AN ABSTRACT OF THE THESIS OF

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Title: The Tidal Exchange of Callianassa californiensis Larvae between

the Ocean and the Salmon River Estuary, Oregon

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During the Callianassa californiensis larval release period, weekly zooplankton samples were taken through daylight tidal cycles near the mouth of a small, fast flushing estuary on the Central Oregon coast. Although C. californiensis adults are confined to estuaries and embayments, stage I zoeal larvae were shown to be exported from the Salmon River estuary to the nearshore ocean. Physical features of the Salmon River estuarine environment appear to dominate any Callianassa larval behavior that would lead to retention within the estuary. Larval recruits to the adult population at the Salmon River must come from the nearshore region which probably contains Callianassa larvae flushed from estuaries all along the coast.

The relative effects of temperature, salinity, spring/neap tide series, tidal position, the number of days elapsed from January 1, 1979, upwelling, and river discharge on larval density were examined using correlation and multiple regression techniques. The results supported the contention that larvae were exported to the nearshore ocean and the

hypothesis that larvae would be retained in the nearshore ocean despite upwelling if they remained below the surface Ekman layer.

The Tidal Exchange of <u>Callianassa</u> <u>californiensis</u> Larvae
between the Ocean and the Salmon River Estuary, Oregon

by

Gary Ellis Johnson

A THESIS

submitted to

Oregon State University

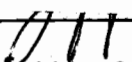in partial fulfillment of
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BETWEEN THE OCEAN AND THE SALMON RIVER ESTUARY, OREGON *

I. INTRODUCTION

The population dynamics of benthic invertebrates confined to
estuaries as adults are strongly affected by the tidal exchange of
estuarine and nearshore waters if the species have planktonic larvae.
These effects are common since about 70% of benthic species in temperate
latitudes have a planktonic phase in their life cycles (Thorson, 1950).
Tidal exchange is the vehicle whereby larvae are lost seaward from the
parent population and by which recruits may be transported into the
estuary from the nearshore ocean. The purpose of this thesis is to
determine the effects of tidal exchange on the recruitment of an
estuarine benthic invertebrate population.

There are two basic mechanisms supplying planktonic larvae for
recruitment to estaurine benthic invertebrate populations: retention of
larvae within the parent estuary and the input from the nearshore ocean
of mixed larvae previously exported from the parent estuary and adjacent
estuaries. Studies of recruitment in estuaries have often dealt with
or alluded to retention mechanisms (for example: oysters by Carriker,
1951 and Wood and Hargis, 1971; barnacles by Bousfield, 1955; flounder
by Pearcy, 1962; herring by Graham, 1972; and decapod crustaceans by
Sandifer, 1975). These studies related retention to the ability of the
larvae to regulate their position in the water column of two-layered
estuaries having a net landward flow in the bottom layer. DeWolf (1973)
disagreed with the contention of these authors 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. Estuarine circulation patterns permit retention and previous authors implicitly assumed that the input of larval recruits from the nearshore ocean was of negligible consequence. Larvae transported seaward were assumed to be effectively lost or dead.

The nearshore oceanic zone must be a source of recruits for stable populations of benthic invertebrate species inhabiting fast flushing estuaries where the physical characteristics preclude retention (Rogers, 1940). Carriker (1959) reported that Crassostrea virginica and Mercenaria mercenaria larvae produced at Home Pond, Long Island, a shallow salt-water pond with a 50% exchange ratio, were lost to Long Island Sound and that recruits were regularly transported into the estuary from the Sound. Sporadic sets of Mya arenaria in Barnstable Harbor, Mass. were attributed to the rapid flushing of the estuary and the irregular input of larvae from Cape Cod Bay (Ayers, 1956). Planktonic larval recruitment to North American west coast estuaries has not been reported.

At a small estuary on the Central Oregon coast with a 68% exchange ratio, I investigated the hypothesis that larvae 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. Zooplankton were sampled weekly at a station near the mouth of the Salmon River estuary during the Callianassa californiensis larval release period. On each sampling date, samples were taken consecutively through one daylight tidal cycle, providing flood and ebb tide

estimates of total numbers of C. californiensis larvae entering and leaving the estuary. The possibility for retention was studied and an hypothesis was formed concerning the source of recruits to the adult population within the Salmon River estuary. The relative effects of various environmental factors on larval density variation were examined statistically to form hypotheses concerning the triggering of larval release and details of an hypothesized recruitment mechanism.

Callianassa californiensis Biology

Callianassa californiensis is a burrowing decapod crustacean which inhabits intertidal and subtidal sandy substrates within embayments and estuaries from Alaska to Baja California (MacGinitie, 1934). Within estuaries, C. californiensis is found only in the regions of predominately marine influence. At the Salmon River, C. californiensis is confined to the lower 3 km of the estuary (Figure 1). It is the most abundant macroinfaunal species in the most extensive intertidal habitat (+5 to +3 ft MLLW) found within Oregon estuaries (Gonor, et al., 1979).

Locally two species of Callianassa are present, C. gigas and C. californiensis. C. gigas is so rare compared to C. californiensis that all Callianassa larvae found in the samples taken in this study were assumed to be C. californiensis.

The annual larval release period in Callianassa californiensis begins in late spring to early summer at this latitude (McCrow, 1972) and coincides with the upwelling season in coastal waters. Ovigerous females were found at the Salmon River in April and May, 1979. The larvae are brooded through the naupliar stages and then released into the
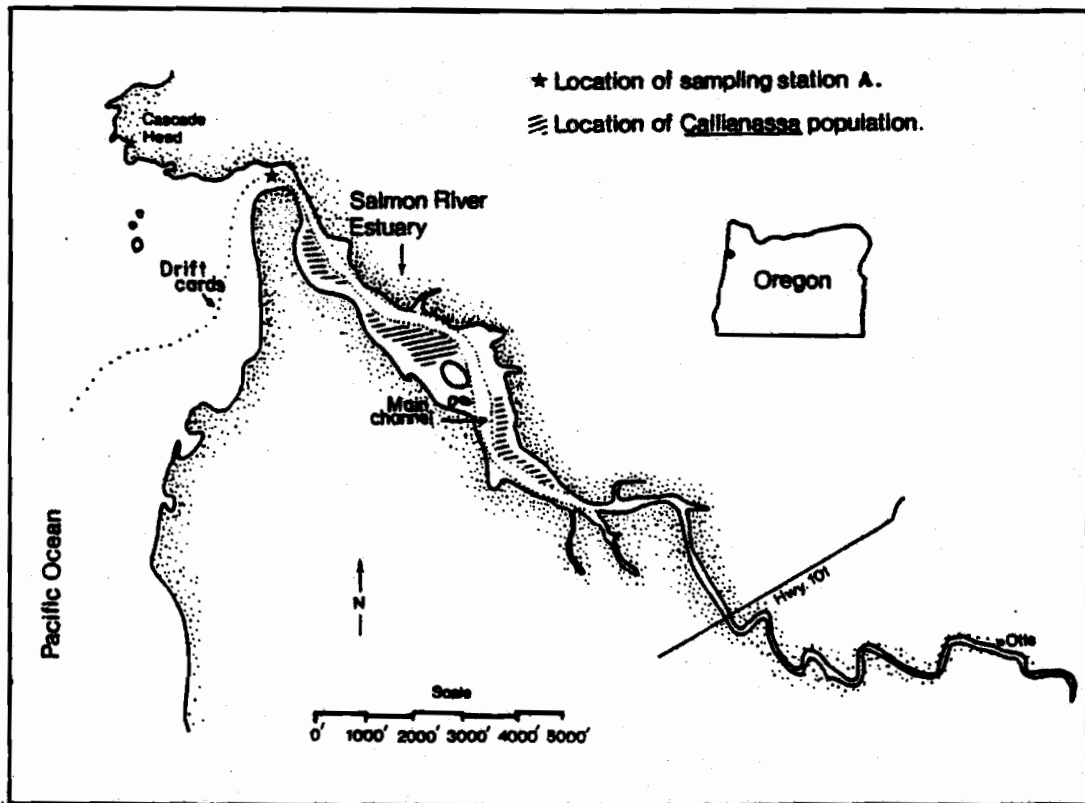
Figure 1: Salmon River estuary, Oregon showing sampling station A,
location of the Callianassa californiensis population,
track of drift cards, and the main channel.

the plankton as first stage zoeal larvae. The carnivorous larvae pass

through five zoeal stages and possibly one megalopal stage before metamor-

phosis and settlement. The estimated duration of planktonic life is six

to eight weeks (McCrow, 1972); the duration of each stage is unknown.

General Characteristics of the Study Site

Along the Oregon coast, nearshore waters (< 10 km from shore)

undergo extensive and sometimes daily changes in biological, chemical,

and physical characteristics (Collins, et al., 1968; Bourke, 1972; and

Smith, 1974). Northerly winds predominate in spring and summer, pro-
ducing a southward flow of surface water. The offshore component of
this flow can lead to upwelling if the winds are persistent or intense
enough. In order to interpret the distribution of plankton in these
waters, the complex coastal circulation during the upwelling season
must be understood. The biological, chemical, and physical changes
produced by upwelling can be observed in the seaward end of estuaries
along the coast (Bourke, 1969; Duxbury, 1979). Consequently, the lower
reaches of an Oregon estuary may be considered to be a tongue of the
nearshore ocean.

The Salmon River estuary (45°N-124°W) is located 137 km (85 miles)
south of the Columbia River (Figure 1). The distance from the estuary
mouth to the head of tide near Otis, Oregon is approximately seven kilo-
meters, and the surface area at MHW is only 0.83 km^2, 62% of which is
intertidal (Oregon Division of State Lands, 1973). The total volume at
MHW is 14.0 X 10^5 m^3 and at MLW is only 4.5 X 10^5 m^3 (Askren, et al.,
1976). The ratio of the tidal prism to total volume is 0.68, indicating
that the estuary, especially the portion nearest the mouth, empties and
fills every few tidal cycles.

Mixed semidiurnal tides dominate the water flow at the Salmon
River estuary. Their average range is 1.6 m (5.28 ft) (see Appendix for
derivation of this estimate), with a diurnal range of 2.3 m (7.6 ft) and
an extreme range of 4.0 m (13.0 ft) (Percy, et al., 1974). Surface cur-
rent velocities near the mouth regularly exceed 1.0 m/s on both ebb and
flood flows and may surpass 2.0 m/s (Askren. et al., 1976). Transport
of suspended sand was frequently observed by the author. Strong

tidal flows over the shallow bottom ($\sim$1 m below MLLW) in the lower three kilometers of the estuary produce a well-mixed water mass passing out of the mouth of the estuary on the ebb tide.

II. METHODS

Hydrography of the Salmon River Estuary

Detailed temperature and salinity measurements were taken to iden-
tify water masses, water movements, and the magnitude of mixing at the
Salmon River estuary. All measurements except those of April 15, 1979
were made at least at 0.5 m depth intervals using the same calibrated
Beckman induction salinometer. Longitudinal and horizontal temperature
and salinity transects were sampled at or near high tide because of the
shallowness of the estuary.

A drift card experiment was performed on August 21, 1979 to follow
the path of ebbed estuarine water into the nearshore ocean. Three ply-
wood drift cards (30 cm X 45 cm with a 45 cm X 20 cm fin) were released
at one-half hour intervals near mid-ebb tide from sampling station A
(Figure 1). The tracks of the fluorescent orange drift cards were
observed with binoculars from Cascade Head and recorded.

For each sampling date, volumes ebbed and flooded were estimated
using a model of the shape of the Salmon River estuary. It was assumed
that the estuary is a rectangular box below MLLW and that above MLLW
the relationship between tide height and surface area is linear. A
linear regression of surface area on tide height was derived from two
known surface area and tide height relationships for the Salmon River
estuary, those at MHW and MLW. Surface areas were then predicted for
high and low slack tide heights for each flow on each sampling date.
Volume was then computed using these high and low slack surface areas

and the change in tide height. A constant change in tide height through-
out the estuary is assumed for the model. The equations and other details
of this volume estimation method, along with the estimates used in this
study, are presented in the Appendix.

Concomitant temperature and salinity measurements using the same
salinometer were obtained with each zooplankton sample. Measurements
taken before and after the collection of each zooplankton sample were
averaged to obtain temperature and salinity measurements for the inter-
vening sampling time. Temperature and salinity data were not taken on
August 6, 1979.

Zooplankton Sampling Design and Methods

Quantitative zooplankton samples (Table 1) were obtained weekly
from June 23 to August 9, 1979, at a permanent station 0.2 km from the
mouth of the Salmon River estuary (sampling station A, Figure 1). A
single sampling station near the mouth was selected because virtually
all of the water present in the lower three kilometers of the estuary
at high tide must pass through this shallow, constricted part of the
channel during ebb tide.

The weekly samples were taken consecutively through one daylight
tidal cycle, except at or near slack tides, by allowing the tidal cur-
rent to pass through a net suspended from a skiff anchored in mid-chan-
nel. Mid-tides were sampled more extensively than other periods in the
tidal cycle because the tidal current was strongest near mid-tides. In
total. 32 flood samples and 29 ebb samples were distributed between eight
pairs of ebb and flood tidal flows.

Table 1: Sampling dates, spring or neap tide series, and number of ebb samples and number of flood samples for each date.

Date	Spring/neap	Number of ebb samples	Number of flood samples
June 23, 1979	spring	4	3
June 30	neap	4	4
July 8	spring	4	4
July 15	neap	4	5
July 22	spring	4	4
July 30	neap	3	3
August 6	spring	3	3
August 9	spring	3	6
Total	spring	18	20
	neap	11	12
	Total	29	32

A 0.5 m diameter, 0.5 mm mesh, conical Nitex net was used to obtain zooplankton samples. The width of the smallest Callianassa larvae sampled was approximately one millimeter. A calibrated Tsurumi-Seiki Kosakusho flowmeter mounted in the net mouth, 12.5 cm from the frame, was used to measure the volume filtered. An average of 227 m^3 (s.d. 88 m^3) was filtered to obtain each sample. The volume sampled was not related (r=0.15, P>0.1) to larval density calculated from the sample. Clogging of the net was not a problem. The flowmeter was periodically checked for interference from macroalgae, especially on ebb tides. An attempt

was made to sample all layers of the water column (average depth two meters) equally, but because of velocity flucuations the net could not be positioned near the bottom. This is probably not a serious problem because of the shallowness and turbulence at the sampling station. In the field, the samples were immediately preserved in 10% buffered formalin in seawater.

In the laboratory, samples were washed through a seven millimeter mesh screen placed over a 0.445 mm sieve to separate macroalgal fragments from the plankton. Small allotments of the plant material caught on the coarse screen were thoroughly washed into the finer sieve until all was washed. Microscopic examination of the algae before and after washing showed that almost all planktonic animals were separated from the algae by this process. The residue of plankton retained on the sieve was preserved in 40% isopropanol. The entire residue of each sample was sorted and all _Callianassa californiensis_ larvae found were staged and counted.

Statistical Methods

The statistical methods used in the data analysis included methods to evaluate ebb and flood differences in _Callianassa californiensis_ larval content and to evaluate the relative importance of certain environmental variables in explaining _C. californiensis_ larval density variation. The following references to larval density apply to each stage separately.

The sample larval density estimates were transformed by the natural logarithm ($\log_e(\#/100m^3 + 1)$) because the effect of environmental fac-

tors on larval density is normally multiplicative rather than additive
(Cassie, 1959a; Ricker, 1975). Also, the transformation deemphasizes
the effect of extremely dense samples. Most statistical procedures used
were applied to $\log_e$-transformed biological data.

The analysis of ebb/flood differences in the content of Callianassa
californiensis larvae treated the total number estimates for each tidal
flow on each of eight sampling dates as a related pair. The total num-
ber of Callianassa larvae passing the mouth of the estuary during a
given flow was estimated as the mean of the raw larval density data
(#/100m^3) for that flow multiplied by an estimate of the total volume
ebbed or flooded (see Appendix). The Wilcoxon matched-pairs signed-rank
test (Siegel, 1956) was applied to the ebb/flood pairs of transformed
total number estimates to test for the significance of the null hypo-
thesis that the total number of C. californiensis larvae leaving the
estuary was the same as that entering during daylight tidal cycles.

Measurements on seven environmental variables at two levels of spe-
cificity are associated with the Callianassa californiensis larval den-
sity estimates for 55 samples. An additional six samples have observa-
tions on all environmental variables except temperature and salinity.
The following variables are specific to each sampling date: number of
days elapsed from January 1, 1979 (DAYS); spring/neap tide series indi-
cator variable (0=neap and 1=spring, SGNP); Bakun's upwelling index
(Bakun, 1980) (UPWG); and river discharge (RDIS). Temperature (TBAR),
salinity (SBAR), and tidal position (TPOS) are sample specific variables.

The tidal position variable was designed to reflect the effect of
tide height changes on the physical, chemical, and biological character-

istics of the water column passing through the mouth of the estuary.
This variable is the ratio of elapsed time between the time when the sam-
ple was taken and the time of the nearest low slack to the total dura-
tion of that particular one-half tidal cycle, ebb or flood (TPOS =

$$\frac{\text{time of sample midpoint} - \text{time of nearest low slack}}{\text{duration of } \frac{1}{2} \text{ tidal cycle}}$$

). TPOS ranges from -1 to +1; ebb
flows have negative and flood flows have positive values. TPOS values
of -1 and +1 are at high slack tides and zero values are at low slack
tides (see Figure 8 for a graphical presentation). Except for periods
near or at slack tides when tide height changes slowly or not at all,
time and tide height are approximately linearly related during each one-
half tidal cycle.

The seven environmental factors measured do not have the same types
of relationships with larval density. Temperature and salinity have
direct biological relationships with larval density. However, the mag-
nitude of these direct effects is regulated by those variables influenc-
ing temperature and salinity, which are SGNP, TPOS, UPWG, and RDIS.
Although DAYS is not an indirect-effect variable, it was treated as such
to expedite the data analysis. The following pathway represents the
the relations between the seven environmental factors and Callianassa
californiensis larval density: indirect effect variables ⟶ direct-
effect variables ⟶ larval density. In the determination of the
relative importance of an environmental factor in explaining larval den-
sity variation, preference was given to temperature and salinity. Besides
having a direct effect on larval density, these two variables are repre-
sented by accurate quantitative measures, are sample specific, and they
serve as indicators of the history of a water mass.

In the analysis of environmental effects on larval density, ebb and flood samples were separated to obtain more homogeneous sample sets than would be the case if they were pooled. These sample sets were standardized separately. The standardization used was the difference between the observed value and the mean divided by the standard deviation for each variable $(\frac{x_i - \bar{x}}{s.d.})$. Standardization permitted valid comparison of regression coefficients because after standardization variables were expressed in the same units. Samples from August 6, 1979, were not included in the environmental effects analysis because of the missing temperature and salinity data.

The basic approach used to evaluate relative importance was to reduce the initial number of indirect-effect variables by exploratory correlation (Ricker, 1975) because seven environmental factors were too many to reliably model larval density with only 29 flood and 26 ebb samples. Then, the relative importance of the remaining variables, plus temperature and salinity, was analyzed using partial correlation and multiple regression techniques. For each correlation and regression coefficient, a two-tailed test of statistical significance was applied. Significance levels of these coefficients are indicated by asterisks: *, $P < .1$; **, $P < .01$; ***, $P < .001$.

Partial correlations between the indirect-effect variables remaining after exploratory correlation and larval density were obtained and, if any spurious relationships or insignificant correlations were uncovered, these variables were removed from further analysis. The association of the remaining indirect-effect variables and temperature and salinity was then reviewed. If a plausible hypothesis could be formed

concerning the effect temperature and salinity had on larval density, as regulated by the indirect-effect variables in question, and if this hypothesis was consistent with the trends shown by correlations between larval density and temperature and salinity, then the hypothesized pathway(s) were accepted as reasonable. I concluded that the variables most highly correlated with larval density were most important in explaining larval density variation. It was expected that variables not measured but which affected larval density would cloud this analysis. The main advantage of the correlation approach was to gain a detailed understanding of the relationships between the variables.

Forward and backward stepwise regression were used to select the best multiple regression model describing the observed variation in Callianassa californiensis larval density. The indirect-effect variables remaining after exploratory correlation, plus temperature and salinity, were initially inserted into the regression model. The criterion for entry or removal of a variable was the magnitude of the change in the residual variability compared to that achieved by the existing model. Those variables forming the best model were assumed to be more important in explaining larval density variation than those not in the model. The standard regression coefficients were then used to determine the relative importance of the variables in the model; this is valid even though the environmental factors are intercorrelated (Ricker, 1975).

III. RESULTS

Hydrography of the Salmon River Estuary

During spring the estuarine water column is well-mixed, with res-
pect to temperature and salinity, on the seaward side of a salt-wedge
that is approximately 1.5 km long (Figure 2A). The region of marine
influence extends approximately three kilometers upstream from the mouth.
However, during periods of low river discharge (Figure 2B) salt water
penetrates at least as far as the Hwy. 101 bridge, five kilometers from
the mouth. The seasonality of river discharge results in seasonal dif-
ferences in the temperature and salinity structure. The Salmon River
should be classified as a well-mixed or Type D estuary in the lower
reaches and a partially stratified or Type B estuary in the upper reaches
(Pritchard, 1955).

It is clear from temperature and salinity data taken in horizontal
transects across the estuary that the water over the tide flats has much
the same temperature and salinity structure as that at an equivalent
depth in the adjacent main channel. There are no pockets of stagnant
water in the lower reaches of the estuary. Although I have observed
eddies along the shore, these features are ephemeral and disappear at
ebb tide.

Temperature and salinity measurements were taken through a tidal
cycle at sampling station A. The water column passing this location was
well-mixed throughout the tidal cycle (Table 2), so all of the vertical
measurements at station A at a given time were averaged. Average values
of temperature and salinity through time were negatively correlated with
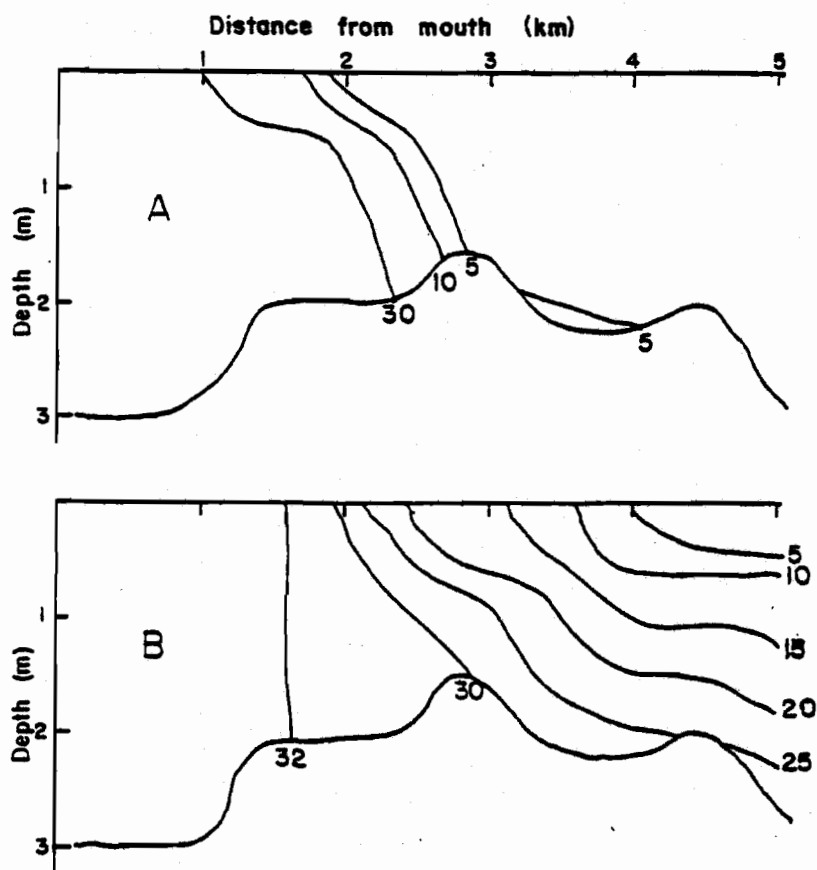
Figure 2: Longitudinal distribution of salinity at high tide at the Salmon River estuary on (A) April 15, 1979 (river discharge = 17.4 cms) and on (B) July 15, 1979 (river discharge = 1.5 cms). Contours in parts per thousand.

Table 2: Vertical distribution of temperature (^{O}C) and salinity (^{O}/oo) at different times in a tidal cycle at station A on June 30, 1979.

| | Ebb | | | | Low slack | | Flood | | | |
| | 0645h | | 0919h | | 1230h | | 1432h | | 1735h | |
Depth	T	S	T	S	T	S	T	S	T	S
0.0 m	11.8	31.7	13.9	16.0	14.6	11.3	13.3	31.2	13.7	31.6
0.5	11.6	31.6	13.7	16.5	14.6	11.3	13.3	31.2	13.7	31.6
1.0	11.6	31.9	13.7	17.8	14.6	11.3	13.4	31.4	13.7	31.7
1.5	11.7	31.9	13.7	17.9	14.6	11.3	13.4	31.5	13.6	31.6
2.0	11.6	31.9					13.4	31.4	13.7	31.6
2.5	11.7	31.5					13.4	31.2	13.6	31.6

each other (Figure 3). A comparison of Figures 2B and 3 indicates that the low salinity, high temperature water passing the mouth late in the ebb originated at least three kilometers up the estuary. These data are useful in estimating the magnitude of the exchange of estuarine and nearshore waters.

It is realistic to assume that 100% of the ebbed water is lost to the nearshore region. The temperature and salinity of the flood tide reaches a stable structure within two hours after low slack (Figure 3). This implies that undiluted nearshore water is entering the estuary during most of the flood flow.

Other evidence supporting the assumption of complete exchange involves the summer alongshore current which runs southward, parallel to
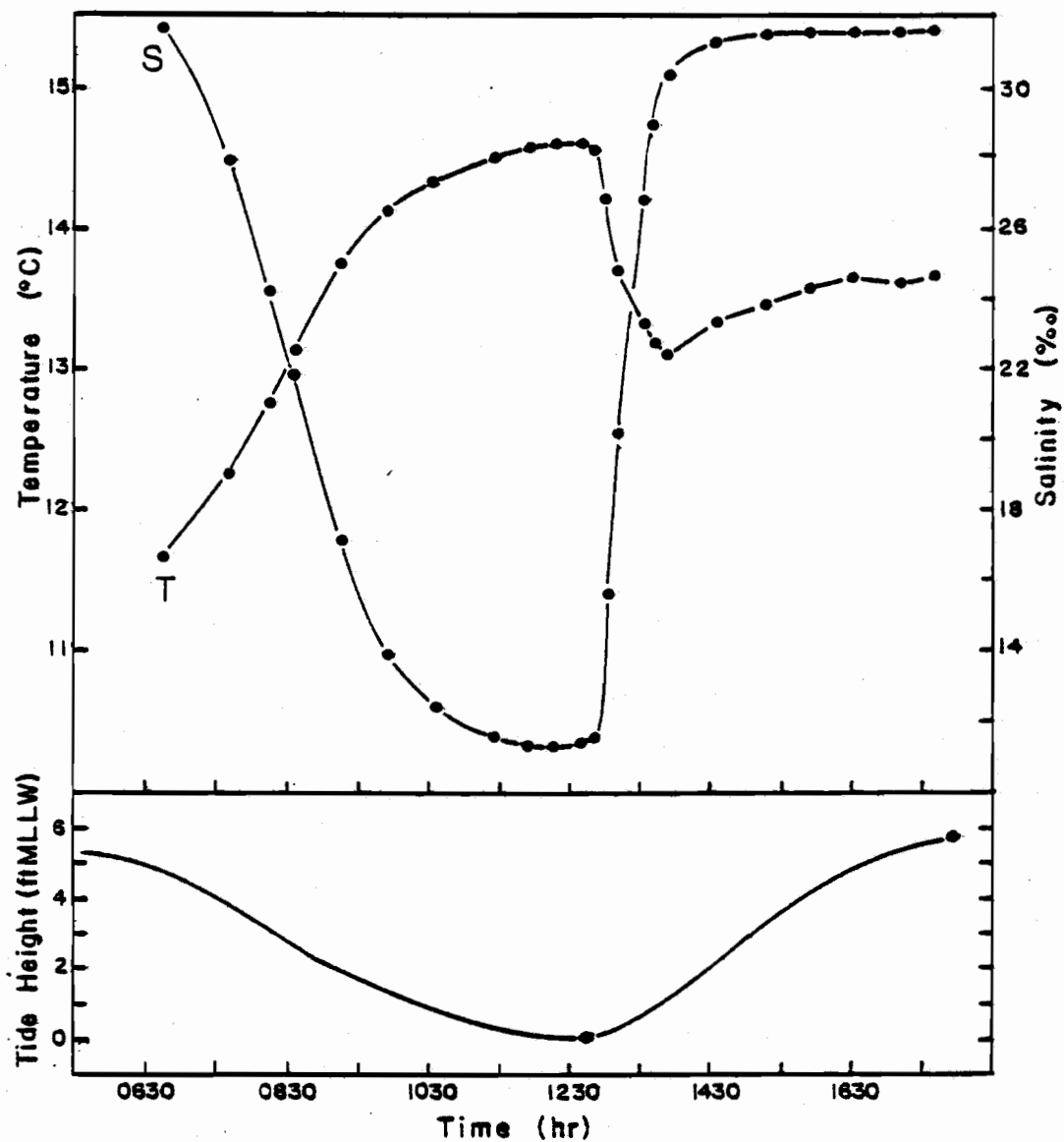
Figure 3: Variation in temperature, salinity, and tide height
(estimated from tide table) through a tidal cycle on
June 30, 1979 (neap tide series) at station A near the
mouth of the Salmon River estuary.

Table 3: Estimates of the flushing time of the Salmon River estuary from data taken in mid-May, 1976 when river discharge was about 3.4 cms (compiled from Askren, et al., 1976).

Method	Flushing time (tidal cycles)
Classical tidal prism	1.5
Fraction of freshwater approach	2.0
Ketchum's modified tidal prism	3.6
Dyer-Taylor segmented approach	5.7

the coastline, at velocities ranging from 8.6 to 26 km per day (Huyer, et al., 1975). The average path taken by the three drift cards released on August 21, 1979 was to the south, parallel to the spit, then westward into the main alongshore current and finally to the southwest (Figure 1). Ebbed water does not remain behind Cascade Head but enters the nearshore current system where, on the average, it spends three hours per tidal cycle. During this time the ebbed volume will be carried approximately two kilometers southward. Because tidal currents are usually orders of magnitude less strong than the alongshore flow, most of the ebbed water entering the nearshore current system is swept southward and does not return to the estuary.

Askren, et al. (1976) used four methods (Table 3) to compute the flushing time (that required to replace the existing freshwater in the estuary at a rate equal to the river discharge) of the Salmon River estuary during mid-May, 1976 when river discharge was 3.4 cms. Flushing

time estimates for May would be shorter than those for summer because river discharge in greater in May than in summer months. However, these methods do not take into account the effect of upwelling which decreases flushing time (Duxbury, 1979). The flushing time estimates of a few days given by these methods are assumed to be reasonable for summer conditions.

The Physical Environment During the Sampling Period

The discharge of the Salmon River was low during the sampling period, decreasing from 2.2 to 1.1 cms (Oregon Department of Water Resources, 1980). Because this small amount of variation could not have altered the temperature and salinity structure of the estuary appreciably, this variable was not included in the analysis of the effects of   . environmental factors on larval density.

The range and magnitude of the temperature and salinity observations for each zooplankton sample taken during the study are given in Figure 4. Temperatures ranged from 7.32 $^\circ$C to 18.16 $^\circ$C with an approximately equal frequency distribution. Salinities ranged from 13.16 $^\circ$/oo to 34.63 $^\circ$/oo but were strongly skewed to the higher salinities. In 47% of the observations, salinities were greater than 33.10 $^\circ$/oo.

The identification of water types from Figure 4 was slightly biased because complete tidal cycles were not sampled. Tidal positions near the slack tide in the middle of the tidal cycle were sampled more intensively than those near the slack tides at the ends of the cycle. Spring tidal cycles were sampled from low-low to low-high to high-low and neap tidal cycles were sampled from low-high to low-low to high-high. The
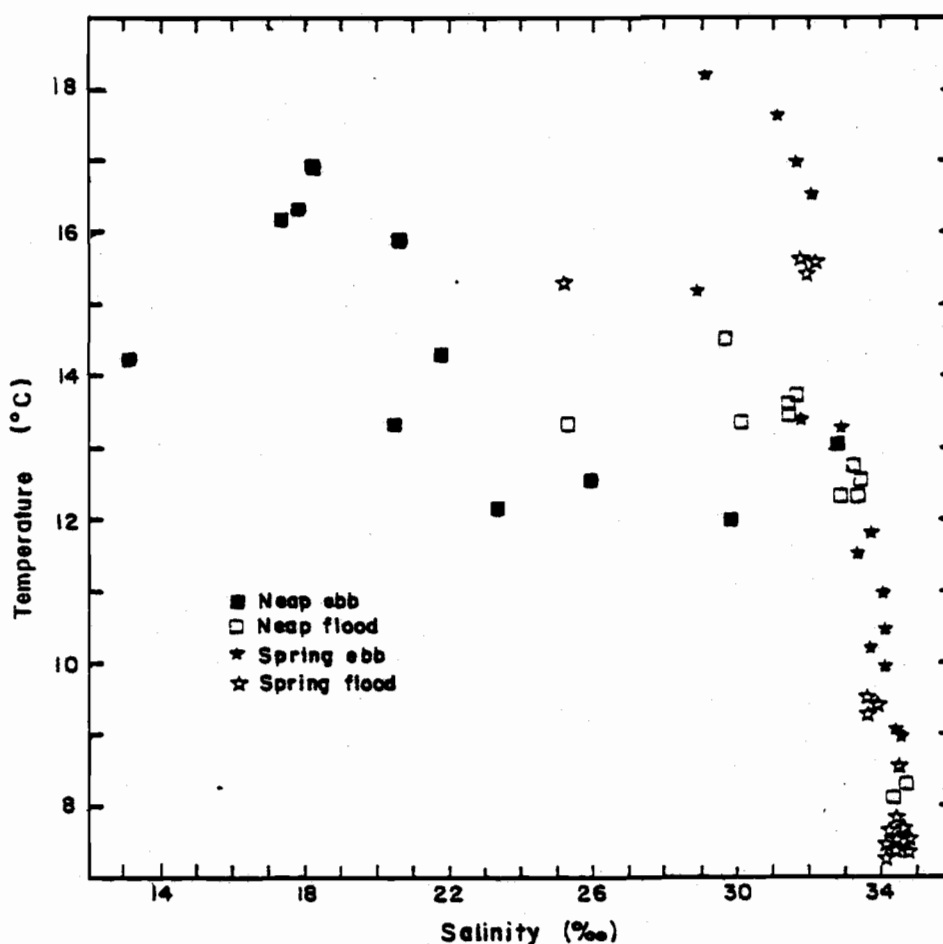
Figure 4: Temperature and salinity diagram from measurements
taken concurrently with zooplankton samples taken near
the mouth of the Salmon River estuary during summer 1979.

bias was accounted for in partial correlation and multiple regression

analyses by controlling for the effect of TPOS.

After accounting for the effects of tidal position and upwelling on

the relations between temperature and salinity and spring/neap tide ser-

ies, spring flood flows apparently were cooler and more saline than neap

flood flows (Table 4). Neap ebb flows generally were much less saline

than spring ebb flows. Ebb temperatures were not related to spring/neap

Table 4: Total and partial correlation coefficients of tempera-
          ture (TBAR) and salinity (SBAR) with spring/neap tide
          series (SGNP) and upwelling (UPWG) for ebb (n=26) and
          flood (n=29) flows.

Correlates	Controlling for:	Ebb	Flood
TBAR-UPWG	---------	-.51**	-.58**
TBAR-UPWG	TPOS	-.61**	-.60***
TBAR-UPWG	TPOS,SGNP	-.61**	-.69***
SBAR-UPWG	---------	.05	.50**
SBAR-UPWG	TPOS	.08	.59***
SBAR-UPWG	TPOS,SGNP	.28	.60***
TBAR-SGNP	---------	-.24	-.42*
TBAR-SGNP	TPOS	.04	-.35*
TBAR-SGNP	TPOS, UPWG	-.02	-.53**
SBAR-SGNP	---------	.81***	.31
SBAR-SGNP	TPOS	.83***	.11
SBAR-SGNP	TPOS,UPWG	.84***	.22

tide series, possibly because other independent factors, such as solar
heating, were involved. The sampling bias produced a spurious correla-
tion between ebb temperatures and spring/neap tide series.

The pattern of change in temperature and salinity values through
a tidal cycle generally was the same for both spring and neap tide ser-
ies (Figures 5 and 6). As a flood tide progressed, temperature decreas-
ed (TPOS-TBAR r=-.26) and salinity increased (TPOS-SBAR r=.52**; TBAR-
SBAR r=-.71***). As an ebb tide progressed, temperature increased
(TPOS-TBAR r=.56**) and salinity decreased (TPOS-SBAR r=-.83***; TBAR-
SBAR r=-.50**). The ebb patterns were more pronounced for neap tide
series than for spring tide series.

According to Bakun's index of upwelling (Bakun, 1980), of the eight
sampling dates, five were during active upwelling, two were during
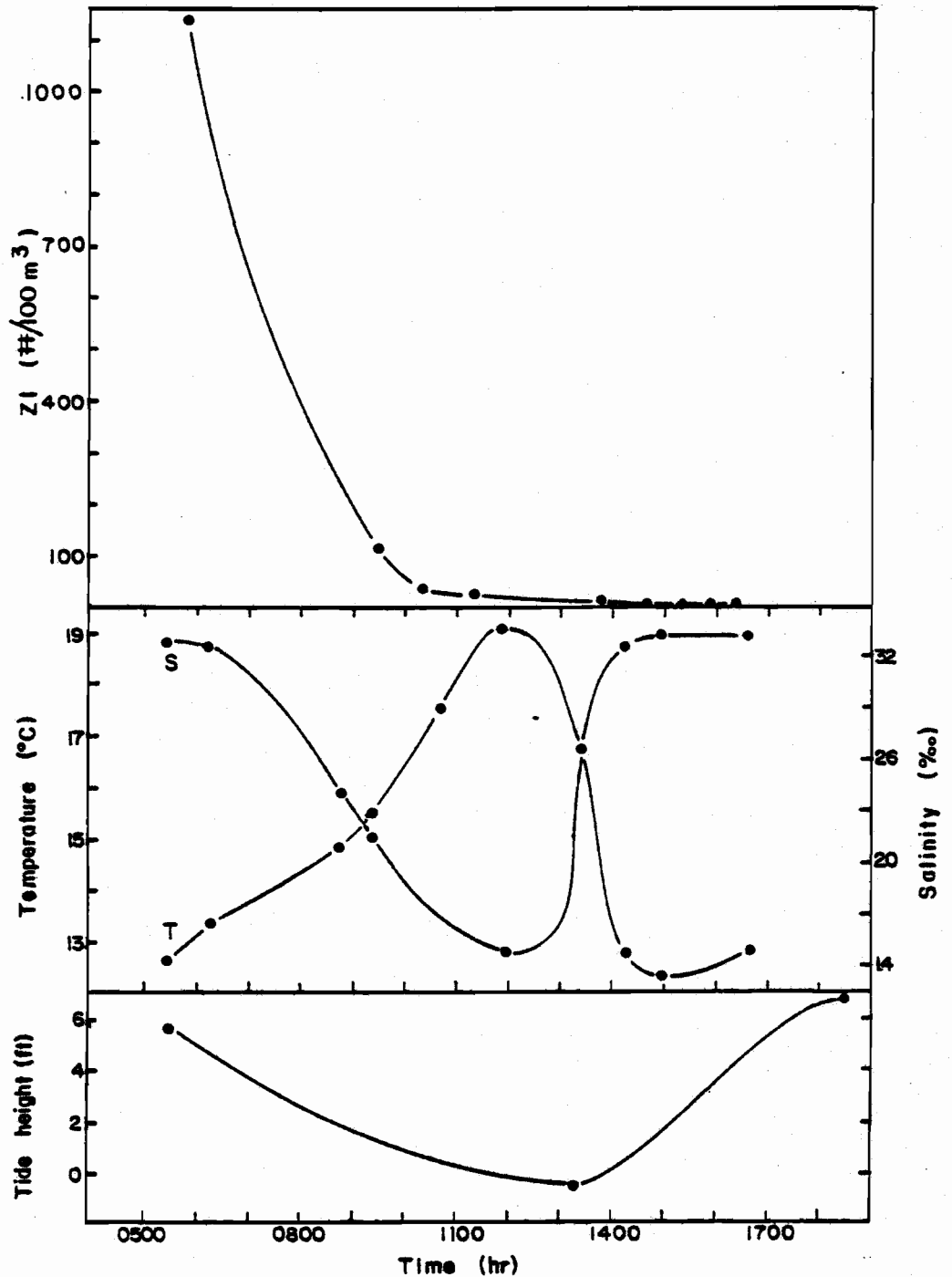
Figure 5: Variation in Z1 density, temperature, salinity, and
tide height (estimated from tide table) through a tidal
cycle on July 15, 1979 (neap tide series) at station A
near the mouth of the Salmon River estuary.
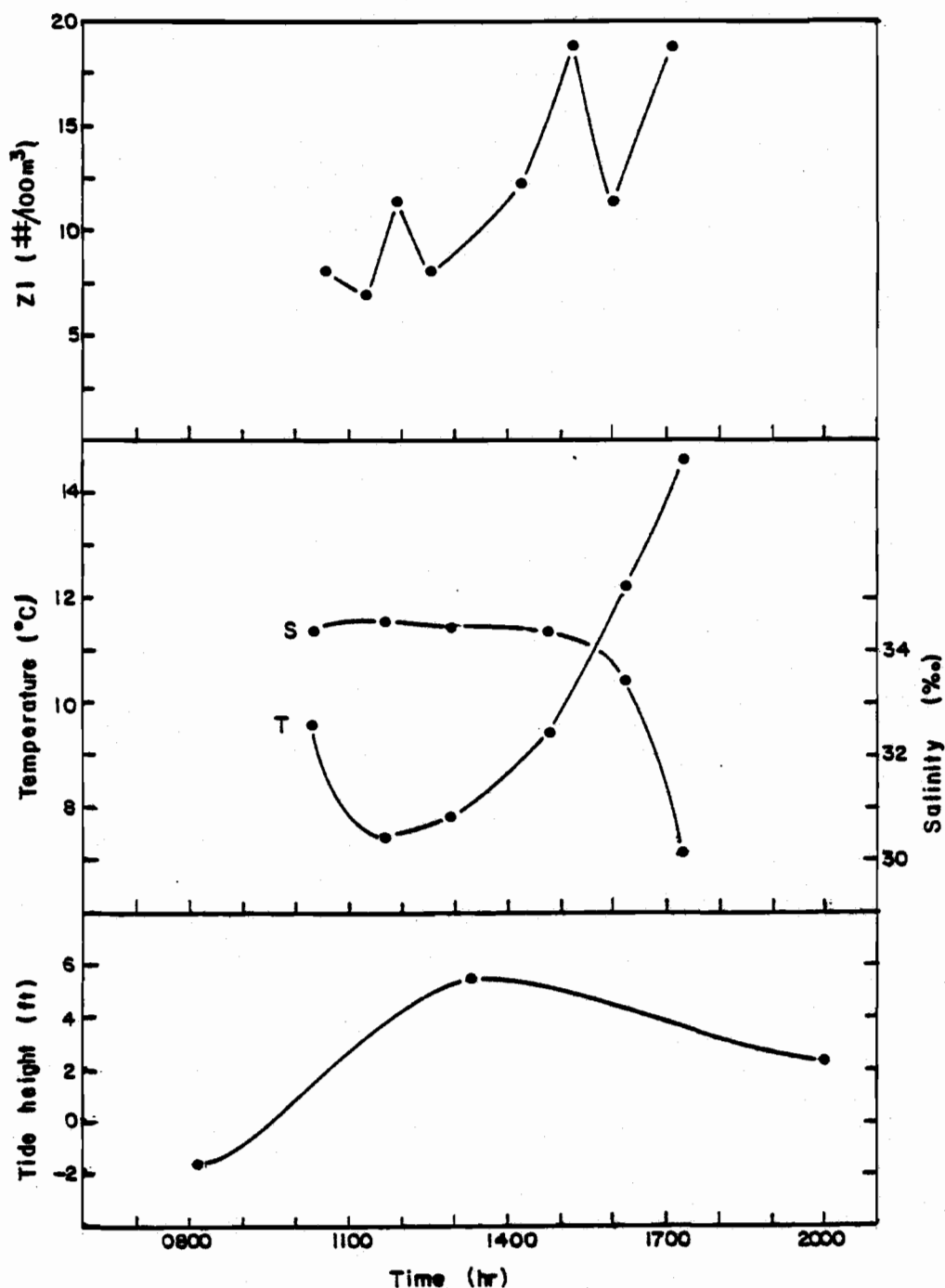
Figure 6: Variation in Z1 density, temperature, salinity, and tide height (estimated from tide table) through a tidal cycle on July 22, 1979 (spring tide series) at station A near the mouth of the Salmon River estuary.
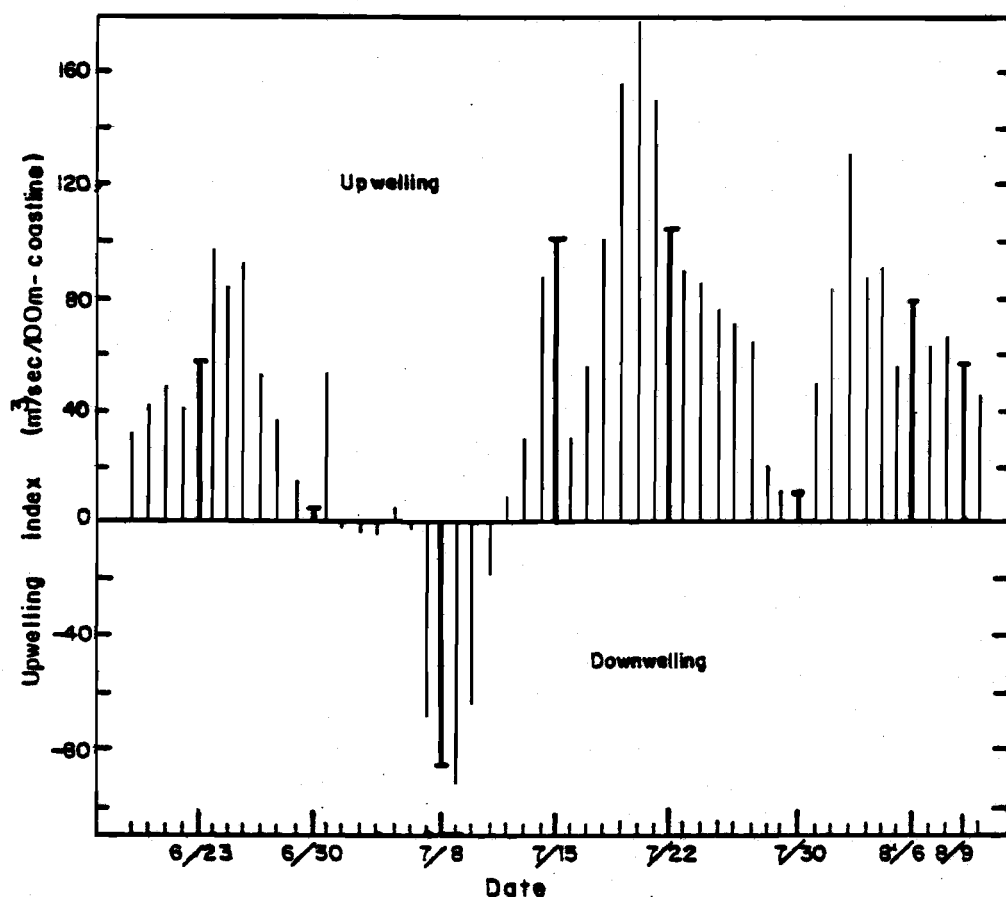
Figure 7: The state of upwelling off the central Oregon coast (45°N-125°W) during late June, July, and early August, 1979. Thick bars indicate zooplankton sampling dates.

relaxed upwelling, and one was during a downwelling event (Figure 7). These changes in the state of upwelling were evident in the temperature and salinity observations. As the magnitude of 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 (Table 4). The relation between upwelling and salinity for ebb flows was masked by the effect spring/neap tide series had on salinity. These results agree with those of Bourke (1969) and Duxbury (1979).

Table 5: Multiple regressions of temperature (TBAR) and salinity (SBAR) on tidal position (TPOS), upwelling (UPWG), and spring/neap tide series (SGNP) for ebb and flood flows separately. R^2 is the coefficient of multiple determination for the full model. All variables were standardized. Ebb n=26 and flood n=29.

	Ebb		Flood	
	Regression coefficients of the full model		Regression coefficients of the full model	
	TBAR	SBAR	TBAR	SBAR
TPOS	.5274**	-.5382***	-.0532	.4284**
UPWG	-.4890**	.0872	-.6051***	.4949***
SGNP	-.0117	.5320***	-.4465**	.1656
R^2	.5676	.9080	.5673	.5377

Table 5 gives an estimate of the relative influence the indirect-effect variables had on temperature and salinity for ebb and flood flows separately. Ninety-one percent of the variation in ebb salinity data can be accounted for by SGNP and TPOS, with UPWG having a minor effect. In the other three regressions, the indirect-effect variables only account for about one-half of the variation in the temperature and salinity data, implying that other factors were involved.

Biological Results

General

The ebb and flood tide mean proportions of stage I zoea out of all Callianassa californiensis larvae found in the samples for each sampling

Table 6: Ebb and flood tide means, variances, and coefficients of dispersion ($d=(s^2-\bar{x})/s^2$) for Z1 density ($\#/100m^3$).

	n	$\bar{x}$	s^2	d
Flood	32	63.7	16,027	0.996
Ebb	29	146.4	81,282	0.998
Total	61	103.0	47,951	0.998

date before August 9, 1979, was greater than or equal to 95%. Flood sample mean larval density increased through the last half of the sampling period, but only on August 9 did the proportion of first stage larvae decrease markedly and noticable numbers of later stage larvae begin to appear in the samples. Larvae older than stage I were more common in flood samples than ebb samples. Because of the large number of zero data points for stages II through megalope, the following data analyses will involve only stage I zoea (hereafter called Z1). The high proportion of Z1 in the samples shows that the sampling period included much of the larval release period at the Salmon River estuary in 1979.

Ebb sample mean Z1 density was greater than flood sample mean Z1 density over all sampling dates and the variance greatly exceeded the mean (Table 6). The proportion of nonrandom variance, represented by the d-statistic (Cassie, 1959b), is nearly one in all cases, implying that the influence of chance on Z1 density variation is negligible compared to the influence of other factors.

The changes in Z1 density through spring and neap tidal cycles for two representative sampling dates are given in Figures 5 and 6. A well-defined pattern is evident for the neap example, July 15, and an ill-defined pattern is evident for the spring example, July 22. On July 15, a high number of Z1 were present in the plankton early in the ebb, there-after decreasing steadily. The bulk of these larvae apparently did not return on the following flood tide. On July 22, the ebb following the flood was enriched with Z1 but the densities were very much less than those on July 15. These patterns for all samples will be analyzed in detail in the next two sections.

Ebb and flood tide differences in Z1 content

Samples immediately before and after slack tide are a first appro-ximation of ebb and flood tide differences in Z1 content. The water late in one flow and early in the next, reverse flow is most likely to have undergone the least change from one flow to the next. The larval densities of these ebb and flood pairs of samples have the greatest prob-ability of being similar.

Table 7: Z1 density ($\#/100m^3$) from samples immediately before and after slack tide on each sampling date.

	6/23	6/30	7/08	7/15	7/22	7/30	8/06	8/09
Slack	high	low	high	low	high	low	high	high
Flood	1.7	0.5	0.0	0.4	8.2	2.0	106.9	97.3
Ebb	20.9	9.4	34.6	27.8	11.9	16.6	90.2	185.3

There were appreciable changes in Z1 density after both high and low slack tides (Table 7). After high slack the ebb flow was enriched with Z1 and after low slack the flood flow was depleted of Z1. These patterns could be indicative of the changes occurring from one flow to the next during a complete tidal cycle. Except for August 9 samples (the six highest Z1 densities for flood samples), ebb sample densities were usually greater than flood sample densities (Figure 8).

Estimates of total larval numbers were greater for ebb flows than for flood flows on six of eight sampling dates (Table 8). Application of the Wilcoxon matched-pairs signed-rank test to the $\log_e$-transformed total number estimates resulted in the rejection of the null hypothesis
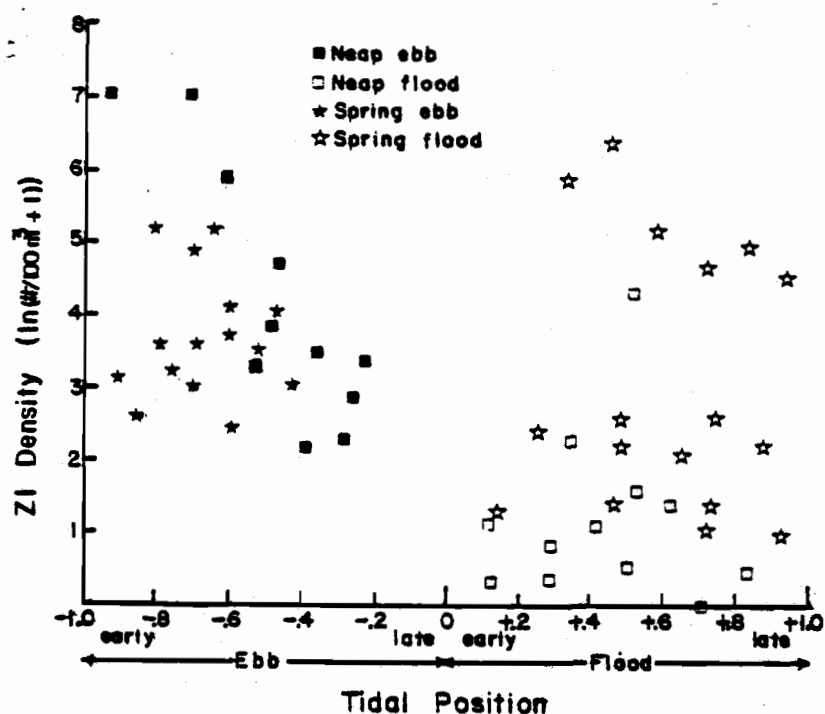
Figure 8: Scatterplot of Z1 density versus tidal position. Samples are classified as spring or neap tide series and ebb or flood flow.

Table 8: Tidal prism, mean Z1 density ($\#/100m^3$), and total number Z1 estimates for ebb and flood tides on each sampling date.

Date	Flow	Tidal prism ($X10^5\ m^3$)	Mean Z1 density ($\#/100m^3$)	Total # Z1	Log_e-total #
6/23	flood	9.02	5.2	46,904	10.76
	ebb	6.10	39.6	241,560	12.40
6/30	flood	8.38	0.5	4,190	8.34
	ebb	7.70	378.0	2,910,600	14.88
7/08	flood	8.80	3.6	31,680	10.36
	ebb	5.76	35.0	201,600	12.21
7/15	flood	11.22	2.1	23,786	10.08
	ebb	8.52	327.7	2,792,004	14.84
7/22	flood	8.60	8.7	14,820	9.60
	ebb	5.51	15.4	84,854	11.35
7/30	flood	8.59	28.7	246,533	12.42
	ebb	6.27	16.6	104,082	11.55
8/06	flood	9.25	124.7	1,153,475	13.96
	ebb	6.55	210.8	1,380,740	14.14
8/09	flood	12.86	250.2	3,217,572	14.98
	ebb	11.04	127.4	1,406,496	14.16

that the total number of Z1 ebbed equaled the total number of Z1 flooded at $\alpha = .05$ for a one-tailed test. Even though ebb volumes were approximately 73% of flood volumes, ebb densities were sufficiently large to result in more larvae being exported from the estuary than were imported.

Table 9: Total correlation coefficients of Z1 density
($\log_e(\#/100m^3 + 1)$) with the environmental
factors measured.

Flow	n		DAYS	SGNP	TPOS	TBAR	SBAR	UPWG
Flood	29	Z1	.80***	.48**	.06	-.75***	.45*	.19
Ebb	26	Z1	-.07	-.23	-.41*	-.15	.23	.22
Total	55	Z1	.37**	.18	-.46***	-.24*	.01	.10

Influences of environmental factors on Z1 density

Differences in patterns of the relations between Z1 density and the
environmental factors measured are evident in Figures 5 and 6 and Table
9. This justified separate analysis of the influence of environmental
factors on Z1 density for ebb and flood samples.

Flood tides

The indirect-effect variables with the highest total correlations
with Z1 density for flood samples are DAYS, SGNP, and UPWG (Table 9).
The variable TPOS had no apparent relation to Z1 density (Table 9 and
Z1-TPOS·SGNP,DAYS=-.06) and was dropped from further analyses of flood
samples. After taking the first and second order partial correlations
of Z1 density with DAYS, SGNP, and UPWG, it was apparent that the indi-
rect-effect variables most strongly associated with changes in flood
sample Z1 density were DAYS and SGNP (Table 10).

The strong correlation between Z1 and DAYS was not entirely due to
the effect DAYS had on temperature and salinity (Z1-DAYS·TBAR,SBAR=
.66***). Since temperature and salinity account for only 31%

Table 10: Zero, first, and second order partial correlation
coefficients of Z1 density ($\log_e(\#/100m^3 + 1)$) with
SGNP, UPWG, and DAYS for flood tide samples (n=29).

| Variables | Z1 density with: | | |
controlled for:	DAYS	SGNP	UPWG
none	.80***	.48**	.19
DAYS	NA	.55**	-.04
SGNP	.83***	NA	.27
UPWG	.80***	.51**	NA
DAYS,SGNP	NA	NA	.06
DAYS,UPWG	NA	.55**	NA
SGNP,UPWG	.81***	NA	NA

of the association between DAYS and Z1 density, this association reflec-
ted some other biological and/or physical process.

Changes in SGNP were much more strongly associated with changes in
temperature than in salinity (Tables 4 and 5). Temperature partial
correlation explained 68% of the association between Z1 and SGNP (Z1-
SGNP·TBAR=.28). There was a strong negative correlation between Z1 and
TBAR (Table 9 and Figure 9). From this analysis it is inferred that
spring tide series were characterized by lower temperatures than were
neap tide series and that this temperature decrease was associated with
an increase in Z1 density.

The spring tide periodicity to flood tide Z1 density might also
reflect a greater flux of larvae into the nearshore ocean during extreme
tidal ranges.

The multiple regression analysis of Z1 density variation (Table 11)
led to the same results as did the correlation analysis: DAYS, SGNP, and

Table 11: Partial regression coefficients and t-statistics for standardized environmental variables in the best multiple regression model of flood tide Z1 density ($\log_e(\#/100m^3 + 1)$). $R^2 = .80$ and n=29.

Variable	Regression coefficient	t-statistic
constant	2.23***	13.76
DAYS	1.07***	5.18
SGNP	0.45*	2.45
TBAR	-0.56*	-2.49
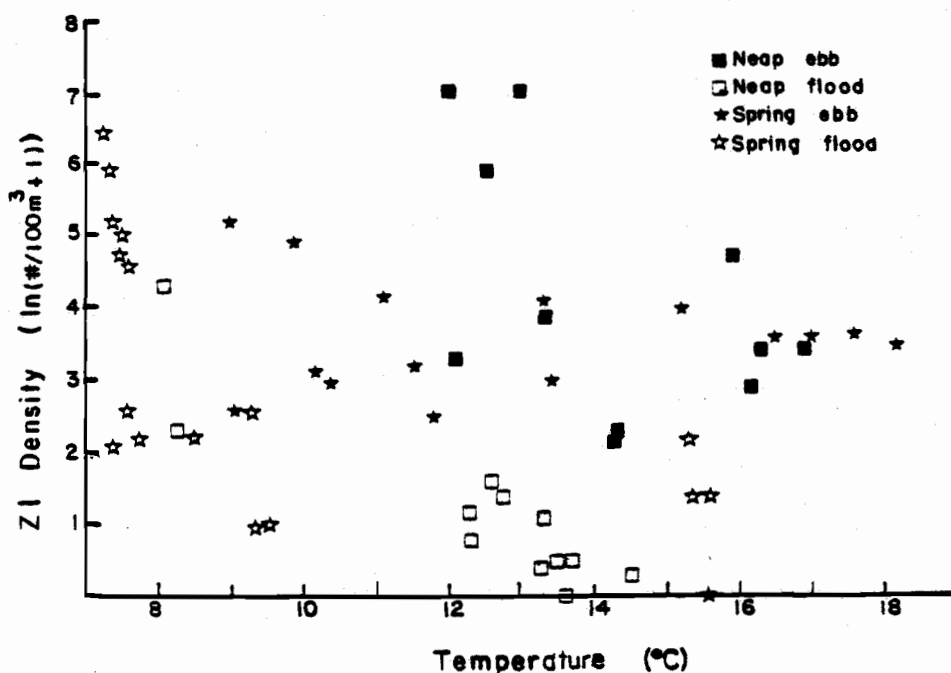
Figure 9: Scatterplot of Z1 density versus temperature. Samples are classified as spring or neap tide series and ebb or flood flow.

TBAR were found to be more important in explaining Z1 density changes than the other variables included in the analysis. The regression coefficients of the best multiple regression model of flood tide Z1 density showed that DAYS was relatively more important than SGNP and TBAR, which had comparable importances (Table 11).

Ebb tides

The indirect-effect variables with the highest total correlations with Z1 density for ebb samples were SGNP, TPOS, and UPWG (Table 9). DAYS had no apparent association with Z1 density and was not included in the subsequent analyses of ebb samples.

The partial correlations of Z1 density with SGNP, TPOS, and UPWG (Table 12) resulted in the rejection of UPWG as an important variable in explaining Z1 density variation. SGNP and TPOS each mask the moderate strength of the relation the other has with Z1 density (Table 12) due to the sampling bias mentioned earlier.

Table 12: Zero, first, and second order partial correlation coefficients of Z1 density ($\log_e(\#/100m^3 + 1)$) with SGNP, TPOS, and UPWG for ebb tide samples (n=26).

Variables controlled for:	Z1 density with:		
	SGNP	TPOS	UPWG
none	-.23	-.41*	.22
SGNP	NA	-.61**	.21
TPOS	-.54**	NA	.24
UPWG	-.22	-.42*	NA
SGNP,TPOS	NA	NA	.22
SGNP,UPWG	NA	-.62**	NA
TPOS,UPWG	-.53*	NA	NA

Table 13: Ebb tide sample total correlations between Z1 density $(\log_e(\#/100m^3 + 1))$, TBAR, SBAR, and TPOS for spring (above diagonal) and neap (below diagonal) tide series. Spring ebb n=15 and neap ebb n=11.

|	Z1	TBAR	SBAR	TPOS
Z1	1.00	-.06	.01	.01
TBAR	-.50**	1.00	-.86***	.52**
SBAR	.87***	-.66***	1.00	-.65***
TPOS	-.88***	.70***	-.95***	1.00
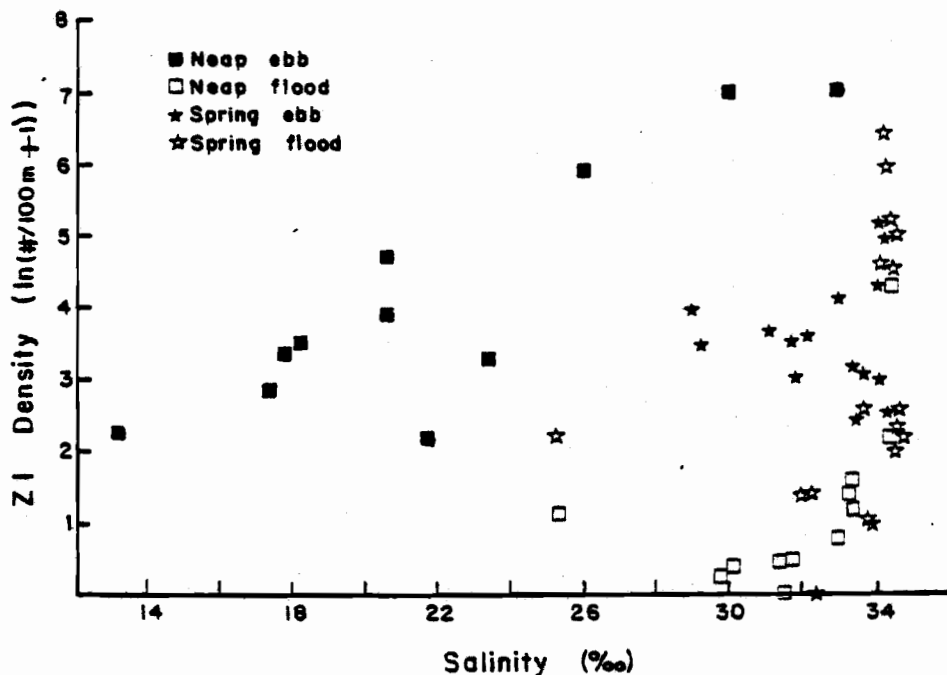
Figure 10: Scatterplot of Z1 density versus salinity. Samples are classified as spring or neap tide series and ebb or flood flow.

A comparison of the spring and neap tide relations between Z1, TPOS, TBAR, and SBAR is given in Table 13 and Figures 8, 9, and 10. As TPOS increased (early to late ebb) during a neap tide series, temperature increased and salinity decreased, in correlation with a decrease in Z1 density. Although the environmental variables for spring tide samples followed the same pattern as those for neap samples, Z1 densities did not.

The negative correlation between SGNP and Z1 density for ebb samples implies a neap tide periodicity to larval release in Callianassa californiensis. Possible mechanisms for such periodicity might incorporate changes in temperature and/or salinity between spring and neap tide series. Other environmental factors that might trigger larval release, such as photoperiod or pressure, were not studied. After correcting for the sampling bias, SGNP was still strongly correlated with SBAR (SGNP-SBAR·TPOS=.83***). However, SBAR was positively correlated with Z1 density which was itself negatively correlated with SGNP. This implies that the observed neap tide periodicity of larval release was not associated with salinity differences between the two tide series. Apparently neither was temperature because, after accounting for the sampling bias, SGNP and TBAR were not significantly related (SGNP-TBAR· TPOS=.04) for ebb samples.

The ebb tide correlation of Z1 density with TPOS (r=-.41**) indicates that early ebb samples contained greater Z1 densities than late ebb samples. Partial correlations show that neither TBAR, SBAR, and SGNP alone account for the Z1-TPOS relation (Z1-TPOS·TBAR=-.39*; Z1-TPOS·SBAR=-.40*; and Z1-TPOS·SGNP=-.61**). However, SGNP and SBAR

Table 14: Partial regression coefficients and t-statistics for standardized environmental variables in the best multiple regression model of ebb tide Z1 density $(\log_e(\#/100m^3 + 1))$. $R^2 = .58$ and n=26.

Variable	Regression coefficient	t-statistic
constant	3.85***	22.31
SGNP	-1.68***	-5.30
SBAR	1.81***	5.08
TBAR	0.31	1.45

together account for the Z1-TPOS relation (Z1-TPOS·SGNP,SBAR=-.01). Ebb Z1 densities were highest in the high salinity water early in the ebb during neap tide series. Therefore the correlation analysis shows SGNP and SBAR to be relatively more important in explaining Z1 density variation than the other variables included in the analysis.

Stepwise multiple regression of ebb tide Z1 density results in SGNP and SBAR as the first two variables to enter and the last two to leave the model (Table 14). The R^2 value of this model is 54%. The greatest increase in R^2 made by adding one more variable was made by adding TBAR, producing an R^2 value of 58%. Addition of more variables after this did not increase R^2 significantly. Therefore, selection of the best multiple regression model of ebb Z1 density variation (Table 14) results in SGNP and SBAR being most important, followed by TBAR, in explaining such variation.

IV. DISCUSSION

The 1979 _Callianassa californiensis_ larval release period lasted until late July at the Salmon River estuary. Release was apparently not synchronized within the population nor were there an identifiable number of broods. Temperature and salinity were not correlated with the observed neap tide periodicity of larval release. This periodicity could have been related to the longer duration of water coverage over the tide flats during neap tides than during spring tides, which made more time available for release. Environmental cues associated with larval release remain unknown.

Once released into the plankton, the larvae were exported to the nearshore ocean by the tidal exchange of estuarine and nearshore waters. Of the total number of stage I _Callianassa_ zoea passing the sampling station on all sampling dates except August 9, 88% passed out on the ebb tide. This exportation of Z1 from the estuary was documented by the analysis of ebb/flood Z1 contents and was also indicated by patterns found in the ebb tide Z1 density data.

The most important variables in explaining ebb tide Z1 density variation, spring/neap tide series and salinity, were associated with greater densities of larvae early in the ebb than later. Larvae released early in the ebb are most likely to be exported from the estuary. The timing of release is also reflected in the lack of pattern for spring ebb samples (Figure 6) as opposed to the well-defined pattern for neap ebb samples (Figure 5). This difference was probably caused by the difference in tide heights at the low slack sampled for the two tide series

(spring high-low average 1.9 ft; neap low-low average 0.2 ft). The spring ebb salinities sampled were never below 28 ^{o}/oo, but the neap ebb salinities went as low as 13 ^{o}/oo (Figure 10). The wide range of neap salinities produced a pattern in the change of Z1 density. The positive relation between Z1 density and salinity indicates that the larvae were most prevalent in estuarine waters that are a tongue of the nearshore ocean. These waters are greatly affected by tidal exchange and, hence, it is expected that Z1 released into these waters would be exported to the nearshore ocean.

The data obtained in this study support the conclusion that, given a flushing time of a few tidal cycles and a planktonic larval life of six to eight weeks, all Callianassa californiensis larvae released from the population at the Salmon River must be exported from the estuary to the nearshore ocean. No retention mechanism was discovered in this study.

The assumption that there is no retention mechanism is supported by an analysis of possible locations of larval sinks within the estuary. Tidal marsh creeks are not a significant sink because diking has reduced their surface area to a negligible amount and the remaining creeks tend to drain almost completely at ebb tide. There are no eddies or other hydrographic features present of the magnitude required to retain sufficient numbers of larvae for recruitment to the adult population. The depression near the Hwy. 101 bridge was sampled at high tide on July 15, 1979, and found to contain few Callianassa larvae.

The residual water at low tide was not sampled during the summer of 1979 because priority was placed on obtaining consecutive samples through a tidal cycle at station A where most of the water in the estuary

passed. However, it is improbable that large numbers of larvae were concentrated in the residual water because:

1) There was no build-up of Z1 in the ebb samples through the sampling period. This would be expected if larvae were retained release continued.

2) No later stage larvae were found in ebb samples until late in the sampling period when they were also present in flood samples. Furthermore, flood samples, not ebb samples, were the first to contain noticable numbers of stage II zoeal larvae.

3) Water passing the mouth of the estuary late in the ebb had the physical and biological characteristics of the upper estuary. It was relatively warm, of low salinity, and contained freshwater species of zooplankton. In qualitative samples taken along a longitudinal transect of the estuary on August 5, 1978, Callianassa larvae were not found in this type of water.

4) The larvae could not swim against the ebb current. Mileikovsky (1973) reports that decapod crustacean larvae generally swim vertically at speeds of 23.3 to 117 cm/min. These, if used as estimates of horizontal swimming speed, are far less than the 1.0 to 2.0 m/sec velocities of tidal currents at the Salmon River estuary.

Severe scouring of the bottom by tidal currents, especially in the main channel, would preclude temporary settlement of the larvae there during ebb tides. Sand waves averaging 1.5 m in length and .25 m in height are prominent features of the main channel bottom. Also, crus-

tacean premetamorphic larval stages are not known to burrow in bottom sediments and Callianassa zoeal larvae are not morphologically adapted for such behavior.

Since the physical characteristics of the Salmon River estuary appear to dominate any Callianassa larval behavior that would lead to retention, nearly all C. californiensis larvae released there must be lost to the nearshore ocean by tidal exchange. Therefore the nearshore zone must be the source of recruits to the adult population.

If the nearshore ocean is the source of recruits, then this population faces similar problems in recruitment to those faced by open coast intertidal populations with planktonic larvae. The main recruitment problem is for final stage larvae to be near an adult habitat when settlement time arrives. In some species, larvae swept seaward metamorphose into post-larvae which can swim back toward land, as do rock-lobster larvae off Australia (Phillips, et al., 1975) or larvae may be carried back toward land by a deeper onshore flow, as is a coastal copepod, Calanus marshallae (Peterson, 1980). Larvae may also be retained in nearshore waters throughout the planktonic period, as is probably the case with C. californiensis. Offshore transport by advection could be avoided by an interaction between the behavior of the larvae in controlling their vertical position in the water column and nearshore circulation patterns.

Although planktonic larvae can be widely dispersed horizontally, they may be retained in the nearshore ocean by systems of eddies and countercurrents (Johnson, 1939; Knudsen, 1960; Chittleborough and Thomas, 1969; and Efford, 1970). Coe (1953) attributed the sporadic settling of Donax gouldi on Southern California beaches to "vagaries" of oceanic

currents. Efford (1970) hypothesized that Emerita analoga larvae, which
spend approximately four months in the plankton, are retained relatively
near the adult population from which they came by travelling roughly
equivalent distances in currents and countercurrents. Efford postulated
that larvae were transferred from one current to another by eddies form-
ed between the opposing flows. This hypothesis would be difficult to
test since, at this time, there is no known method available to effi-
ciently tag sufficient numbers of larvae to track their movements.
Lough (1975) made stepwise oblique plankton hauls from the bottom to the
surface off the Oregon coast and found the majority of the larvae of
intertidal crab species at the two stations closest to land, one and
three miles away. He attributed nearshore retention to an onshore com-
ponent of the surface current and to females avoiding the release of the ·
bulk of their larvae during the upwelling season. All of these studies
have lacked detailed information on the distribution of larvae with
depth and on the coastal circulation.

Recent advances in the understanding of nearshore circulation off
the Oregon coast during upwelling provide the basis for an hypothesis
about a mechanism for nearshore retention of the larvae of intertidal
invertebrates released into these waters. Peterson, et al. (1979) sam-
pled zooplankton at discrete depths along transects perpendicular to the
Oregon coast during summer periods of active and relaxed upwelling.
They investigated how the highest concentration of zooplankton was
maintained within the region of most active upwelling, that within 15 km
of shore. They concluded that the Ekman layer of offshore surface tran-
sport is probably no more than a few meters thick and that plankton

avoiding this layer would not be transported offshore. This nearshore retention mechanism could also apply to intertidal invertebrate planktonic larvae, such as those of Callianassa californiensis.

The analysis of environmental effects on flood tide Z1 densities provides data supporting such an hypothesis. The following discussion assumes that flood samples are representative of the nearshore ocean and applies only to stage I Callianassa zoea.

The strong correlation between DAYS and Z1 density probably represents a build-up of Callianassa larval density in the nearshore area during the sampling period. Although highest flood Z1 densities occurred on the last two sampling dates, the trend is still apparent without these data (Z1-DAYS r=.51**, n=20). This apparent build-up could reflect an increase in the total number of brooding females releasing larvae as the season progressed. The density of Z1 in the incoming nearshore oceanic water early in August, 1979 increased to levels comparable to those in water leaving the estuary earlier in the larval release period. This nearshore density increase, despite dilution and mortality, signifies that Callianassa larvae were entering the nearshore ocean in prodigeous quantities from estuaries along the Oregon coast.

This observed increase in larval density occurred despite upwelling. There were episodes of upwelling throughout the sampling period and there was active upwelling on the last two sampling dates (Figure 7). Apparently Callianassa californiensis larvae were not significantly transported offshore by upwelling circulation. If larvae were transported by upwelling away from the shore where they would otherwise be present, one would expect a negative correlation between UPWG and Z1, given

all other factors held constant; such was not the case. The first order partial correlation of Z1 and DAYS controlling for UPWG is unchanged from the total correlation of Z1 and DAYS, but the first order partial correlation of Z1 and UPWG goes from +.26 to -.04 when DAYS is controlled. These correlations imply that there was a build-up of Z1 in the nearshore region despite upwelling. This supports the hypothesis that C. californiensis larvae are retained in the nearshore ocean during upwelling because they avoid the upper few meters of the water column.

Water enters estuaries from greater nearshore depths during spring tide series than during neap tide series. This was shown in this study by the positive correlation between SBAR and SGNP and the negative correlation between TBAR and SGNP. Surface waters are warmer and less saline than deeper waters. In both ebb and flood samples, Z1 density was positively associated with salinity and negatively associated with temperature. However, Z1 densities for flood samples were significantly correlated with temperature and not salinity, implying that the larvae may be densest in water at least a few meters below the surface. The spring tide periodicity to flood tide Z1 density further substantiates the formation of the hypothesis that Callianassa larvae, in at least stage I zoea, can control their position in the water column. This hypothesis could be tested by sampling for Callianassa larvae at discrete depths along transects perpendicular to the coastline.

I have indirectly shown that the nearshore ocean is the source of recruits to the Callianassa population at the Salmon River estuary. A study designed to directly confirm that this is the case should use the sampling design of this study, but also include night sampling, to

quantify the input of stage V and megalope from the nearshore ocean to the estuary. The net input of these larvae from the nearshore to the estuary would be assumed to represent the number of potential recruits for that tidal cycle. This assumption should be confirmed by benthic sampling in the adult habitat for newly settled individuals. Such a study would provide direct evidence that the nearshore ocean is the source of recruits to the Callianassa population at the Salmon River estuary.

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APPENDIX

V. APPENDIX: Volume Estimation

Estimation of the volume ebbed and flooded for each tidal flow sampled in this study required knowledge of the surface areas at slack tides and tidal height changes. Since no Salmon River tide height corrections were available from tide tables referenced to Yaquina Bay, Oregon, the correction used was an average of those given for the Siletz and Nestucca River mouths (high water -1.1 ft and low water -0.3 ft). These corrections were applied to obtain tide heights for the slack tides on each of the sampling dates of this study. Estimates of mean tide heights were obtained by applying the difference between the high and low water corrections (-0.8 ft) to the estimates of MHW and MHHW for Yaquina Bay at the Marine Science Center dock (Oregon Division of State Lands, 1973). Because MLLW is zero by definition, the low tide estimates, MLW and MLLW, were left unchanged. Therefore, the mean tide heights used in this study were: MLLW=0.0 ft; MLW=1.54 ft; MHW=6.82 ft; MHHW=7.58 ft. This produced the average tidal range estimate of 5.28 ft presented in the section of this thesis on the general characteristics of the study site. This estimate differs from that given by Percy, et al. (1974), 5.8 ft. I do not know how they obtained their estimate.

The surface area of the estuary at a given tide height was predicted from a linear regression of surface area on tide height (Equation 1). The raw data in this regression were the tide heights and surface areas at MHW and MLW. The y-intercept of Equation 1 is assumed to be the surface area at MLLW.

$$\text{surface area } (km^2) = 0.171 + (0.317)(\text{tide height } (m)) \qquad \text{Eq. 1}$$

The volumes ebbed or flooded were derived using Equation 2. The volumes on each side of this equation represent the volume ebbed or flooded, not the total volume within the estuary at a particular tide height. All volumes are $X\ 10^5\ m^3$.

$$\text{volume} = V3 = \text{volume below MLLW} + \text{volume above MLLW} \qquad \text{Eq. 2}$$
$$= V1 + V2,$$

where,

$$V1 = (\text{surface area at MLLW})(H1)(X\ 10^6)\text{ and}$$

$$V2 = (A1)(H2)(X\ 10^6) + \tfrac{1}{2}(A2 - A1)(H2)(X\ 10^6),$$

where,

- $A1\ (km^2)$ = surface area at low tide or MLLW, which ever tide height was greatest,

- $A2\ (km^2)$ = surface area at high tide,

- $H1\ (m)$ = tide height at MLLW minus tide height at low slack for low tides below MLLW, otherwise H1=0,

- $H2\ (m)$ = tide height at high slack minus tide height at low slack or MLLW, whichever low tide height was greatest.

This method produced an estimate of $9.3\ X\ 10^5\ m^3$ for the volume between MHW and MLW which compares favorably with the estimate of $9.5\ X\ 10^5\ m^3$ given by Askren, et al. (1976). It should be recognized that the volume estimates used are crude. The resulting calculated volumes are given in Table 1 of this Appendix.

The only bathymetric map of the Salmon River estuary available was obtained from the Army Corps of Engineers in Portland, Oregon. This map, made in 1939, was used to produce an estimate of the volume of the lower 2.5 km of the estuary. This estimate was two orders of magnitude lower than that given by Askren, et el. (1976). This map was judged to be too old for use in volume estimation in 1979.

Table 1: Estimates of ebbed and flooded volumes at
the Salmon River estuary for slack tide heights
during the sampling period, June-August, 1979.
See text for explanation of symbols.

Date	Low tide ht.	A1	High tide ht.	A2	H1	H2	V1	V2	V3
6/23/79	-0.49	0.17	1.80	0.74	0.49	1.80	0.83	8.19	9.02
	0.73	0.40	1.80	0.74	0.00	1.07	0.00	6.10	6.10
6/30/79	0.15	0.22	1.77	0.73	0.00	1.62	0.00	7.70	7.70
	0.15	0.22	1.86	0.76	0.00	1.71	0.00	8.38	8.38
7/08/79	-0.49	0.17	1.77	0.73	0.49	1.77	0.83	7.97	8.80
	0.76	0.41	1.77	0.73	0.00	1.01	0.00	5.76	5.76
7/15/79	-0.06	0.17	1.83	0.75	0.06	1.83	0.10	8.42	8.52
	-0.06	0.17	2.16	0.86	0.06	2.16	0.10	11.12	11.22
7/22/79	-0.37	0.17	1.77	0.73	0.37	1.77	0.63	7.97	8.60
	0.82	0.43	1.77	0.73	0.00	0.95	0.00	5.51	5.51
7/30/79	0.37	0.29	1.65	0.69	0.00	1.28	0.00	6.27	6.27
	0.37	0.29	1.95	0.79	0.00	1.58	0.00	8.59	8.59
8/06/79	-0.49	0.17	1.83	0.75	0.49	1.83	0.83	8.42	9.25
	0.67	0.38	1.83	0.75	0.00	1.16	0.00	6.55	6.55
8/09/79	-0.67	0.17	2.23	0.88	0.67	2.23	1.15	11.71	12.86
	0.31	0.27	2.23	0.88	0.00	1.92	0.00	11.04	11.04