

RECRUITMENT OF LARVAE OF THE GHOST SHRIMP, CALLIANASSA CALIFORNIENSIS  
(CRUSTACEA, DECAPODA), IN THE SOUTH SLOUGH ESTUARY, OREGON

by

GLICERIA ESTANDIAN PIMENTEL

A THESIS

Presented to the Department of Biology  
and the Graduate School of the University of Oregon  
in partial fulfillment of the requirements  
for the degree of  
Master of Science


August 1986

APPROVED:

Paul P. Rudy  
Dr. Paul P. Rudy

An Abstract of the Thesis of  
Gliceria Estandian Pimentel for the degree of Master of Science  
in the Department of Biology to be taken August 1986  
Title: RECRUITMENT OF LARVAE OF THE GHOST SHRIMP, CALLIANASSA  
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ESTUARY, OREGON

Approved: \_\_\_\_\_

  
Dr. Paul P. Rudy

Weekly zooplankton samples were collected at mid-tide at the mouth of the South Slough Estuary on the southern Oregon coast to study the recruitment of Callianassa californiensis larvae into the adult population in the estuary. The results show that early zoeal stages are transported into and from the estuary with the tides but significantly more C. californiensis first-stage zoea were exported from the estuary during ebb tides than were imported during flood tides. Retention of larvae is apparently not a possible mechanism of recruitment because of the physical characteristics of the South Slough Estuary.

The effects of five environmental factors on larval density variation were examined by correlation and multiple regression. The results support the hypothesis that Callianassa californiensis larvae are exported to the nearshore ocean where they develop into later stages and that these later stages are retained nearshore where they are

potentially available for transport back to the estuaries along the coast.

## VITA

NAME OF AUTHOR: Gliceria Estandian Pimentel

PLACE OF BIRTH: Mountain Province, Philippines

DATE OF BIRTH: May 20, 1958

## GRADUATE AND UNDERGRADUATE SCHOOLS ATTENDED:

University of Oregon  
University of the Philippines

## DEGREES AWARDED:

Master of Science, 1986, University of Oregon  
Bachelor of Science, 1978, University of the Philippines

## PROFESSIONAL EXPERIENCE:

Instructor I, Department of Zoology, University of the  
Philippines, Diliman, Quezon City, 1981-84

Research Associate, Biological Research Department, National  
Institute of Science and Technology, Manila, Philippines,  
1978-79

## AWARDS AND HONORS:

National Science Development Board Undergraduate Scholarship,  
1974-78

University of the Philippines-National Science and Technology  
Authority Graduate Scientific Manpower Training Scholarship,  
1979-81

Delta Kappa Gamma World Fellowship, 1984-86

Fulbright-Hays Mutual Exchange Scholarship, 1984-86

## ACKNOWLEDGMENTS

I would like to express my deep gratitude to Dr. Paul Rudy and to Dr. James Carlton for their insightful suggestions and assistance in the preparation of this manuscript. My sincere appreciation is given to Dr. Martin Posey for his input especially in the early phase of this research, and to Dr. Jennifer Purcell for lending me a Bogorov tray which made my life in the laboratory a lot easier. Special thanks are due to my good friend Sonia Javier who extended invaluable assistance in all phases of this research, and to my family for the encouragement and moral support they gave me throughout the duration of my studies here in the United States. I also thank the O.I.M.B. staff for their help in various ways. This research was supported in part by a Fulbright-Hays Mutual Exchange Scholarship Thesis Grant.

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## INTRODUCTION

### Background Information

Recruitment into a benthic estuarine population requires that larvae or juveniles remain within the estuary or return to it (Sandifer, 1973, 1975). Depending upon the species, adult behavior may either enhance retention of larvae in the estuary or export of larvae from the estuary (Cronin and Forward, 1982; Strathmann, 1982; Sulkin and Van Heukelem, 1982). The behavior of larvae with a long planktonic phase may also influence their dispersal. For example, strong swimmers such as crustacean larvae can control their vertical position in the water column, and thus influence horizontal transport (Sandifer, 1973, 1975; Day and McEdward, 1983). Laboratory experiments have demonstrated that larvae respond to environmental factors such as the salinity of ebb and flood waters (Hughes, 1969; Latz and Forward, 1977), temperature (Ott and Forward, 1976), light (Thorson, 1964; Rebach, 1983), and gravity and hydrostatic pressure (Carriker, 1951; Hardy and Bainbridge, 1951; Knight-Jones and Qasim, 1955; Sulkin, 1973; Wheeler and Epifanio, 1978). Responses include changes in swimming velocity (e.g. barokinesis) and directional swimming (e.g. phototaxis and geotaxis).

Studies on the dispersal of estuarine larvae along the continental shelf and nearshore waters have been mostly done in boreal and temperate seas (Scheltema, 1975). The fate of larvae transported

offshore is unclear. Johnson (1939) showed that large numbers of sand crab, Emerita analoga, zoea were carried as far as 125 miles off the coast of southern California where they are thought to perish. Efford (1970), on the other hand, observed new recruits on beaches each year, and concluded that E. analoga were returned to the coast by eddies formed between longshore currents and their counter-currents. Knudsen (1960) and Lough (1976) postulated that a hydrographic mechanism must exist to explain coastal retention of larvae. Peterson et al. (1979) showed that copepod populations along the Oregon coast are maintained by upwelling events, and Boicourt (1982) examined circulation processes in the nearshore area to explain larval transport in two estuaries in the Atlantic coast.

The distribution of larvae is, therefore, controlled by both active behavior and passive transport mechanisms (Norcross and Shaw, 1984). In estuaries, tidal and riverine input are the primary factors that create the vertical gradient in net directional transport. Tidal currents in estuaries influence vertical migration, especially where planktonic organisms have to maintain a critical density in areas subject to strong dispersive tidal flows (Grindley, 1964; Woodmansee, 1966). Bousfield (1955) showed that the vertical distribution of barnacle larvae influenced their horizontal transport within the estuary. Based on their distributional differences with passively transported particles, Wood and Hargis (1971) concluded that oyster larvae could actively control their vertical distribution during a tidal cycle. This conclusion has been challenged. Based on field and

laboratory studies on barnacle cyprids, deWolf (1973) claimed that passive transport by currents can account for the distribution of larvae.

The physical characteristics of estuaries and their applications to biological phenomena were considered by Pritchard (1951) and Burt and McAllister (1959) but Nelson (1917) first proposed the idea of synchrony between selective swimming and tidal cycles, based upon his observations on oyster larvae. Ketchum (1954) and Ayers (1956) have shown the loss of larvae by mortality and by transport out of a well-mixed estuary. Ayers suggested that in estuaries with a high flushing rate, there is no possibility for endemic larvae to complete development and that settlement is solely from mature larvae carried in with the flooding tide. However, Christy and Stancyk (1982) showed that in a well-mixed estuary in the Atlantic coast, few larval forms were significantly imported or exported in spite of the fact that more water was exported from the estuary than was imported at all tidal cycles. Moreover, large exports of water were not necessary to effect transport of larvae, and imports or zero fluxes occurred despite water exports. Only crab zoea were significantly transported out of the estuary.

For estuarine decapod crustacean populations, there appear to be two mechanisms of recruitment of young: (1) recruitment by retention of larvae, and (2) recruitment by immigration of juveniles and adults. Different species in an estuary exhibit various combinations of these two mechanisms, and the tendency of a species to exhibit one more than the other is influenced primarily by the degree of its dependence

upon the estuary (Sandifer, 1975).

This study is an investigation of the mechanism of recruitment of Callinassa californiensis larvae into adult populations in estuaries. The ghost shrimp C. californiensis Dana, 1854, is an estuarine, burrowing thalassinid decapod crustacean found in marine sloughs and bays from Alaska to Baja California (Stevens, 1928; Haig and Abbott, 1980; Bird, 1982; Rudy and Rudy, 1983; Posey, 1985). It is very common in Oregon and Washington where it occupies large expanses of estuaries. In Oregon estuaries, Callinassa is the most abundant large macro-infaunal species in the most extensive intertidal habitat: +5 to +3 ft above MLLW (Gonor et al., 1979).

In Oregon, the principal breeding period of Callinassa is late spring and early summer, depending on when and how fast the water warms (Tucker-McCrow, 1972). Ovigerous females are reported to be present year round in California (MacGinitie, 1935). In Oregon, ovigerous females are most abundant in June and July, and by mid-August become scarce again; three or four broods are produced at about six-week intervals. Females brood larvae to the first zoeal stage. Hatching is probably triggered by warmer temperatures of an ebbing tide (Tucker-McCrow, 1972), suggesting that the tidal cycle may have a significant effect on the timing of larval release. Planktonic larval life consists of five zoeal stages and one megalops stage, and lasts about six to eight weeks (Tucker-McCrow, 1972; Johnson and Gonor, 1982). Johnson and Gonor (1982) indirectly showed that the nearshore ocean is the source of recruits for the Callinassa population in the Salmon

River Estuary in Oregon. Their conclusions were based largely upon the density differences in stage-one zoea during ebb and flood tides and upon the fact that later stages were first observed during an incoming tide. Only daytime samples were collected by Johnson and Gonor.

#### Study Area

The study area is the South Slough Estuary, in Coos Bay, Oregon. The Slough is 8.1 km long with an average width of 0.66 kilometers. It joins the Coos Bay Estuary 1.6 km above the mouth of the Bay, and is therefore part of the marine subsystem of the Coos Bay Estuary (Figure 1).

The Slough is thus relatively long compared to its width, which suggests that there may be little lateral variation in salinity. Moreover, it is shallow, having an average depth of 2.2 m (Boyce, 1977). These factors, combined with high energy resulting from wave surge and tidal currents within the marine subsystem of the Coos Bay Estuary, suggest that little vertical stratification in salinity may occur here. Freshwater runoff is small (Harris et al., 1979) so longitudinal gradients may also be small. Moreover, the flow ratio, that is the ratio of the volume of the river flow per tidal cycle to the tidal prism, ranges from 0.0009 in August to 0.0313 in February (see Appendix B). South Slough therefore is a well-mixed estuary according to the classification of Burt and MacAlister (1959).

The surface area of the Slough south of the bridge at Charleston is 5.3 sq km, and approximately 75.4 sq km of land drain into it

(Oregon Department of Transportation, 1978). Drainage is accomplished chiefly by means of small streams. Average annual freshwater inflow is estimated to be  $2.8 \text{ m}^3/\text{sec}$ , ranging from monthly average values of  $0.2 \text{ m}^3/\text{sec}$  in August to  $6.6 \text{ m}^3/\text{sec}$  in February. Extreme values of monthly runoff are  $0.03 \text{ m}^3/\text{sec}$  and  $12.6 \text{ m}^3/\text{sec}$ . Thus, except under extreme conditions, the effect of freshwater runoff directly into the South Slough may be relatively small.

Tides are of the mixed semi-diurnal type, having two high and two low waters of unequal height in a lunar day. Heights normally range from  $-0.6 \text{ m}$  to  $2.8 \text{ m}$  relative to mean lower low water, and the mean tide range is  $1.7 \text{ m}$  (Oregon Department of Transportation, 1983). Harris et al. (1979) used three independent techniques (see Appendix B) for the calculation of the volume of the tidal prism ( $V_p$ ). All three estimates were in good agreement with each other; and based on the average tide range of  $1.7 \text{ m}$  a representative value is,  $V_p = 9.4 \times 10^6 \text{ m}^3$ . This results in an exchange ratio of 0.48; thus, on an average tide range of  $1.7 \text{ m}$ , 48% of the Slough is discharged on the ebb tide.

The single zooplankton sampling station throughout the study is at the South Slough bridge on Highway 240 (Cape Arago Highway), crossing the narrow mouth of the Slough at Charleston (Figure 1). All of the tide water going into and out of the Slough must pass through this narrow channel below the bridge. The narrowness of this channel causes higher tidal velocities than in other parts of the Slough, reaching  $0.9 \text{ m}/\text{sec}$  during the strongest flow of flood tide, and scour of the bottom occurs here (Oregon Department of Transportation, 1983).



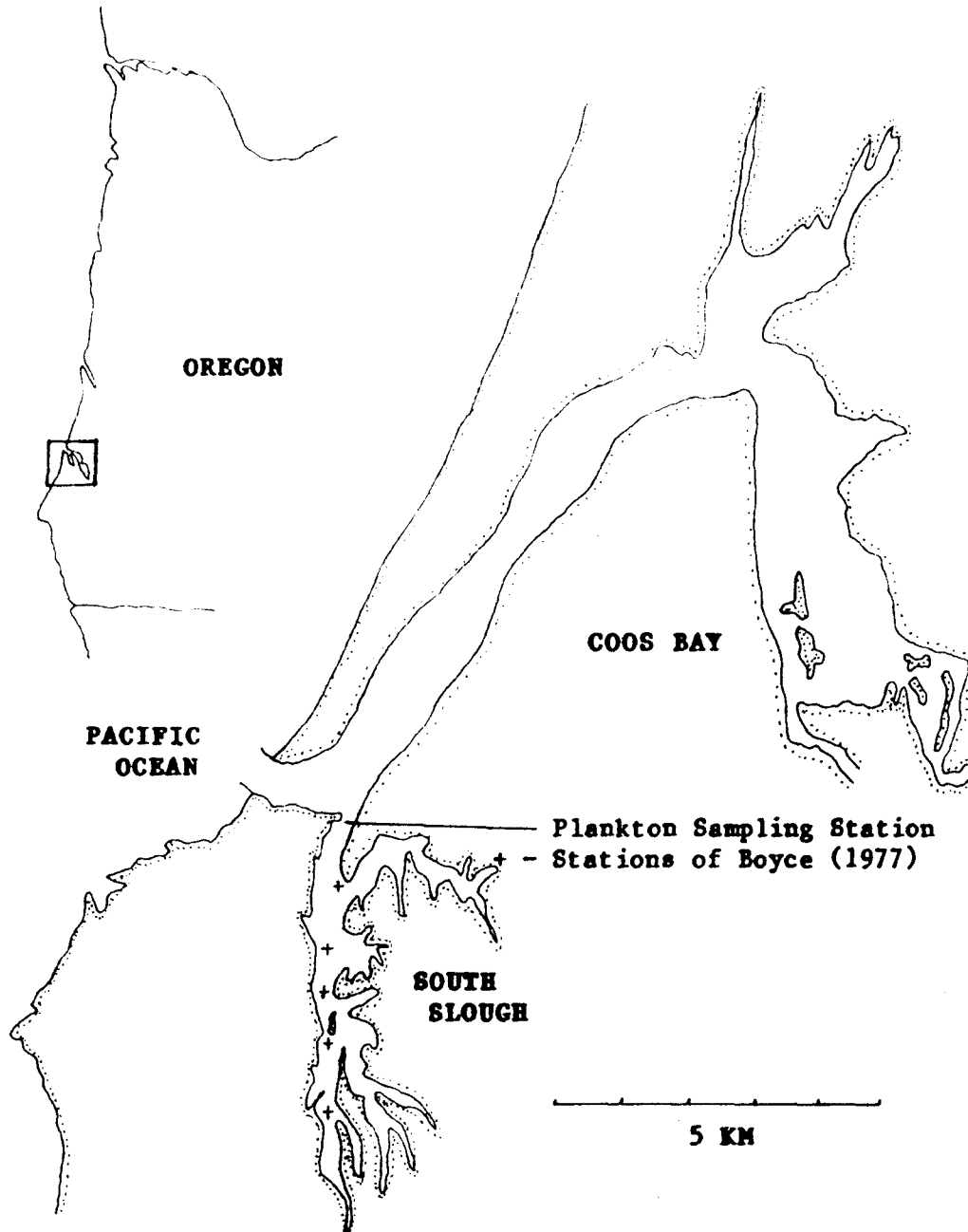


Figure 1. Map of the study site.

## METHODS

### Zooplankton Sampling

During the Callinassa larval release period (late spring to early summer), weekly zooplankton samples were collected at mid-tide (between high water and low water, or vice versa) during one daily tidal cycle. At each mid-tide, three quantitative samples were taken consecutively by allowing the tidal current to pass through a conical nylon 0.5 m ring net (0.5 mm mesh) suspended from the bridge. The semi-diurnal tides characteristic of the area, therefore, resulted to the collection of 12 samples per week, 6 flood, and 6 ebb samples. Mid-tides were sampled because the water velocities were highest during these times. This enabled extensive and non-selective sampling since avoidance of the net by swimming larvae will be reduced or eliminated by the swift tidal current. A preliminary zooplankton sampling at the fixed station on July 5, 1985 showed that early and late in the ebb or flood tide, water currents are too slow to enable unbiased plankton sampling.

To determine the volume of water filtered, a calibrated General Oceanics flow meter with a standard rotor was mounted off-center in the net mouth. The three mid-tide samples were collected at three different depths in the water column: 0.5 - 1.5 (surface), 2.0 - 3.5 (middle), 4.0 - 5.0 m (bottom). During sampling, a weight was attached

to the plankton net to maintain it at a specific depth range. A van Dorn bottle was used to collect water for determinations of temperature and salinity at the different sampling depths. Salinity was measured with an optical refractometer while temperature was measured by means of a glass mercury thermometer mounted inside the van Dorn bottle. Weekly sampling lasted 11 weeks (July 12 to September 21, 1985).

In the field, the samples were immediately fixed in 10% buffered formalin in seawater (Steedman, 1976). In the laboratory, macro-algal fragments and other debris were removed by passing the preserved samples through three metal U.S.A. Standard Testing sieves (4.0, 1.4, 0.246 mm respectively) after removing the macroplankters. Microscopic examination of the algae after washing ensured that all of the zooplankters were collected. The residue of the sample retained in the finest sieve was preserved again in 10% buffered formalin in seawater. The entire sample was then examined under a dissecting microscope for Callianassa larvae, all of which were staged and counted. In the study area, other species of Callianassa are reported to be rare (Rudy and Rudy, 1983), thus all Callianassa larvae collected were considered to be those of Callianassa californiensis. The different larval stages were identified using the descriptions given by Tucker-McCrow (1972).

Tides were classified as neap or spring depending on which phase of the moon the sampling date was closer to. Sampling dates closer to the new or full moon were classified as spring, and neap if closer to the first or last quarter.

### Statistical Analyses

Measurements of temperature and salinity at the three sampling depths were analyzed to test the null hypothesis that there is no difference in temperature or salinity at the three sampling depths during ebb and flood tides. The Kruskal-Wallis one-way analysis of variance (Sokal and Rohlf, 1981) was applied to four sets of data: ebb temperatures, ebb salinities, flood temperatures, and flood salinities. These tests were done to verify whether station A was well-mixed with respect to temperature and salinity during the sampling dates. The Kruskal-Wallis test is applicable even with varying sample sizes, and at  $\alpha=0.10$  or  $\alpha=0.05$ , the chi-square approximation is good even with samples as few as five.

All larval counts were  $\log_e$ -transformed to minimize the effects of very dense samples over less concentrated ones. There were very few zoeal stages II to VI (hereinafter referred to as C2 to C6); thus, for statistical analyses, only the first-stage zoea (hereinafter referred to as C1) counts were used.

The Wilcoxon matched-pairs signed rank test (Sokal and Rohlf, 1981) was used for the null hypothesis that the concentration of C1 larvae in the flood tide is equal to the concentration of C1 larvae in the ebb tide for the whole daily tidal cycle during the sampling dates. The Wilcoxon matched-pairs signed rank test was also used for the null hypothesis that the C1 content of daytime ebb/flood tides is equal to the C1 content of night-time ebb/flood tides. Ebb flows that follow daytime high tides were considered as daytime ebb tides while ebb flows

that follow night-time high tides were considered as night-time ebb tides. The same classification was used to separate daytime and night-time flood tides. The times of sunrise and sunset for each sampling date were used to delineate day and night, respectively. The Kruskal-Wallis one-way analysis of variance was used to analyze whether larval concentration was equal among the three sampling depths.

The method of partial correlation (Snedecor and Cochran, 1984) was used to analyze the relationship of five environmental variables to each other and to Cl density variation. The five variables included were: temperature (TEMP), salinity (SLNT), neap/spring tide series (NPSP), day/night sampling (DYNT), and number of days elapsed since January 1, 1985 (DAYS). DYNT is a variable which reflects the effect of daylight on larval numbers, and DAYS is a variable which reflects the seasonality of larval release in C. californiensis.

Using the forward selection method (Snedecor and Cochran, 1984) to determine the best predictors of larval density variation in C. californiensis, a regression analysis was done on TEMP, SLNT, NPSP, DYNT, and DAYS. Forward selection is a method that examines all the independent variables available and includes only the variables that result in regression models with F-values that fall within a pre-determined set of criteria. The criterion for selection used in this analysis was that the variable/s entered must result in a model with an F-value significant at  $\alpha=0.10$ . Indicator variables were used for NPSP and DYNT: 1=neap, 0=spring; 1=day, 0=night. Data on TEMP, SLNT, and DAYS were standardized so that all data points were expressed

in the same units. The method of standardization was done by the formula:

$$\frac{x_i - \bar{x}}{s.d.}$$

This enabled the comparison of the regression coefficients to determine which factors exert the greatest effect on Cl density. For significance tests, unless given explicitly, the significance levels are indicated as follows: \*\*\* =  $P < 0.001$ , \*\* =  $P < 0.01$ , and \* =  $P < 0.05$ .

## RESULTS

### The Physical Environment

Water temperatures during the sampling period ranged from 10.0 to 17.2 °C, with an average of 13.7 °C. Weekly mean temperatures for both ebb and flood waters were significantly correlated with each other ( $r=0.737$ ,  $P<0.001$ ). High flood temperatures were generally followed by high ebb temperatures, and vice versa (Figure 2). Although the mean temperatures for both ebb and flood waters are not different (ebb=13.6, flood=13.7;  $t=0.26$ ,  $P>0.80$ ), flood mean temperatures were higher than ebb mean temperature during the first five sampling dates but lower during the rest of the study period. The high temperatures of flood tides suggest that a large fraction of flood waters entering South Slough are of estuarine origin. The most possible source of estuarine water aside from South Slough is the Coos Bay Estuary. The reversal of ebb and flood temperatures on the sixth sampling date may reflect the differential heating and cooling of the South Slough and Coos Bay estuaries. South Slough, being of smaller volume and shorter flushing time than the Coos Bay Estuary, is more easily heated up or cooled down depending on the prevailing weather conditions.

Salinities during the sampling period ranged from 30.5 to 34.0, ppt with a mean of 32.3 ppt. Weekly mean salinities of ebb and flood waters were not significantly correlated ( $r=0.463$ ,  $P>0.10$ ), and

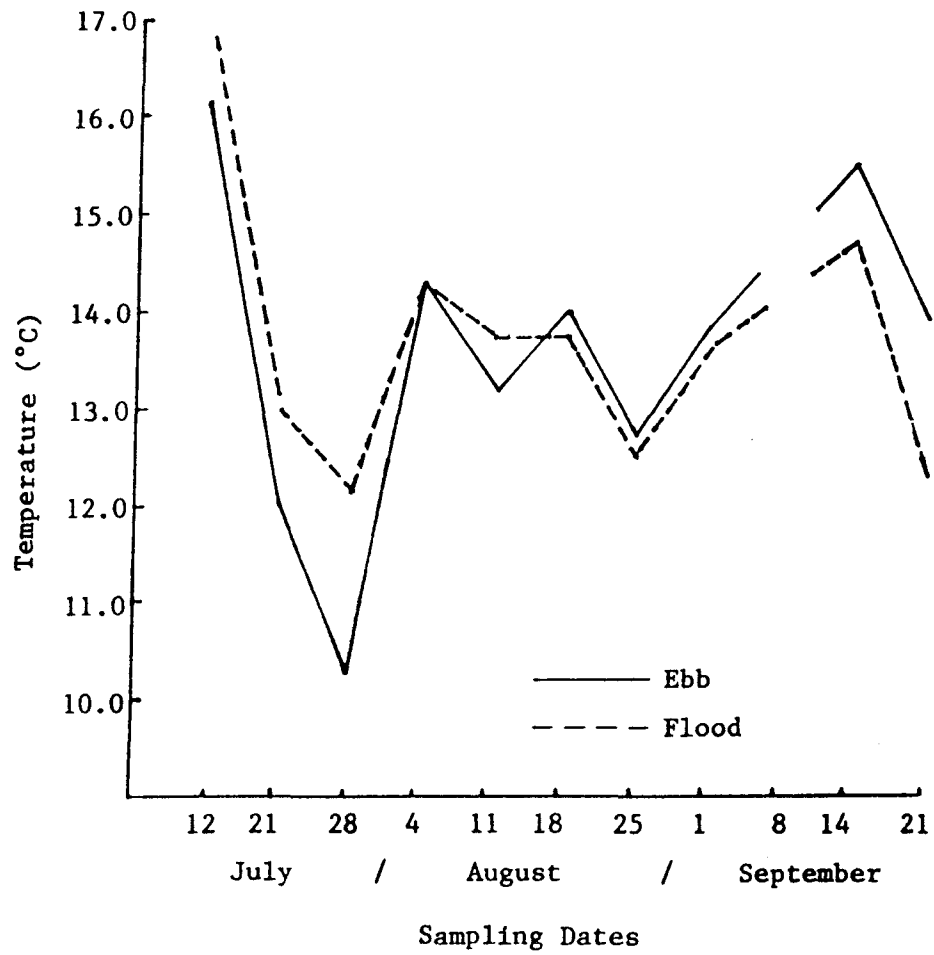


Figure 2. Weekly mean temperatures of ebb and flood flows during the sampling period.



therefore did not fluctuate in the same direction together (Figure 3).

Tables 1 and 2 show the temperatures and salinities of ebb and flood samples, respectively, that were maintained at depth. Because of the variable water velocities at mid-tides, only 25 ebb and 34 flood samples were maintained at the desired depth. The Kruskal-Wallis tests on the four sets of data yielded non-significant results (Table 3). Thus, during the sampling dates, the water column at the sampling station is well-mixed with regards to the distribution of temperature and salinity. Figure 4 shows temperature-salinity diagrams of ebb and flood flows during three sampling dates when all the sampling depths for each date were represented by equal numbers of samples. The diagrams show that variations in temperature or salinity among the sampling depths are generally small except for the flood temperature on August 11 which shows the entry of very warm water into the South Slough estuary.

During the sampling period, tide heights ranged from a low of -0.4 m to a high of 2.4 m relative to mean lower low water. These extreme tides both occurred during one tidal cycle on July 28. The tidal prism ( $V_p$ ) for this tidal cycle is  $1.5 \times 10^7 \text{ m}^3$ . Tidal prism values for the duration of the study are given in Table 4. These are rough estimates from available data on the average surface area of South Slough, and the tidal heights published in NOAA (1984). The mean  $V_p$  during the study is  $7.6 \times 10^6 \text{ m}^3$ , a value lower than the average given by Boyce (1977) and Harris et al. (1979).

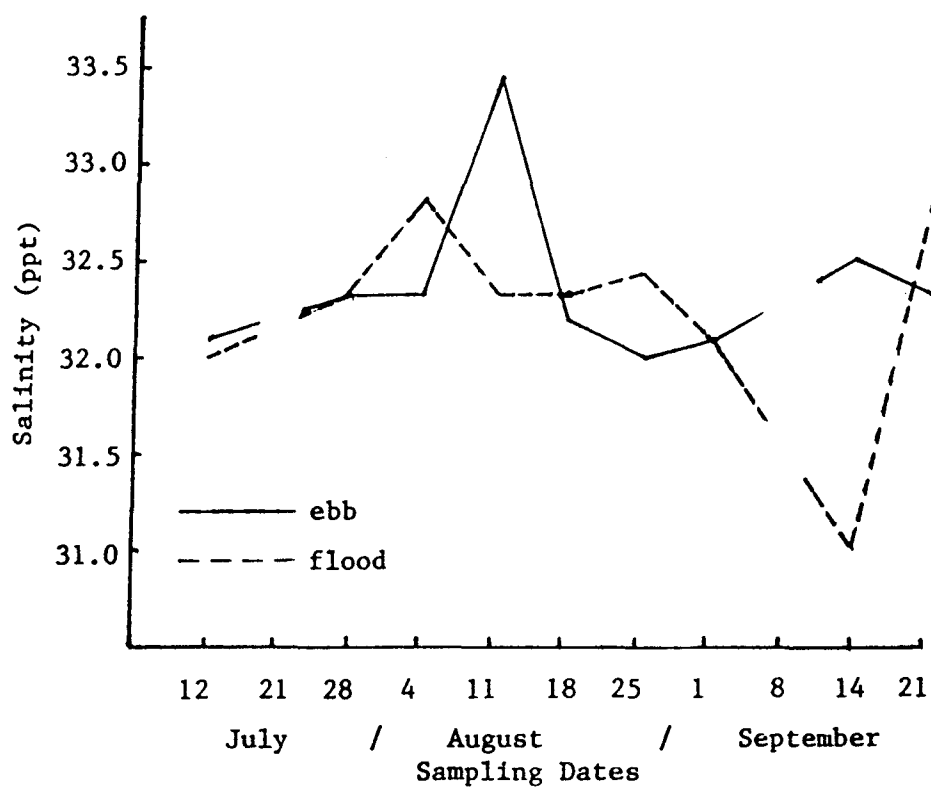


Figure 3. Weekly mean salinities during the sampling period.

Table 1. Temperature and salinity of water samples collected at three depths at the sampling station during ebb flows.

Sampling Date	Temperature			Salinity		
	Surface	Middle	Bottom	Surface	Middle	Bottom
July 12	16.5	17.0	-	32.5	32.0	-
	15.0	17.2	-	32.0	32.0	-
	-	16.0	-	-	32.0	-
	-	15.0	-	-	32.0	-
July 21	-	-	-	-	-	-
July 28	10.5	-	-	32.5	-	-
	10.0	-	-	32.0	-	-
Aug. 4	14.0	-	-	32.2	-	-
Aug. 11	14.6	14.6	14.6	32.0	32.0	32.0
	12.0	11.8	11.6	33.0	33.0	33.0
Aug. 18	13.8	-	-	33.0	-	-
	14.1	-	-	32.0	-	-
Aug. 25	12.6	12.6	12.5	32.0	32.0	32.0
Sept. 1	-	15.3	15.3	-	31.8	32.0
Sept. 14	-	-	-	-	-	-
Sept. 21	14.0	14.0	13.8	32.0	32.0	32.0

Table 2. Temperature and salinity of water samples collected at three depths at the sampling station during flood flows.

Sampling Date	Temperature			Salinity		
	Surface	Middle	Bottom	Surface	Middle	Bottom
July 12	17.2	16.0	-	32.0	32.0	-
	17.0	17.0	-	32.0	32.0	-
	-	17.0	-	-	32.0	-
July 21	-	-	-	-	-	-
July 28	13.0	12.5	-	32.0	32.0	-
	12.5	11.8	10.5	32.5	32.5	-
Aug. 4	14.0	14.0	13.8	32.5	32.6	34.0
	14.3	-	-	32.5	-	-
Aug. 11	11.0	15.5	15.0	32.0	32.0	32.0
	14.2	13.2	13.5	32.5	32.5	32.5
Aug. 18	14.3	-	-	32.0	-	-
Aug. 25	12.3	12.3	12.3	32.0	32.0	32.0
	12.5	12.5	12.7	32.5	33.0	33.0
Sept. 1	15.3	-	-	31.0	-	-
	13.8	14.6	14.3	32.0	32.0	32.0
Sept. 14	-	-	-	-	-	-
Sept. 21	12.0	12.3	12.5	33.0	33.0	33.5

Table 3. Results of Kruskal-Wallis one-way analysis of variance on temperature and salinity at the three sampling depths.

Data Set	Chi-square	Probability
Ebb temperatures	3.39	0.25
Ebb salinities	3.09	0.25
Flood temperatures	0.94	0.75
Flood salinities	1.39	0.50

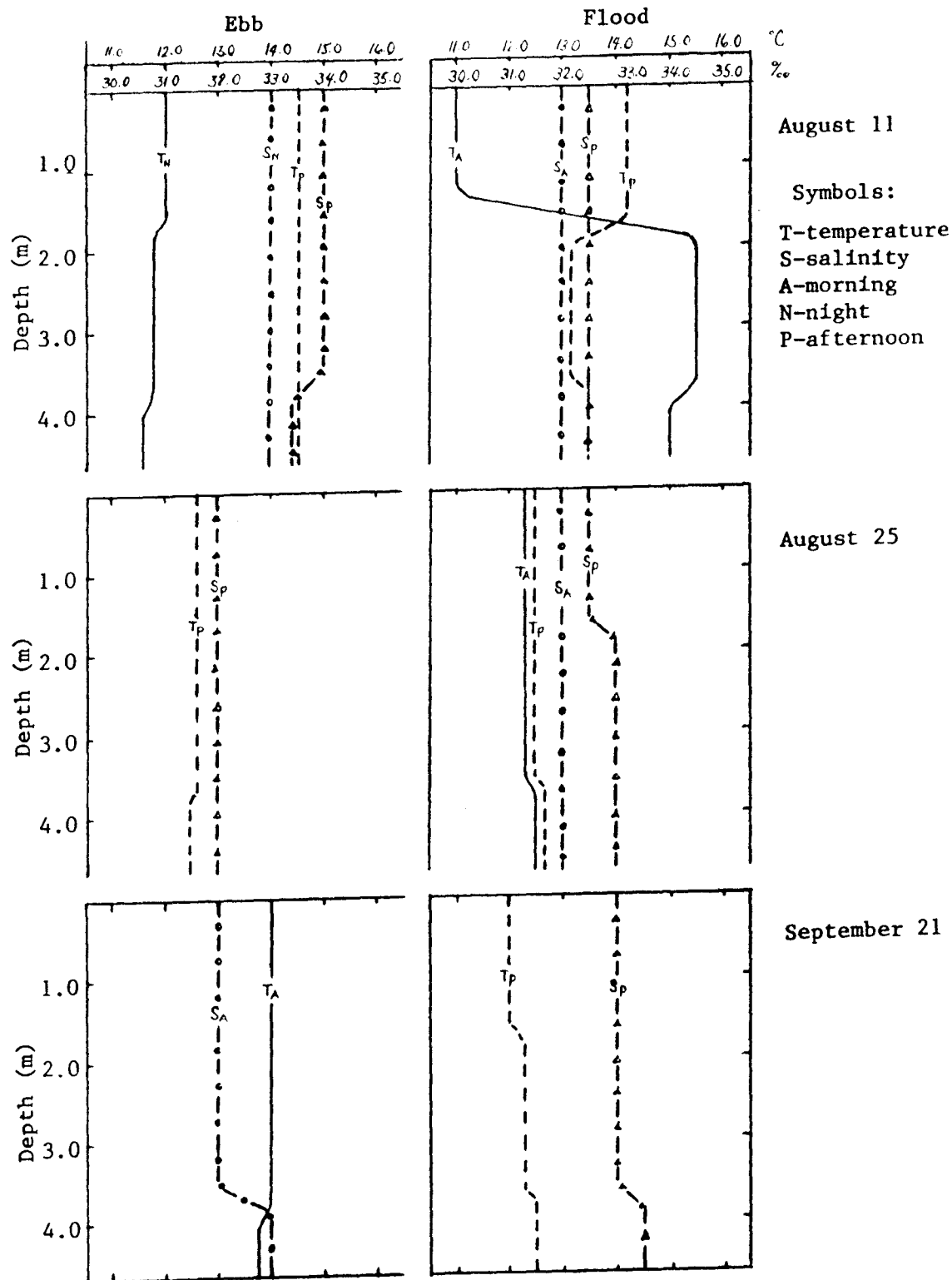


Figure 4. Temperature-salinity diagrams during dates when the sampling depths were represented by equal numbers of samples.

Table 4. Sampling dates, volume of the tidal prism ( $V_p$ ) and total number of Cl larvae per flow.

Date	Neap/ Spring	Flow	$V_p$ ( $\times 10^6 m^3$ )	Mean Cl den- sity (#/100m <sup>3</sup> )	Total Cl (#/flow)
7/12/85	Neap	Ebb	2.12	111,836.0	$2.37 \times 10^9$
		Flood	5.84	782.7	$4.57 \times 10^7$
		Ebb	9.55	123,398.0	$1.18 \times 10^{10}$
		Flood	6.37	15,699.7	$1.00 \times 10^9$
7/21/85	Neap	Ebb	2.21	645.7	$7.88 \times 10^7$
		Flood	11.15	32.0	$3.57 \times 10^6$
		Ebb	5.84	7.0	$4.09 \times 10^5$
		Flood	6.37	6,190.7	$3.94 \times 10^8$
7/28/85	Spring	Ebb	2.65	270.0	$7.15 \times 10^7$
		Flood	9.02	1,090.3	$9.83 \times 10^7$
		Ebb	14.86	6,497.7	$9.65 \times 10^8$
		Flood	7.43	211.7	$1.57 \times 10^7$
8/4/85	Neap	Ebb	10.61	38,563.3	$4.09 \times 10^9$
		Flood	10.08	10.0	$1.01 \times 10^6$
		Ebb	6.37	133.3	$8.49 \times 10^6$
		Flood	5.84	249.0	$1.45 \times 10^7$
8/11/85	Neap	Ebb	1.59	24,821.0	$3.95 \times 10^8$
		Flood	6.37	1,622.7	$1.06 \times 10^8$
		Ebb	10.08	582.7	$5.87 \times 10^7$
		Flood	4.78	217.7	$1.04 \times 10^7$
8/18/85	Spring	Ebb	12.74	3,416.3	$4.35 \times 10^8$
		Flood	11.67	2.7	$3.15 \times 10^5$
		Ebb	7.96	21.0	$1.67 \times 10^6$
		Flood	8.49	111.3	$9.45 \times 10^6$
8/25/85	Neap	Ebb	2.65	150.3	$3.98 \times 10^6$
		Flood	8.49	176.0	$1.49 \times 10^7$
		Ebb	6.37	7,149.3	$4.55 \times 10^8$
		Flood	12.74	12.0	$1.53 \times 10^6$
9/1/85	Spring	Ebb	10.08	662.0	$6.67 \times 10^7$
		Flood	9.55	368.6	$3.52 \times 10^7$
		Ebb	7.43	18.7	$1.39 \times 10^6$
9/7/85	Neap	-	-	-	-
9/14/85	Spring	Ebb	8.49	67.3	$5.71 \times 10^6$
		Flood	11.67	356.3	$4.16 \times 10^7$
9/21/85	Neap	Ebb	2.65	200.9	$5.32 \times 10^6$
		Flood	5.84	944.7	$5.52 \times 10^7$

Plankton Study: Phenology of Callianassa Larvae

A total of 110 samples was collected at the fixed sampling station, 55 ebb and 55 flood samples. The depth distribution of C1 larvae during ebb and flood flows was analyzed for the null hypothesis that there is no difference in the distribution of C1 larvae at all sampling depths. Because of the strong tidal currents at the sampling station, only 25 ebb and 34 flood samples were maintained at depth during sampling (Table 5). The Kruskal-Wallis analysis of variance for both sample sets yielded a non-significant result ( $\chi^2_{\text{ebb}} = 3.412, P > 0.25$ ;  $\chi^2_{\text{flood}} = 0.182, P > 0.50$ ) that led to the conclusion that there is no difference in the distribution of C1 larvae at the three sampling depths. Therefore, at the sampling station, the C1 larvae are uniformly distributed in the water column.

The mean density of Callianassa first-stage zoea ranged from 7.0 to 123,398.0/100 m<sup>3</sup> for the ebb samples, and 2.7 to 15,699.7/100 m<sup>3</sup> for the flood samples. Because the C1 are uniformly distributed in the water column at the sampling station, the total larval content of ebb and flood waters in South Slough were calculated using sample mean larval densities and  $V_p$  values for each flow (Table 4). The calculations resulted in estimates of larval numbers ranging from  $4.09 \times 10^5$  to  $1.18 \times 10^{10}$  and  $3.15 \times 10^5$  to  $1.00 \times 10^9$  for the total volume of water during each ebb and flood tide, respectively.

For the first eight weeks, the mean densities of C1 (#/100m<sup>3</sup>) for all sampling dates were greater during ebb than flood flows except on July 21, (week 2) one week after the ebb tide release of the largest

Table 5. Larval content [ $\log_e (C_l/100m^3 + 1)$ ] of zooplankton samples collected at three depths at the sampling station during ebb and flood flows.  $n_{ebb} = 25$ ;  $n_{flood} = 34$

Sampling Date	Ebb			Flood		
	Surface	Middle	Bottom	Surface	Middle	Bottom
July 12	8.55	12.01	-	6.49	7.13	-
	10.00	12.02	-	10.00	7.52	-
	-	12.30	-	-	10.02	-
	-	11.76	-	-	-	-
July 21	-	-	-	-	-	-
July 28	4.61	-	-	6.58	7.15	6.46
	8.34	-	-	0.00	0.00	-
Aug. 4	7.80	-	-	2.56	5.81	4.98
	-	-	-	5.60	-	-
Aug. 11	11.11	8.34	8.06	7.55	6.57	7.77
	7.23	5.49	4.87	4.96	3.83	6.15
Aug. 18	9.17	-	-	3.04	-	-
	2.48	-	-	-	-	-
Aug. 25	5.00	5.25	4.74	5.16	5.28	5.08
	-	-	-	2.89	2.83	1.39
Sept. 1	-	0.00	4.36	7.26	5.38	6.17
	-	-	-	3.74	-	-
Sept. 14	-	-	-	-	-	-
Sept. 21	6.04	4.70	4.34	7.68	5.12	6.22



observed number of C1 throughout the study (Figure 5). Thus, the C1 content of the July 21 flood tides may consist of a fraction of the C1 that were released in the previous ebb tides. On the tenth and eleventh sampling dates, (Sept. 14 and 21), C1 content of flood tides was greater than that of ebb tides. Figure 5 also shows the presence of three broods of larvae, released at three-week intervals. The predominance of C1 in the samples shows that the sampling period included much of the larval release period of C. californiensis at the South Slough estuary in 1985. It is evident that this study missed the beginning of the Callinassa larval release period. However, the preliminary study on July 5, 1985 resulted in larval numbers that are an order of magnitude less than those reported here.

The highest peak in C. californiensis larval density for both ebb and flood tides occurred in the first week of sampling (Figure 5). On this sampling date, C1 accounted for 100% of the Callinassa larvae in the plankton samples. Later larval stages were first observed on a flood tide on the second sampling date when a low number of C2 were observed. Thereafter, stages C2 and C3 were also observed on both ebb and flood tides along with C1 larvae. Thus, these early planktonic stages are transported into and out of the estuary with the tides. Stages C4 and C5 were not observed in the samples collected at the sampling station. These are zoeal stages that are more abundant in the nearshore ocean than in the estuary (Tucker-McCrow, 1972).

The critical stage for successful recruitment in many decapods has been identified as the megalopa (Tagatz, 1968; Sandifer, 1975).

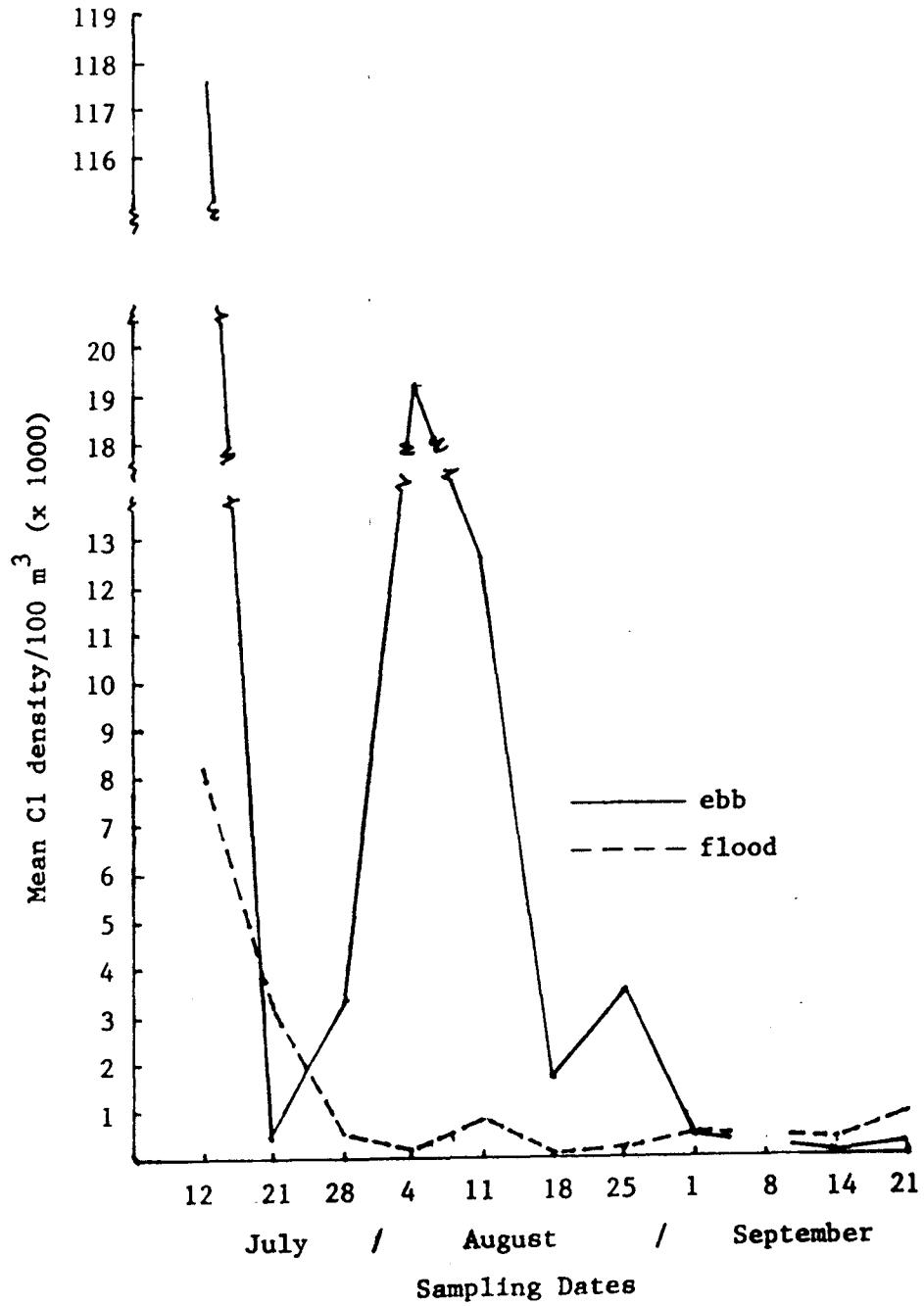


Figure 5. Mean weekly density of Cl at the sampling station.

Callinassa megalops (C6) were first observed on a flood tide on August 18 (Figure 6), and on subsequent ebb tides no megalops were observed to leave the estuary. Two of the three flood samples collected at night during this sampling date contained megalops stages. In these two samples the megalops accounted for 7.0% and 10.5% of the total number of Callinassa larvae in the samples respectively. The remaining fraction of Callinassa larvae in both samples were first-stage zoea.

#### Ebb-Flood Tide Differences in Larval Density

For 10 out of 17 pairs of ebb and flood flows, estimates of C1 density were greater for ebb than for flood flows. The ebb sample mean density was greater than the flood sample mean density, and the variance greatly exceeded the mean (Table 6). Application of the Wilcoxon signed-rank test for the matched pairs of  $\log_e$ -transformed weekly densities for each flow resulted in the rejection of the null hypothesis that the number of C1 larvae passing sampling station A at ebb tide and at flood tide are equal for a one-tailed test ( $P < 0.028$ ). During the tides sampled, ebb volume was only 82% of the flood volume due to the unequal heights of the tides characteristic of the Pacific northwest coast. However, significantly more larvae were exported from the estuary during ebb flows than were imported during flood flows.

#### Environmental Factors Affecting Larval Density

The d-statistic (Cassie, 1959b), that is, the proportion of non-random variance, is nearly one in both ebb and flood flows (Table

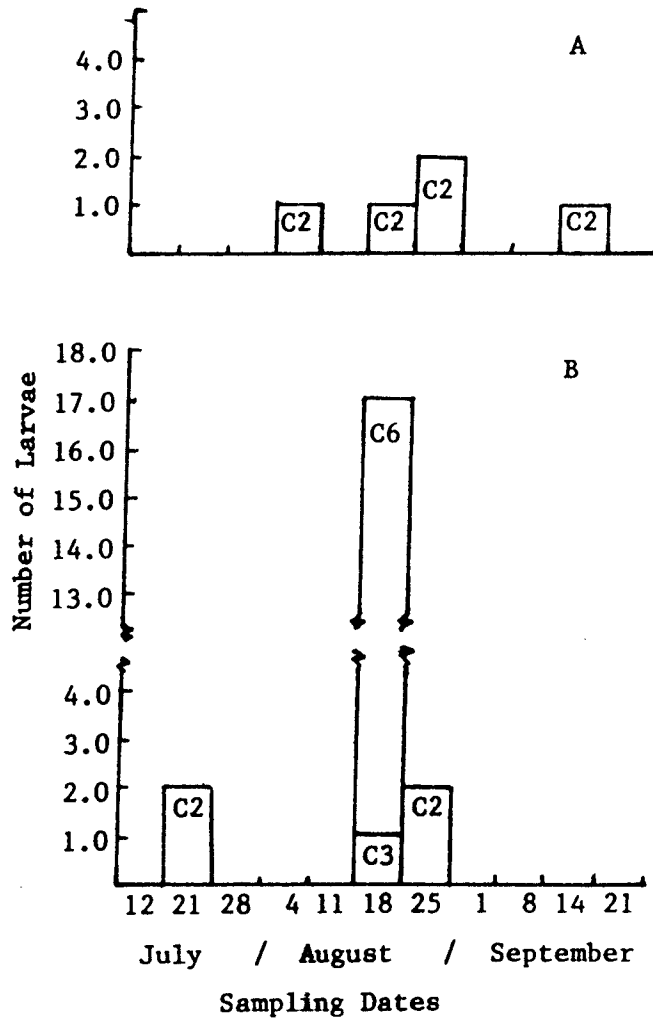


Figure 6. Numbers of C2 to C6 in the combined samples at each sampling date: A, ebb; B, flood.

6); thus, the influence of chance on Cl density variation is negligible. Some factors must exist which regulate the variation in density of Cl of C. californiensis.

For analysis of the influence of environmental factors on larval density variation, only data for Cl were used since there were very few non-Cl larvae. Samples collected on July 21 were not included in the analysis because of missing salinity measurements.

Each environmental factor measured was categorized as either a direct-effect or an indirect-effect variable. Temperature and salinity are direct-effect variables because they have a direct physiological effect on the Callinassa larvae. Since they are sample-specific, and are represented by quantitative values, TEMP and SLNT were given more importance as environmental factors affecting Cl density variation. The extent of the effect of TEMP and SLNT on Cl density variation may be regulated by the variables DAYS, and DYNT, which were thus considered indirect-effect variables. To expedite the analysis, NPSP was also considered an indirect-effect variable. In the analysis of the influences of environmental factors on Cl density, ebb and flood tide data were analyzed separately because of differences in the patterns of the relations between Cl and the environmental factors measured, as evident in Table 6, Table 7, and the result of the Wilcoxon signed-rank test for the Cl content of ebb and flood flows.

Table 6. Mean, variance and coefficient of dispersion ( $d^*$ ) of Cl ( $\#/m^3$ ) for ebb and flood tides.

Flow	n	$\bar{x}$	$s^2$	d
Ebb	55	173.9	223,670.6	0.999
Flood	55	15.6	2,302.8	0.993
Total	110	94.8	118,283.6	0.999

$$*d = \frac{s^2}{\bar{x}^2}$$

Table 7. Simple correlation coefficients of Cl density [ $\log_e (\#/m^3 + 1)$ ] with all environmental factors measured for ebb and flood tide flows.  $n_{ebb} = 48$ ;  $n_{flood} = 48$

Flow		TEMP	SLNT	NPSP	DYNT	DAYS
Ebb	Cl	0.1598	0.0383	0.4818***	-0.3483*	-0.6268***
Flood	Cl	0.3976**	-0.3236*	0.3025*	-0.0345	-0.2547

Table 8. Simple correlation coefficients of environmental factors measured: Ebb, above diagonal; flood, below diagonal.  $n = 48$

	TEMP	SLNT	NPSP	DYNT	DAYS
TEMP		-0.0107	0.2887*	0.3379*	-0.1121
SLNT	-0.3844**		0.2153	0.1703	0.0364
NPSP	0.1904	0.3394*		0.0108	-0.2499
DYNT	0.0778	-0.0713	-0.1205		0.1593
DAYS	-0.4571***	0.0117	-0.2503	0.0224	

### Ebb Tides

Only the indirect-effect variables were strongly associated with Cl content of ebb tides. The variables that showed high simple correlations with Cl are DAYS and NPSP with DYNT showing a weak but still significant correlation (Table 7). Table 8 shows the simple correlation coefficients of the environmental factors with each other.

The highly significant negative correlation of Cl with days implies a reduction in Cl content of ebb flows as the study progressed and this is evident in Figure 5. Neap tide periodicity to ebb tide release of Cl is suggested by the strong positive correlation between Cl and NPSP. Furthermore, Cl release occurs more at night than during the day. This is evidenced by the negative correlation between Cl and DYNT.

To determine whether these indirect-effect variables act singly or in combination to affect Cl density variation, partial correlations between Cl and each of NPSP, DAYS and DYNT were computed (Table 9). These significant partial correlations show that NPSP, DAYS, and DYNT affect ebb tide Cl density variation independently of each other. Furthermore these partial correlations substantiate the results of the simple correlation analysis regarding the effects of NPSP, DAYS and DYNT on Cl density.

Table 10 shows partial correlation coefficients of the indirect-effect variables with TEMP and SLNT. These correlations were computed to determine whether TEMP and SLNT are correlated with each of the NPSP, DAYS, and DYNT when the other two indirect-effect variables are kept constant. These coefficients show that all of the three

indirect-effect variables do not significantly correlate with TEMP and SLNT, except the variable DYNT which had a strong association with TEMP. The significant positive simple and partial coefficients between DYNT and TEMP imply that temperature is higher during the day than at night.

Using the Wilcoxon matched-pairs signed ranks test, a comparison of the  $\log_e$ -transformed total estimates of Cl content of ebb flows following daytime high tides and of ebb flows following night-time high tides was made. This test resulted in the rejection of the null hypothesis that night-time ebb flux equalled daytime ebb flux at  $\alpha=0.01$  for a one-tailed test. This substantiates the strong negative simple correlation between Cl and DYNT. Significantly more Cl are released during ebb tides that occur at night or that follow night-time high tides than during ebb tides that occur during the day or that follow daytime high tides.

Regression analysis using the forward selection method to choose the best predictors of Cl density variation among the five environmental variables measured resulted in the inclusion of only the indirect-effect variables, NPSP, DAYS and DYNT, in the model. The regression coefficients for this model are presented in Table 11. This model resulted in an R-square value of 0.549, which means that 54.9% of the variation in Cl density of ebb tides is explained by the variables NPSP, DAYS and DYNT. A model which included the variables TEMP and SLNT along with the indirect-effect variables resulted in an R-square value of 0.551. The minimal increase in R-square means that TEMP and SLNT do not significantly increase the ability of the model to predict Cl density



Table 9. Partial correlation coefficients of Cl density [ $\log_e (\#/100\text{m}^3 + 1)$ ] on all environmental factors measured during ebb tides.  $n = 48$

Correlates	Controlling for	Coefficient
Cl-DAYS	NPSP,DYNT	-0.5869***
Cl-DYNT	NPSP,DAYS	-0.3838**
Cl-NPSP	DAYS,DYNT	0.4742***
Cl-TEMP	NPSP,DYNT,DAYS	0.1600
Cl-SLNT	NPSP,DYNT DAYS	0.0401

Table 10. Partial correlation coefficients of indirect-effect variables on TEMP and SLNT for ebb tide flows.  $n = 48$

Correlates	Controlling for	Coefficient
DAYS-TEMP	NPSP,DYNT	-0.1100
NPSP-TEMP	DAYS,DYNT	0.2705
DYNT-TEMP	NPSP,DAYS	0.3623*
DAYS-SLNT	NPSP,DYNT	0.0686
NPSP-SLNT	DAYS,DYNT	0.2265
DYNT-SLNT	NPSP,DAYS	0.1590

Table 11. Coefficients of the best regression model of Cl density [ $\log_e (\#/100\text{m}^3 + 1)$ ] variation on the environmental factors measured for ebb tides.  $R^2 = 0.549$

Variable	Coefficient	T-statistic
Constant	6.3952	11.292***
DAYS	-0.4929	-4.808***
NPSP	0.3616	3.572***
DYNT	-0.2737	-2.757**

variation of ebb tides.

#### Flood Tides

The variables with high simple correlations with Cl are TEMP, SLNT and NPSP, with DAYS exerting a very weak ( $P < 0.10$ ,) but still important association with Cl (Table 7). The variable DYNT had no apparent relationship with Cl and was dropped from further analysis of Cl density variation. Temperature had the strongest association with Cl density. The significant positive simple correlation between Cl and TEMP implies that Cl are generally more abundant in flood waters with higher temperature. On the other hand, the significant negative correlation between Cl and SLNT implies that Cl are more abundant in low salinity flood waters. Neap tide periodicity to flood tide Cl density variation is suggested by the significant positive correlation between Cl and NPSP. The negative simple correlation of Cl with DAYS implies a reduction in Cl content of flood tides as the study progressed, and this is evident in Figure 5.

The correlations of the environmental factors with each other during flood tides are presented in Table 8. To determine whether the direct-effect variables affect Cl variation singly or in concert, partial correlations of Cl with TEMP and SLNT were computed (Table 12). The coefficients show that TEMP and SLNT are both strongly associated with Cl density even when the variables NPSP and/or DAYS were controlled. However, the correlation of Cl with TEMP while keeping SLNT constant, and the correlation of Cl with SLNT while keeping TEMP

constant are not significant. These imply that temperature and salinity act in concert to affect the variation in Cl density. The significant positive correlations of Cl with temperature and the negative correlations with salinity while keeping the indirect-effect variables NPSP and/or DAYS constant, substantiate the results of the simple correlation analysis: that high temperature, low salinity waters generally contain large numbers of Cl larvae. These waters are characteristic of estuaries rather than the ocean. This substantiates the results of the analysis on the physical environment during the sampling period, that a large fraction of the flood waters going into South Slough are of estuarine origin. The most possible source of warm, low salinity water other than the South Slough Estuary is the Coos Bay Estuary. This suggests that a large fraction of the Callianassa larvae entering the South Slough Estuary on the flood tide originated from either the upper Coos Bay estuary or from the South Slough Estuary itself, and only a small fraction originated from the nearshore ocean.

Partial correlation coefficients between the indirect-effect variables, NPSP and DAYS, and the direct-effect variables TEMP and SLNT were computed (Table 13). This was done to determine which variable between NPSP and DAYS is more correlated with TEMP and/or SLNT. These coefficients show that changes in temperature are significantly associated with DAYS but not with NPSP while changes in SLNT are significantly associated with NPSP but not with DAYS. The significant correlations between DAYS and TEMP while keeping NPSP constant show that flood temperatures during the later sampling dates are generally lower

Table 12. Partial correlation coefficients of Cl density [ $\log_e (\#/100\text{m}^3 + 1)$ ] with TEMP and SLNT during flood tides.  $n = 48$

Controlling for	Cl with	
	TEMP	SLNT
TEMP	n.a.	-0.2016
SLNT	0.2732	n.a.
NPSP	0.3633*	-0.4754***
DAYS	0.3269*	-0.3315*
NPSP,DAYS	0.3160*	-0.4662***

Table 13. Partial correlations of indirect-effect variables NPSP and DAYS with TEMP and SLNT for flood tides.  $n = 48$

Correlates	Controlling for	Coefficient
DAYS-TEMP	NPSP	-0.4308**
NPSP-TEMP	DAYS	0.0883
DAYS-SLNT	NPSP	0.1061
NPSP-SLNT	DAYS	0.3536*
TEMP-SLNT	NPSP,DAYS	-0.4909***

Table 14. Coefficients of the best regression model of variation in Cl density ( $\log_e \#/100\text{m}^3 + 1$ ) on the environmental factors measured measured for flood tides.  $R^2 = 0.27$ ;  $n = 48$

Variable	Coefficient	T-statistic
Constant	53.033	2.422*
TEMP	0.168	1.158
NPSP	0.405	2.843**
SLNT	-0.396	2.422*

than at the start of the study. The significant correlation between NPSP and SLNT while controlling for the effects of DAYS shows that neap flood waters rather than spring flood waters are generally characterized by higher salinities. The strong correlation between Cl and NPSP while keeping the other significant variables TEMP, SLNT and DAYS constant, ( $r_{Cl-NPSP,TEMP,SLNT,DAYS} = 0.3849^{**}$ ), shows a neap tide periodicity to flood tide Cl content. This implies that more Cl larvae enter the South Slough Estuary during the neap flood tides than during spring flood tides. This trend is evident in Figure 5.

Regression analysis using the forward selection method to build a model with the best predictors of flood tide Cl density resulted in the inclusion of the variables TEMP, NPSP, and SLNT. The regression coefficients of this model are shown in Table 14. The R-square value is 0.27, thus, this model accounts for only 27% of the variation in Cl density of flood tides. A model that included DYNT and DAYS along with TEMP, NPSP, and SLNT resulted in an R-square value of 0.24. Therefore DYNT and DAYS reduce the ability of the variables TEMP, SLNT, and NPSP to predict the variation in Cl density of flood tides.

## DISCUSSION

The 1985 Callinassa californiensis larval release period lasted until late August at the South Slough Estuary. Release was apparently synchronized, with two to three broods evident during the period of study. These broods appear to be released at three-week intervals, perhaps reflecting the period of time between egg fertilization and development of first-stage zoea. However, no data in literature regarding C. californiensis could be found to substantiate this.

Analysis of simple and partial correlations of larval concentrations with the five environmental factors measured revealed a neap tide periodicity to ebb tide release of larvae. The positive significant correlations between neap/spring tide series and temperature for ebb flows show that neap ebb waters were generally characterized by higher temperatures than spring ebb waters. The smaller volume of South Slough during neap tides than during spring tides would enable faster heating by solar radiation. The higher temperatures may have triggered the release of more larvae during neap tides. Moreover, larval concentrations are apparently greater during ebb tides that occur during the night or that follow night-time high tides. The timing of larval release during the night could be an adaptation to avoid predation on both the adults and the larvae. Adults are assumed to come to the entrance of their burrow to spawn making them susceptible to predation (Posey, 1985), and therefore night-time spawning would be more

advantageous. Moreover, the efficiency of visual predators on the larvae would be considerably less at night than during daytime.

Given a maximum flushing time, i.e. the time to replace the freshwater within the estuary at a rate that is equal to the discharge of the freshwater source (Dyer, 1973), of 0.30 day (see Appendix B) for the South Slough Estuary and a planktonic larval life of 6-8 weeks for C. californiensis, it is difficult for the larvae to maintain themselves in the estuary, and they are therefore exported from South Slough. This is substantiated by the result of the Wilcoxon signed-ranks test for the difference between ebb and flood tide C1 densities showing significant export of C1 from the South Slough Estuary. Furthermore, conditions in the ocean appear to be necessary for development to later zoeal stages. The absence of stages C4 and C5 from the sampling station shows that development into these later stages does not occur in the estuary. The nearshore ocean is therefore the source of later-stage larvae, and this is substantiated by the observation that stages C2 and C3 were first observed at station A on flood tides.

Tide waters from South Slough early in the ebb will be exported farthest into the nearshore ocean (Butler, 1978). Therefore, larvae released early in the ebb are carried farthest into the nearshore ocean, but larvae released late in the ebb may only reach the immediate nearshore region or are exported only up to the confluence between the South Slough Estuary and the Coos Bay Estuary. Once in this confluence, export or retention becomes dependent on the hydrography of the Coos Bay Estuary. During the summer months, the flushing time of Coos Bay

Estuary extends up to 65 tidal cycles (Choi, 1975) or 40.3 days (Arneson, 1976). At this confluence and the immediate nearshore region, there is therefore a mix of C. californiensis larvae released late in the ebb from both estuaries.

On the flood tide, simple and partial correlations of Cl with temperature and salinity show that Cl larvae are most abundant in waters with high temperature and low salinity. These waters are characteristic of estuaries rather than of the nearshore ocean. Therefore, a large fraction of the early-stage larvae entering the South Slough Estuary on the flood tide are from populations of C. californiensis in both Coos Bay and South Slough Estuaries. This would also explain the neap tide periodicity to flood tide Cl density variation. Neap tides would result in less flushing of larvae from the Coos Bay Estuary, thus more larvae will be returned to the South Slough Estuary on the succeeding flood tide. Moreover, larvae will be carried not very far from the immediate entrance of the Coos Bay Estuary where they are potentially available for transport back into the estuaries on the subsequent flood tides.

The megalopa is the critical stage for recruitment in decapod crustaceans (Tagatz, 1968) because it is the stage capable of settlement into the benthic adult population. Callinassa megalops were observed at station A on a flood tide and were assumed to have settled in the estuary because no megalops were observed leaving the estuary on the subsequent ebb tides.

Dispersal of the megalopa is largely through passive transport by water movements, and the direction of transport is dependent on its



position in the water column (Sulkin and Van Heukelem, 1982). Reports of the vertical distribution of the megalopa vary considerably. Tagatz (1968) and Sandifer (1973) reported the megalopa to be most common in bottom waters. However, Williams (1971) and Smyth (1980) reported them to be common in surface waters. These apparent discrepancies may be explained by basic locomotor rhythms affected by endogenous or exogenous control in different species, and the profound changes in behavior at the megalopa stage which result in a depth regulatory mechanism of high precision (Sulkin and Van Heukelem, 1982).

Along the Oregon coast during summer, there is a two-layered system of water currents, a generally southward transport of surface waters with a component to the right of the wind direction away from the coastline, balanced by a northward and onshore transport at depth of cold high salinity waters (Bourke et al., 1971; Peterson and Miller, 1976). It is this upwelling event that helps nearshore retention of copepod populations along the Oregon coast (Peterson et al., 1979). This same phenomenon may work to retain Callinassa californiensis larvae in the nearshore ocean where they are potentially available for transport into estuaries.

## SUMMARY

Temperature and salinity data for the sampling period indicate a well-mixed water column at the sampling station. A large fraction of the flood waters entering South Slough is characterized by high temperatures and low salinities. The source of these waters is tidal exchange with the Coos Bay Estuary, which in turn, is influenced by the nearshore ocean. Temperature stratification of the water column may occur but this stratification is apparently ephemeral. This stratification appears to have no relationship to the distribution of Callianassa californiensis larvae, with first-stage zoea uniformly distributed in the water column during both ebb and flood flows. Because of the mixed semi-diurnal tides characteristic of the Pacific northwest coast, ebb volume in South Slough was only 82% of the flood volume during the sampling dates. Nevertheless, significantly more C. californiensis first-stage zoea were exported from South Slough than were imported.

The highest peak in C. californiensis larval density for both ebb and flood flows occurred in the first week of sampling. Larval release was apparently synchronized, with significantly more larvae being released every three weeks, and with two to three broods evident during the period of study. The time interval between release may reflect the time between egg fertilization and development of first-stage zoea. For the first sampling date, first-stage zoea

accounted for 100% of the Callianassa larvae in the samples for both ebb and flood tides. Zoeal stages II and III were first observed at the sampling station during flood tides, but on subsequent sampling dates, these stages were observed on both ebb and flood flows. Thus, early planktonic larval stages are transported in and out of the South Slough Estuary with the tides.

Callianassa californiensis larval content of ebb tides is strongly correlated with season, neap/spring tide series, and day/night. The intensity of larval release decreased as the study progressed. More larvae are released during ebb tides that occur at night or that follow night-time high tides than during ebb tides that occur in the daytime or that follow daytime high tides. The night-time release of larvae may be an adaptation to reduce predation on the adults during spawning, and on the newly released larvae. Neap tide periodicity is apparent for larval release; thus, significantly more larvae are exported from South Slough during neap ebb tides than during spring ebb tides. These larvae are exported to the nearshore ocean and to the confluence between the South Slough and the Coos Bay estuaries. A large fraction of the larvae is apparently transported back into the Slough, which thus explains the observed neap tide periodicity to flood tide larval density variation.

Aside from neap/spring tide series, variation in C. californiensis larval density is also strongly associated with temperature and salinity. Warm, low salinity waters contained significantly larger numbers of Callianassa larvae. This suggests that the estuarine waters from Coos Bay estuary or the South Slough, itself,

are significant sources of larvae entering the South Slough estuary.

Because of the short flushing time of South Slough of only 0.30 days in contrast to the long planktonic larval phase of 6 - 8 weeks in C. californiensis, larval retention is not a possible mechanism of recruitment into the adult population in the estuary. A large fraction of the Callianassa larvae released into the South Slough must therefore be exported out of the estuary at each ebb tide.

The absence of zoeal stages IV and V from the sampling station shows that development of these later stages does not occur in the estuary. Tucker-McCrow (1972) reported these stages to be abundant in the ocean. Conditions in the ocean appear to be necessary for development of these later larval stages. Furthermore, Callianassa megalops were first observed at the sampling station during a flood tide, and were assumed to have settled in the estuary because no megalops were observed to leave the estuary on the subsequent ebb tides. The two-layered system of water currents along the Oregon coast during summer may help to retain these larvae nearshore where they are potentially available for transport back to the estuaries. Thus, the immediate source of recruits to the Callianassa californiensis population in the South Slough Estuary is the nearshore ocean.

## APPENDIX A

## VOLUME ESTIMATION

The volume of water ebbed or flooded at the South Slough was roughly estimated using data on (1) average surface area of South Slough, and (2) the tide range for that flow as published in the NOAA Tide Tables (1985).

As an example,

Given:

1. Surface area of South Slough =  $5.3 \times 10^6 \text{ m}^2$

2. Tide heights on July 12, 1985

9:31 AM -- 1.3 m

2:01 PM -- 0.9 m

Therefore:

$$\begin{aligned} \text{Volume ebbed} &= \text{surface area} \times \text{tide range} && \text{Eq. 1} \\ &= (5.3 \times 10^6 \text{ m}^2) \times 0.4 \text{ m} \\ &= 2.12 \times 10^6 \text{ m}^3 \end{aligned}$$

## APPENDIX B

## SOME PHYSICAL CHARACTERISTICS

Estimation of the Tidal Prism

The tidal prism ( $V_p$ ) is the volume of water between high tide and the succeeding low tide. The methods of computation of  $V_p$  as reported here have been adapted from Harris et al. (1979).

## 1. Steep Sides

The estimation of  $V_p$  involves the assumption that the sides of the estuary are steep. In this case, the  $V_p$  is simply the product of the surface area of the estuary and the mean tide range. For the South Slough Estuary,

$$\begin{aligned} V_p &= \text{surface area} \times \text{mean tide range} && \text{Eq. 1} \\ &= (5.3 \times 10^6 \text{ m}^2) \times 1.7 \text{ m} \\ &= 9.0 \times 10^6 \text{ m}^3 \end{aligned}$$

## 2. Trapezoidal Approximation

This method is based on the field data of Boyce (1977) on the cross-sectional depth at several stations in South Slough. The station locations are indicated in Figure 1 in the text. His data are presented in Table B-1. His computations resulted in a  $V_p = 9.0 \times 10^6 \text{ m}^3$ .

## 3. Two-dimensional, Non-linear Circulation Model

This model was developed by Butler (1978). The volume flow rate is calculated across several cross-sections. The  $V_p$

was estimated by integrating the volume flow rate at the entrance of South Slough over a rising or falling limb of the tides. This model used four limbs and the values were averaged to give a  $V_p = 9.8 \times 10^6 \text{ m}^3$ .

Table B-1. Field measurements of Boyce (1977) for estimation of tidal prism ( $V_p$ ) of the South Slough Estuary.

	Station I	Station II	Station III	Station IV	Station V	TOTAL
HW Depth	2.0 m	21.3	6.2	16.1	11.2	
LW Depth	0.3 m	4.8	0.2	3.2	1.7	
w	838.4 m	945.1	411.6	838.4	518.3	
L	2088.4 m	1097.6	777.4	990.8	2350.6	
$V_{LW} (\times 10^5)$	4.8 m <sup>3</sup>	49.3	0.4	26.4	20.4	101.3
$V_p (\times 10^5)$	30.4	18.0	5.6	14.4	21.2	89.6

All of these methods were based on a low tide volume of  $10.1 \times 10^6 \text{ m}^3$ . From the three different methods, a mean value was computed and this value was considered a good estimate owing to the close agreement of the values from the preceding methods:

$$V_p = 9.4 \times 10^6 \text{ m}^3$$

#### Flow Ratio

Flow ratio is the ratio of river flow per tidal cycle to the tidal prism. When the flow ratio is greater than or equal to 1.0, the estuary is highly stratified; when this ratio is about 0.25, the estuary is partially mixed, and when it is less than 0.1, the estuary is

well-mixed. The equation for the computation of the flow ratio (F.R.) is as follows:

$$\text{F.R.} = \frac{\text{rate of river inflow (m}^3\text{/sec)} / \text{tidal cycle}}{\text{tidal prism}} \quad \text{Eq. 2}$$

For the range of the flow ratio in the South Slough Estuary, rates of river inflow in February (maximum) and August (minimum) were used:

$$\text{River flow (Feb.)} = 6.6 \text{ m}^3\text{/sec.}$$

$$\text{River flow (Aug.)} = 0.2 \text{ m}^3\text{/sec.}$$

$$\begin{aligned} \text{F.R. (Feb.)} &= \frac{6.6 \text{ m}^3\text{/sec} \times 3600 \text{ sec/hr} \times 12.4 \text{ hrs/tidal cycle}}{9.4 \times 10^6 \text{ m}^3} \\ &= 0.0313 \end{aligned}$$

$$\begin{aligned} \text{F.R. (Aug.)} &= \frac{0.2 \text{ m}^3\text{/sec} \times 3600 \text{ sec/hr} \times 12.4 \text{ hrs/tidal cycle}}{9.4 \times 10^6 \text{ m}^3} \\ &= 0.0009 \end{aligned}$$

Both of these flow ratio values are less than 0.1, therefore, South Slough is a well-mixed estuary during all seasons.

#### Flushing Time

Flushing time is the time necessary to replace the freshwater within the estuary at a rate that is equal to the discharge of the river (Dyer, 1973). However, river flow is not the only factor affecting flushing. The range of the tide which alters the tidal prism is also of major importance. Flushing time (F.T.) is computed by means of the formula:

$$\text{F.T.} = \frac{\text{volume of segment} \times \text{freshwater fraction in segment}}{\text{rate of river inflow (m}^3\text{/sec)}} \quad \text{Eq. 3}$$



For South Slough, the extreme values of the fraction of freshwater in the basin are 0.0191 in February, and 0.0005 in August.

The flushing time therefore is:

$$F.T. (Feb.) = \frac{(5.3 \times 10^6 \text{ m}^2) \times 1.7 \text{ m} \times 0.0191}{6.6 \text{ m}^3/\text{sec}}$$

$$= 0.30 \text{ day}$$

$$F.T. (Aug.) = \frac{(5.3 \times 10^6 \text{ m}^2) \times 1.7 \text{ m} \times 0.0005}{0.2 \text{ m}^3/\text{sec}}$$

$$= 0.26 \text{ day}$$

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