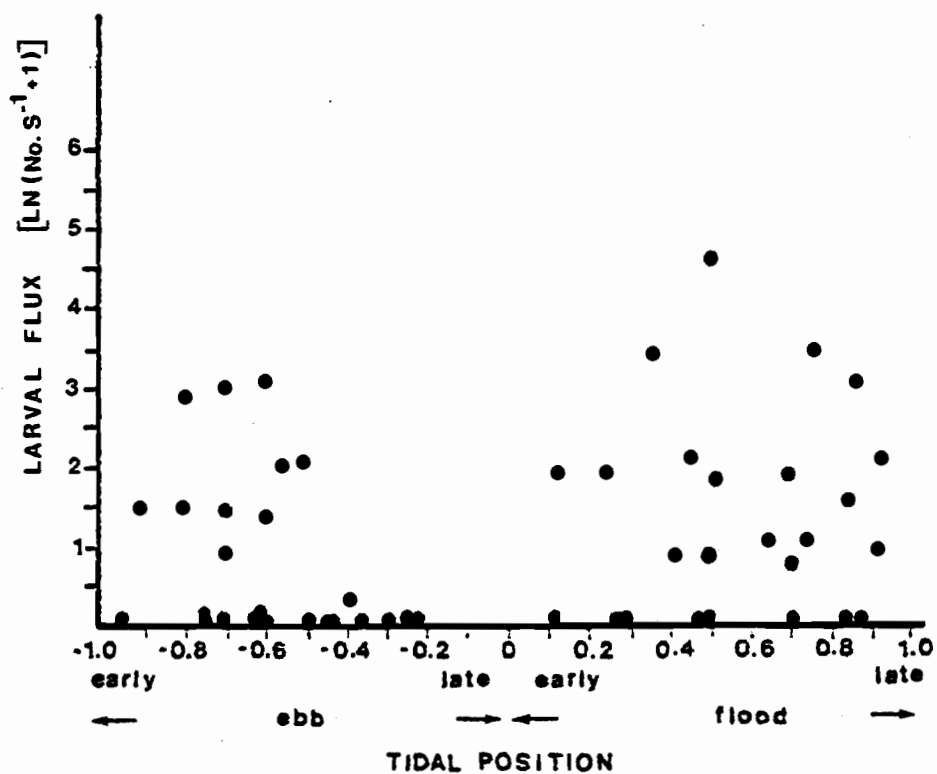


Figure 12. Pinnixa littoralis late zoea, flux through the mouth of the Salmon River Estuary versus tidal position during the summer 1979.

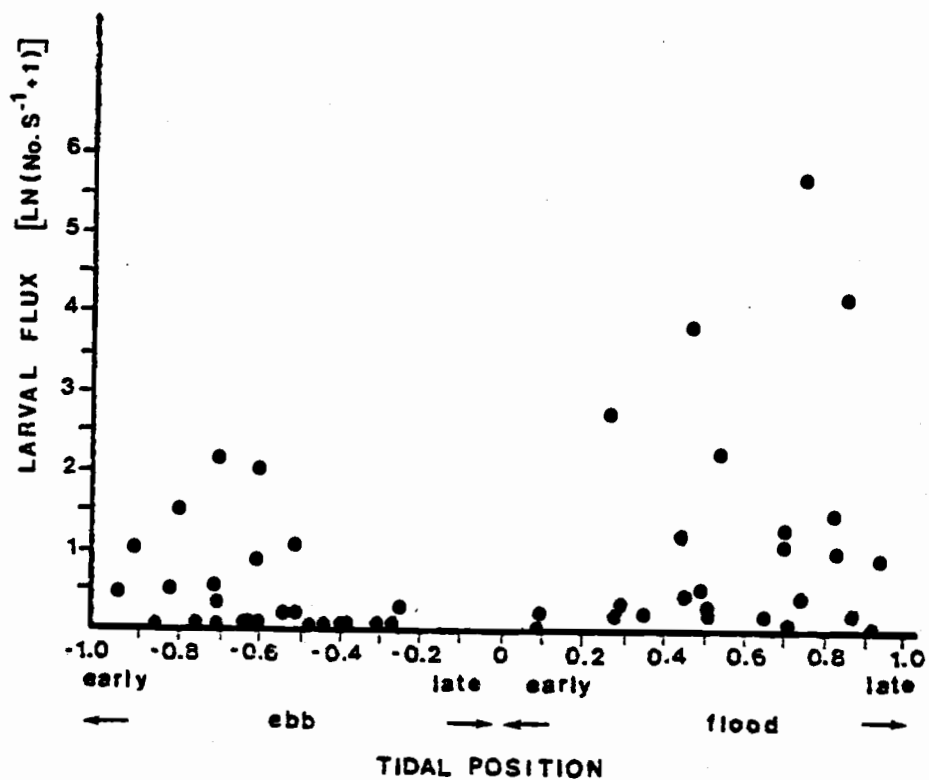


Figure 13. *Pinnixa littoralis megalopa*, flux through the mouth of the Salmon River Estuary versus tidal position during the summer 1979.

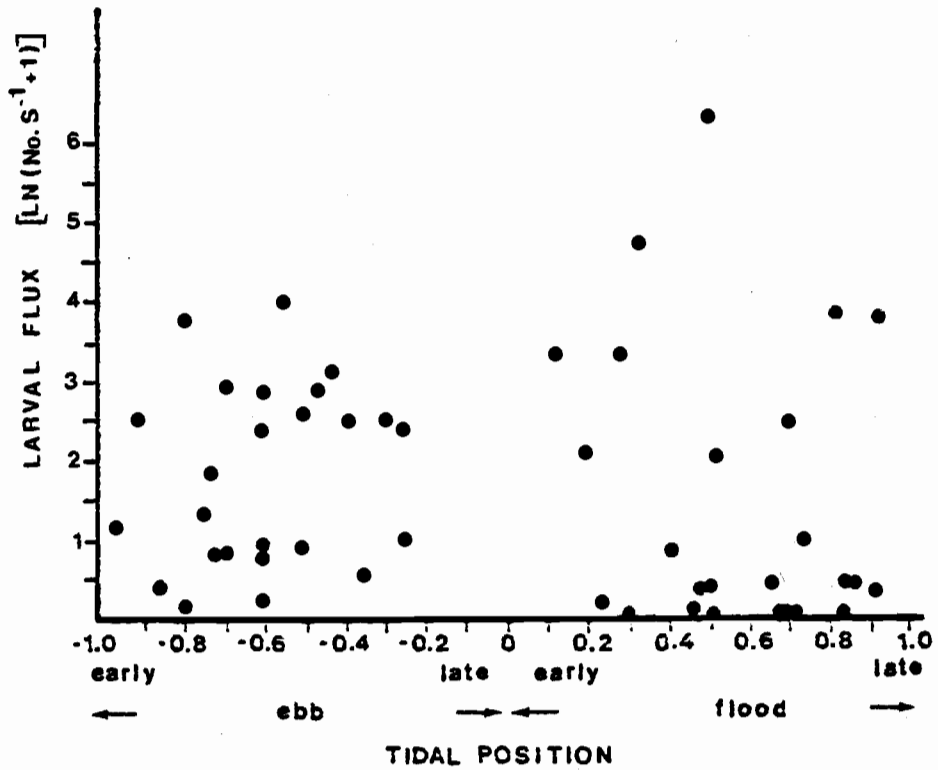


Figure 14. Hemigrapsus oregonensis early zoea, flux through the mouth of the Salmon River Estuary versus tidal position during the summer 1979.

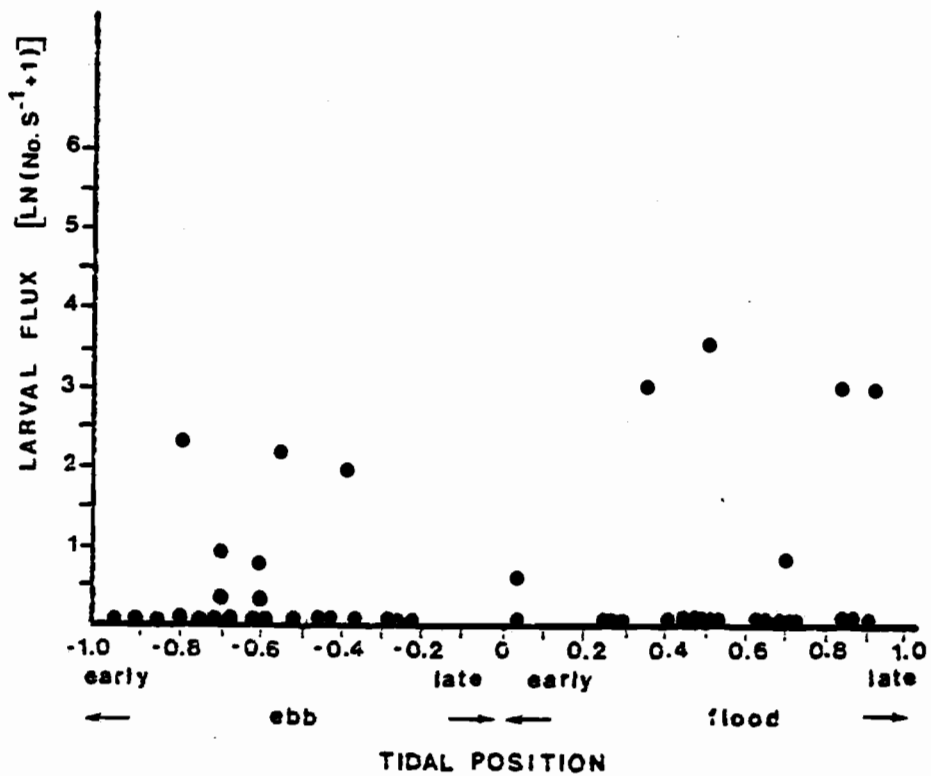


Figure 15. Hemigrapsus oregonensis late zoea, flux through the mouth of the Salmon River Estuary versus tidal position during the summer 1979.

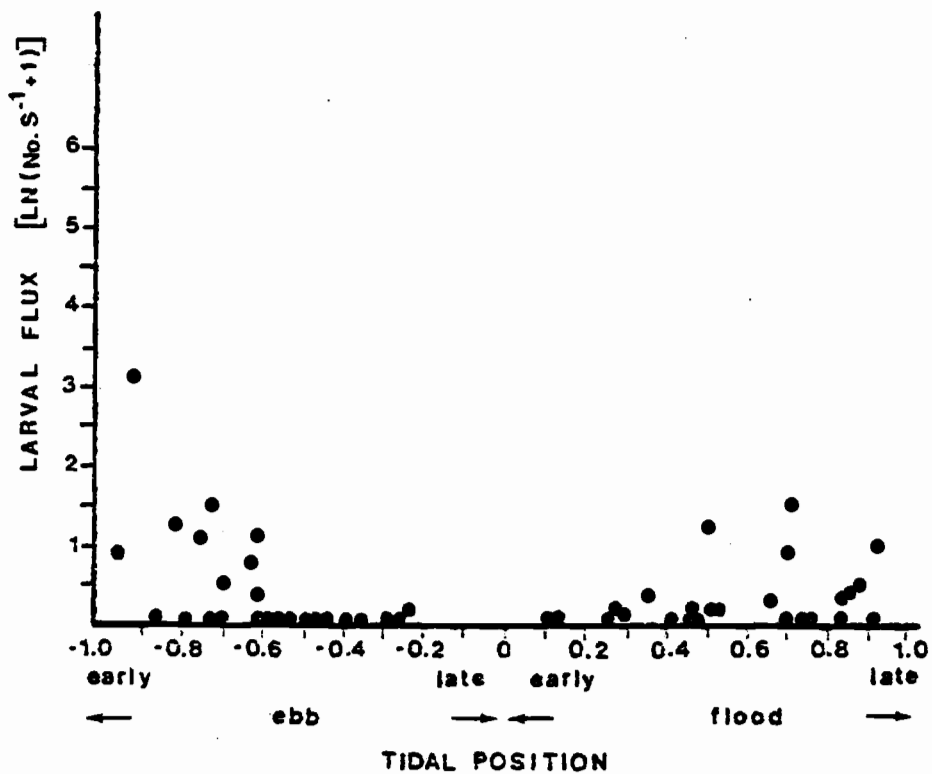


Figure 16. Cancer oregonensis zoea I, flux through the mouth of the Salmon River Estuary versus tidal position during the summer 1979.

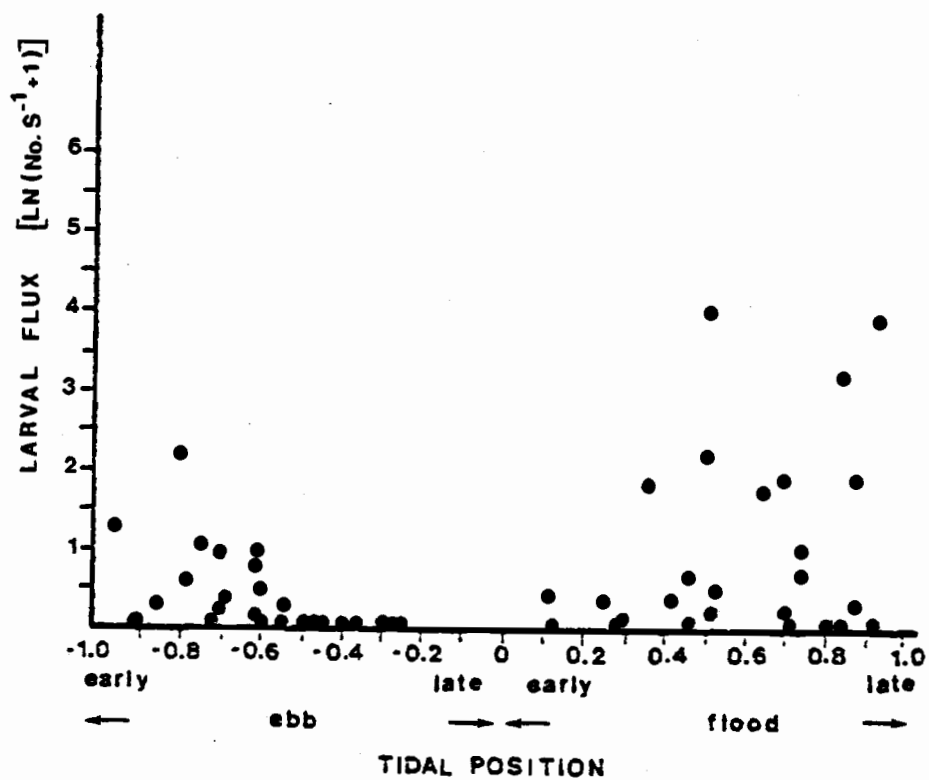


Figure 17. *Pachycheles* spp. zoea I, flux through the mouth of the Salmon River Estuary versus tidal position during the summer 1979.

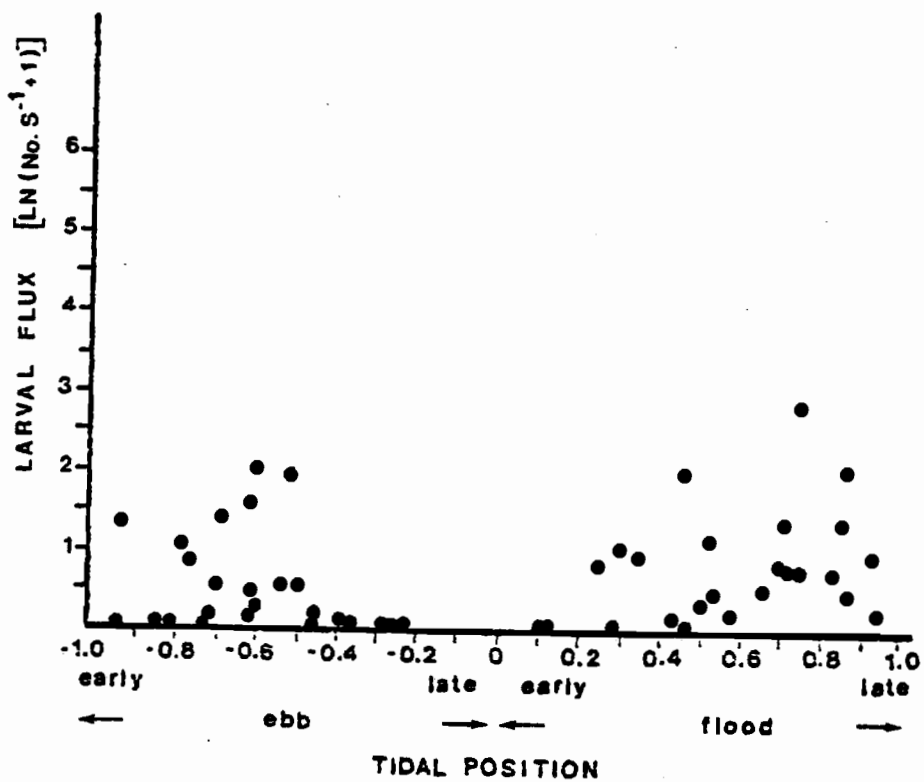


Figure 18. Pagurus granisomanus megalopa, flux through the mouth of the Salmon River Estuary versus tidal position during the summer 1979.

Figure 19. Atylus tridens density versus tidal position.
Samples are classified as ebb or flood flow.

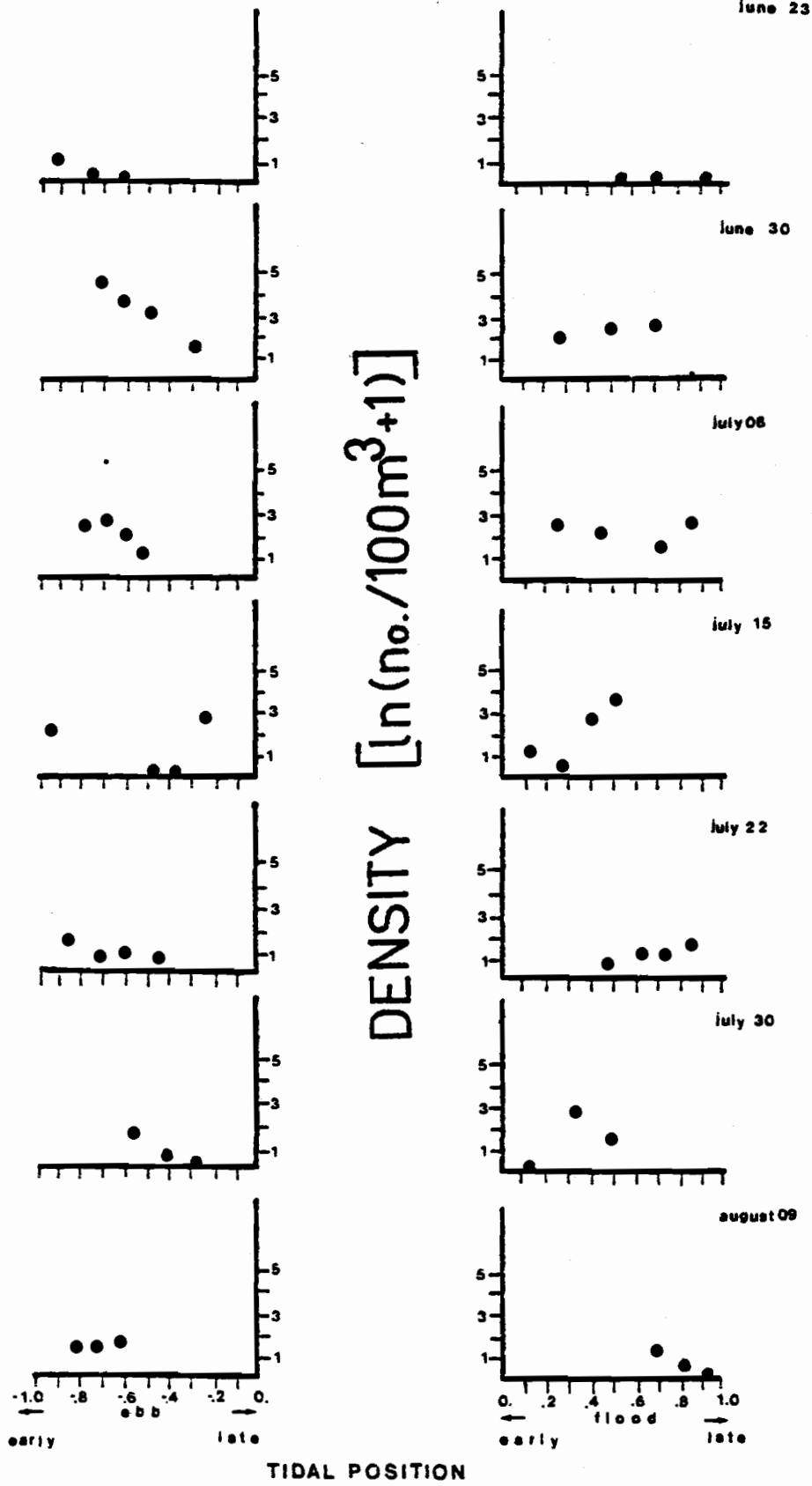


Figure 19.

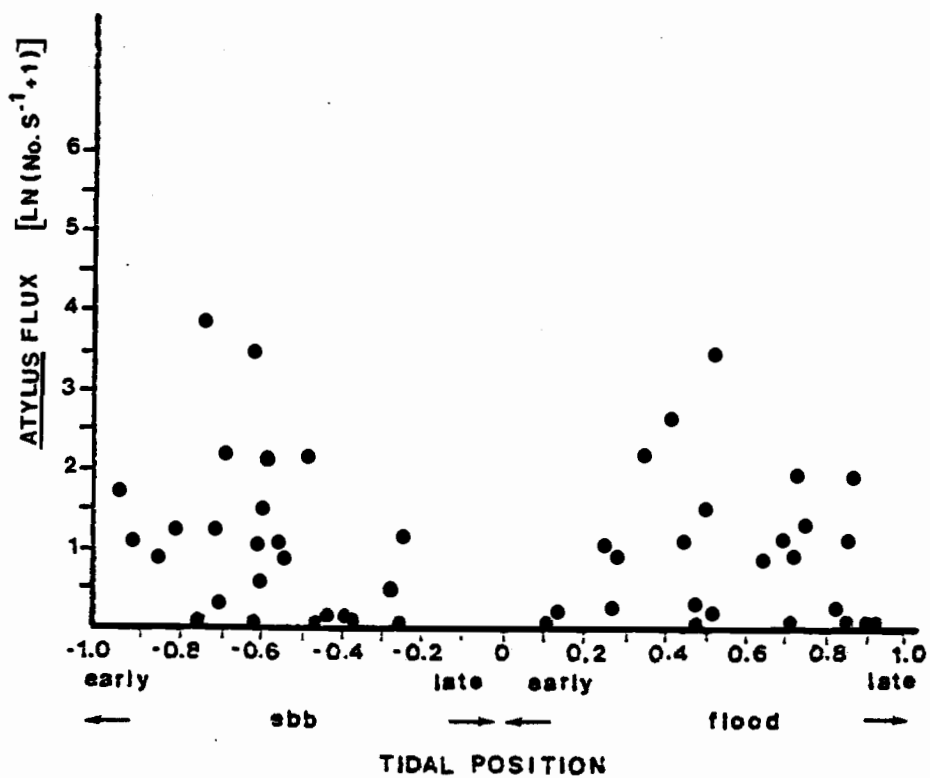


Figure 20. Atylus tridens, flux through the mouth of the Salmon River Estuary versus tidal position during the summer 1979.

Figure 21. Eogammarus confervicolus density versus tidal position. Samples are classified as ebb or flood flow.

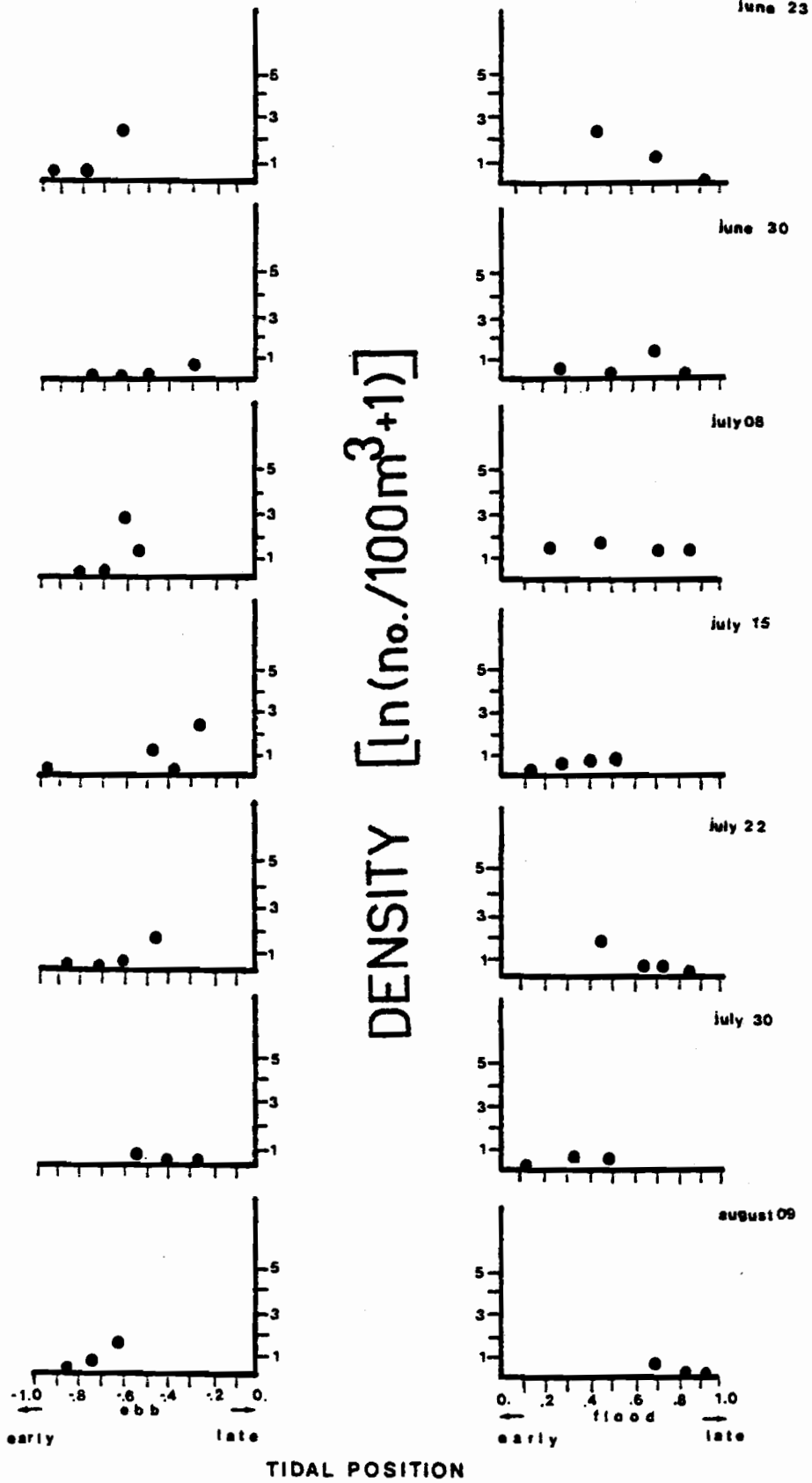


Figure 21.

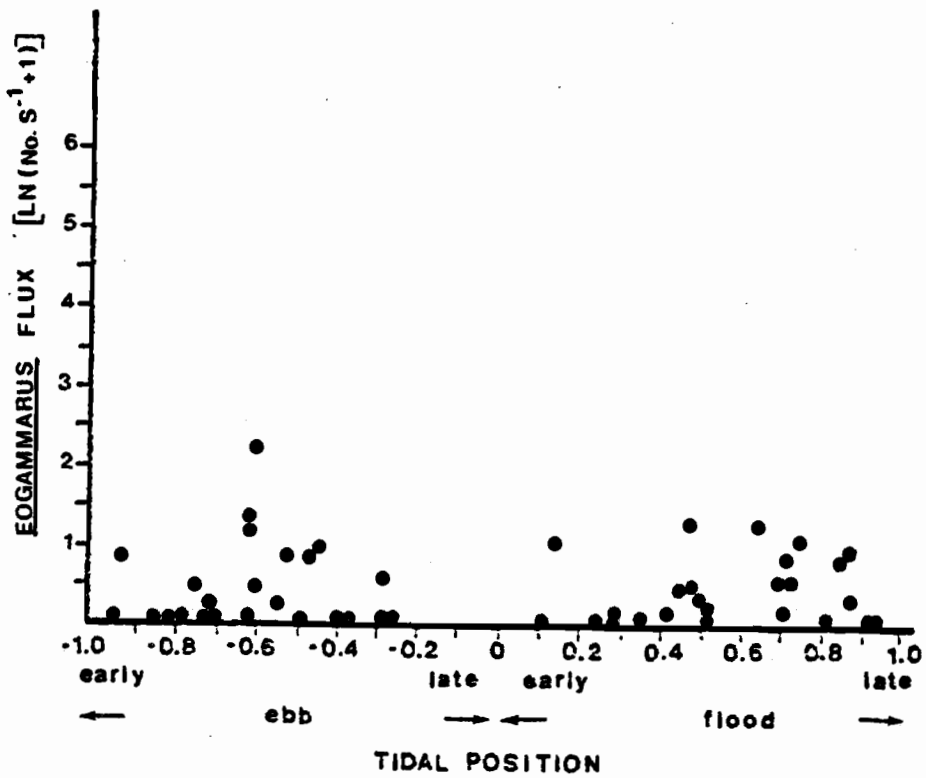


Figure 22. Eogammarus confervicolus, flux through the mouth of the Salmon River Estuary versus tidal position during the summer 1979.

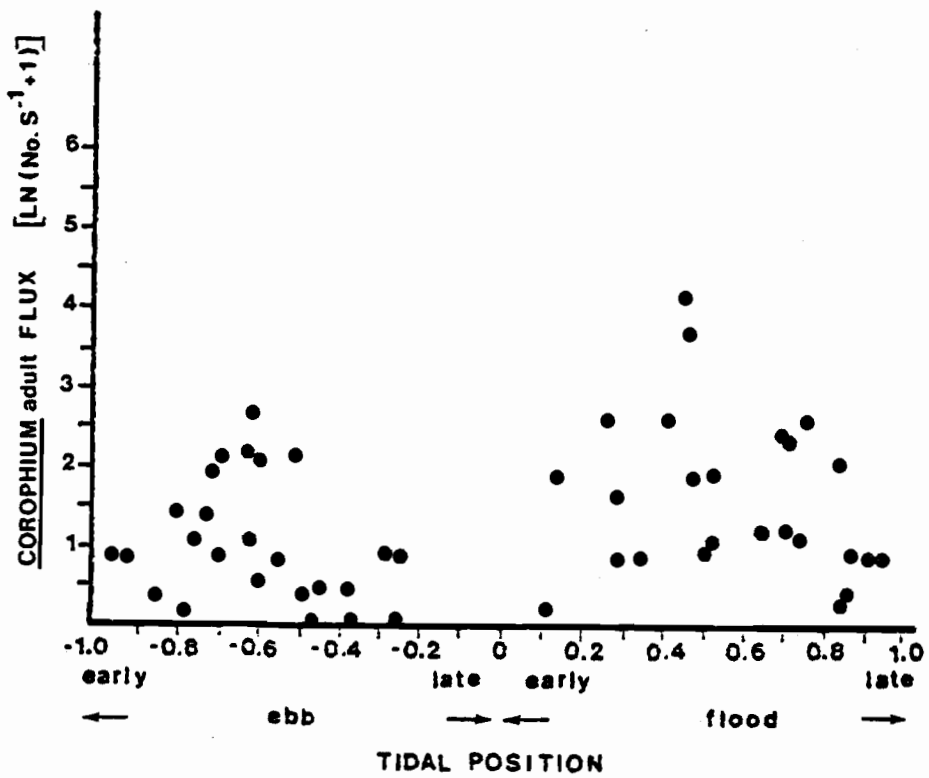


Figure 23. *Corophium brevis* adult, flux through the mouth of the Salmon River Estuary versus tidal position during the summer 1979.

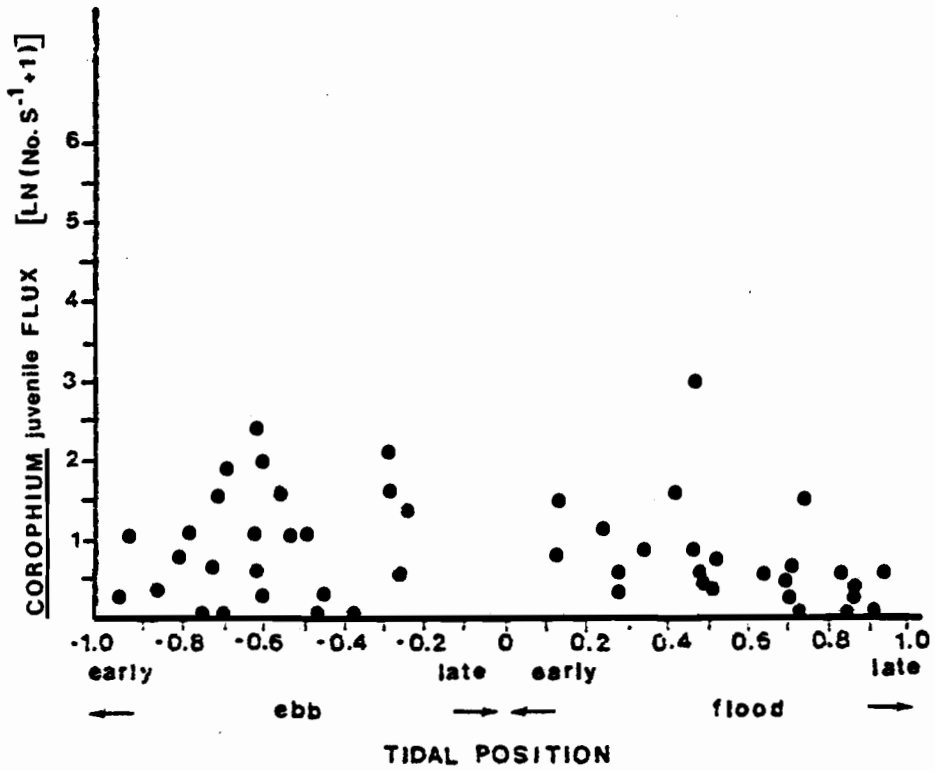


Figure 24. *Corophium brevis* juvenile, flux through the mouth of the Salmon River Estuary versus tidal position during the summer of 1979.

Figure 25. Corophium brevis adult density versus tidal position. Samples are classified as ebb or flood flow.

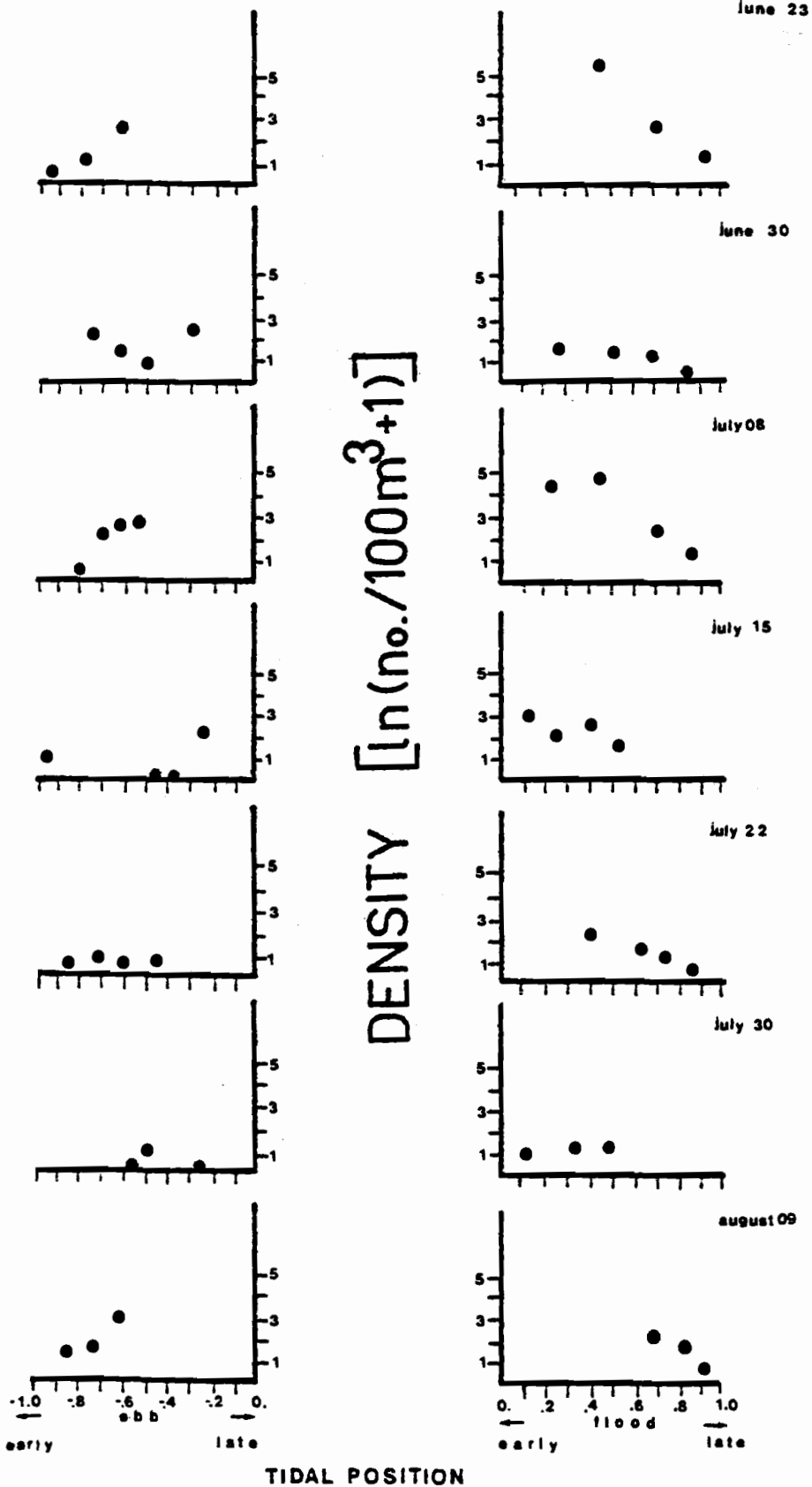


Figure 25.

Figure 26. Corophium brevis juvenile density versus tidal position. Samples are classified as ebb or flood flow.

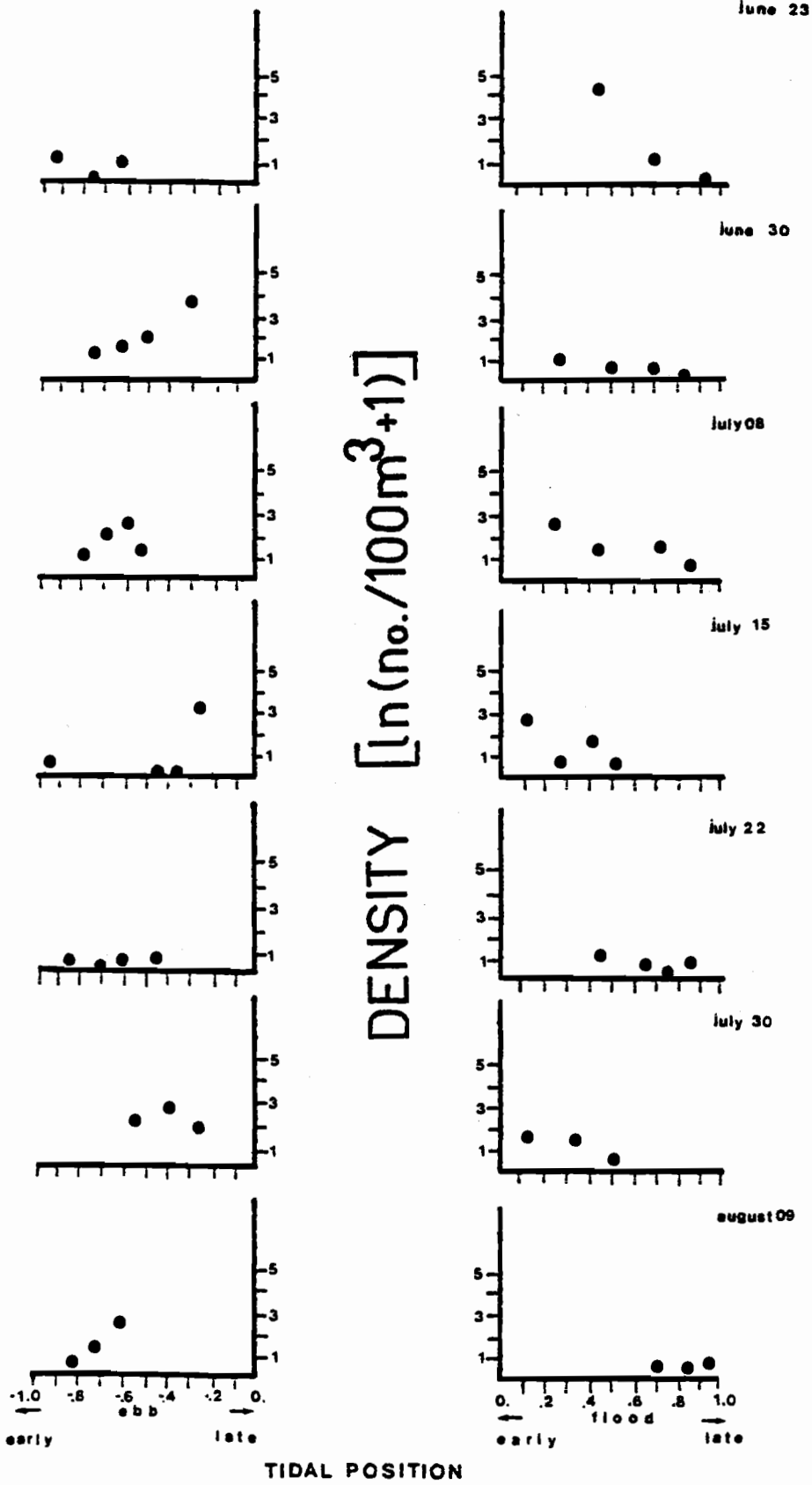


Figure 26.

Figure 27. Neomysis mercedis juvenile density versus tidal position. Samples are classified as ebb or flood flow.

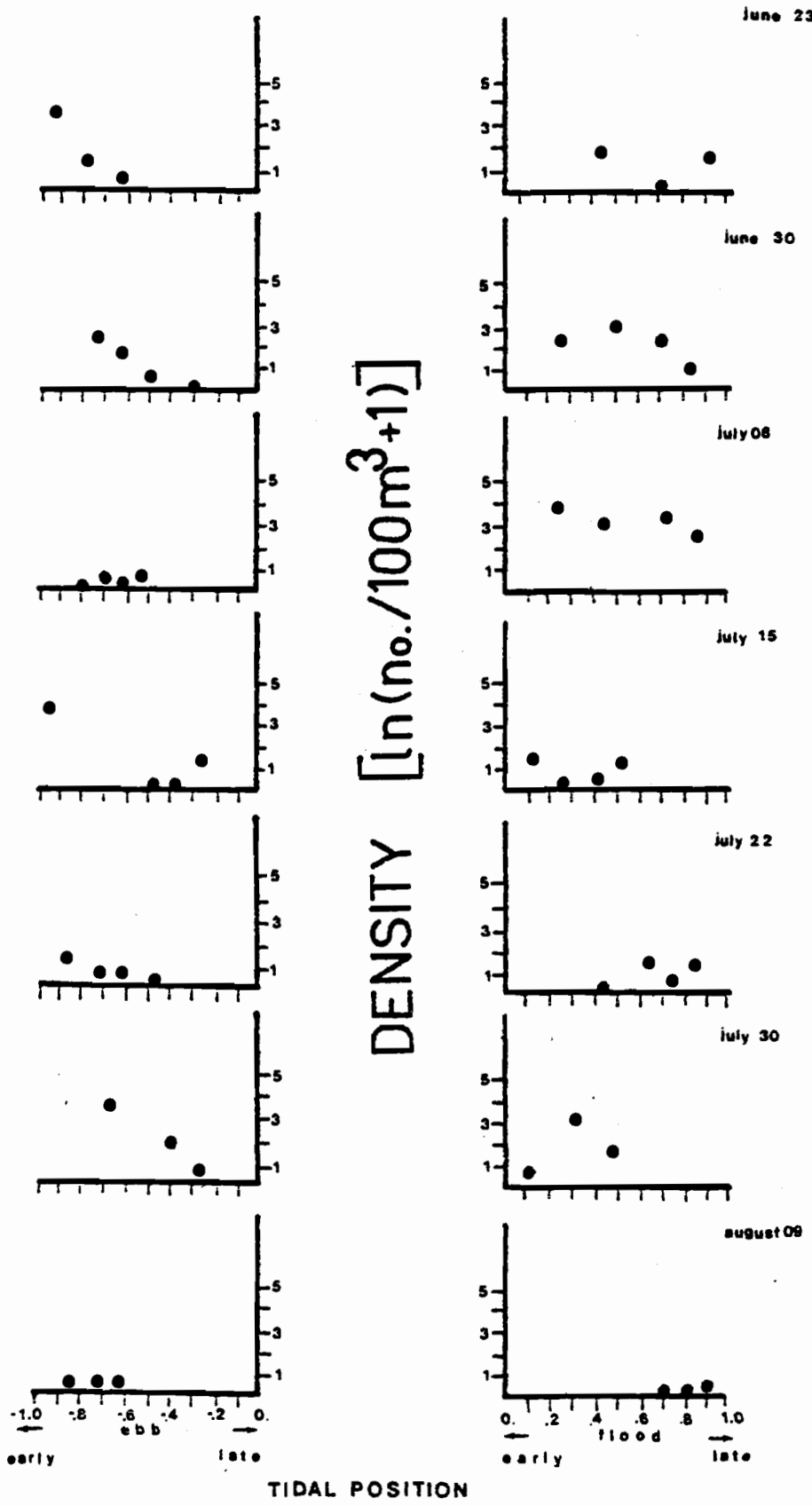


Figure 27.

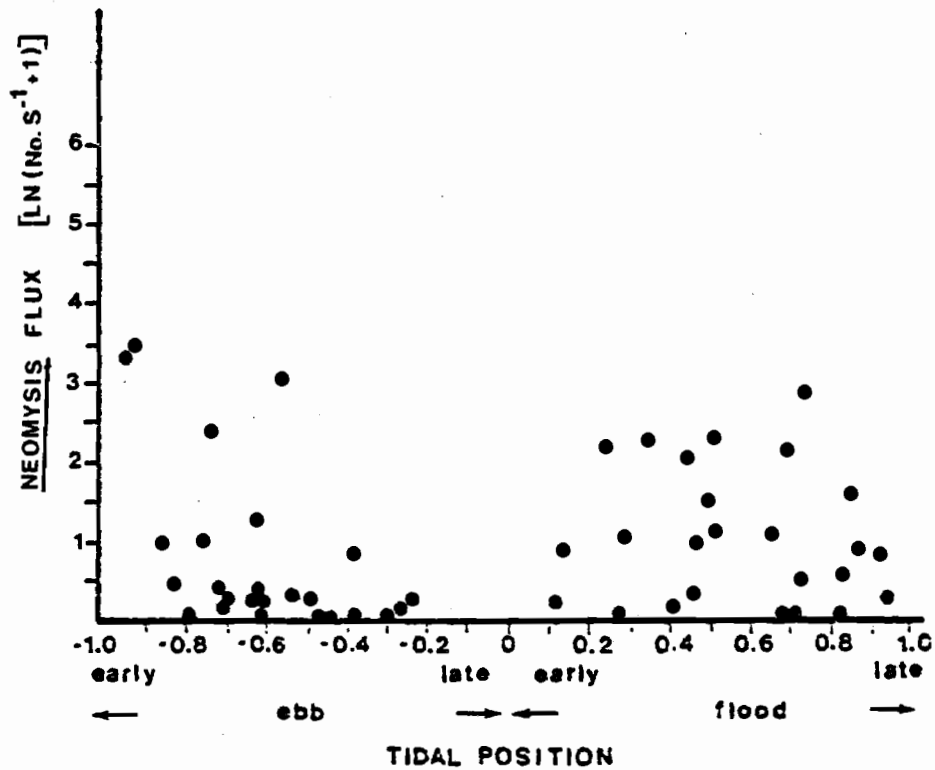


Figure 28. *Neomysis mercedis* juvenile, flux through the mouth of the Salmon River Estuary versus tidal position during the summer 1979.