TRANSPORT OF ZOOPLANKTON IN SOUTH SLOUGH, OREGON

by

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A THESIS

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and the Graduate School of the University of Oregon
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"Transport of Zooplankton in South Slough, Oregon," a thesis prepared by Amy L. Puls in partial fulfillment of the requirements for the Masters of Science degree in the Department of Biology. This thesis has been approved and accepted by:

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An Abstract of the Thesis of

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Title: TRANSPORT OF ZOOPLANKTON IN SOUTH SLOUGH, OREGON

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Dr. Alan Shanks

Planktonic larvae of estuarine organisms exhibit two dispersal patterns, export and retention. The effects of rhythmic vertical migrations by planktonic larvae on dispersal have been well documented. Most of these studies were done in partially-mixed estuaries with non-tidal residual flow.

South Slough, a National Estuarine Research Reserve, is well mixed due to low freshwater input and tidal mixing of the relatively shallow water column. Little is known about the transport of zooplankton in South Slough; therefore, abundances and vertical distributions of multiple species in several taxa were investigated over five semi-diurnal tidal cycles from an anchor station. The data suggest larvae of *Neotrypaea californiensis* and *Hemigrapsus oregonensis* were exported, while pinnotherid larvae and larval fish were retained. Additionally, there were a variety of zooplankters that were imported into South Slough from coastal ocean waters. The role of vertical migration in larval transport is discussed.

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CHAPTER I

INTRODUCTION

After hatching from the egg, but prior to settling to the benthos where the majority of their life-cycle is spent, most marine and estuarine benthic invertebrates progress through one or more planktonic larval stages. Though the larval period is a relatively small part of an organism's life-cycle, what happens to larvae in terms of survival and advection has large consequences. It has long been recognized that larval supply affects the abundance and distribution of benthic populations (Underwood & Fairweather 1989, Grosberg & Levitan 1992). Understanding factors that affect the supply of larvae to a population, such as larval transport, is important for understanding marine and estuarine population dynamics, and is critical for the management of populations, be it for conservation or exploitation.

Planktonic larvae of estuarine organisms are either exported from the estuary shortly after hatching and develop in offshore waters, returning to the estuary as late-stage larvae or juveniles, or, they are retained in the estuary throughout their development (reviewed in Epifanio 1988). There are also coastal invertebrate species, as well as fishes, that utilize estuaries as nursery habitats as larvae and juveniles, later to return to the coastal ocean as adults (reviewed in

Epifanio 1988 and Boehlert & Mundy 1988). The mechanisms by which larvae are transported into and out of estuaries involves physical processes, and in many species, as a growing amount of evidence suggests, the swimming behavior of the larvae.

Because most planktonic larvae are small and swim relatively slowly, their swimming capabilities are inadequate to overcome horizontal current speeds that they typically encounter; however, most larvae swim fast enough to overcome vertical water currents that they typically encounter (Mileikovsky 1973, Chia et al. 1984). By swimming vertically larvae are able to affect their horizontal transport; because, in many instances the speed and direction of water currents vary over the depth of the water column. In estuaries the current direction changes predictably on a regular basis with the ebb and flood of the tide. There is now a large body of evidence that many planktonic larvae of estuarine organisms undergo vertical migrations timed to specific phases of the tide (reviewed in Forward & Tankersley 2001). This behavior, termed selective tidal-stream transport, can result in unidirectional horizontal transport along the estuary or maintenance of their position in a segment of the estuary. This has been best studied in decapods and fish, but the behavior has also been seen in some species of copepods, bivalves, and polychaetes (Forward & Tankersley 2001).

Two general dispersal patterns have been observed in planktonic larvae of estuarine invertebrates, export and retention. Larvae have been observed to export from estuaries in a couple of ways. In partially-mixed estuaries with two-

layer circulation there is a net seaward flow of water at the surface and a net landward flow at the bottom (Pritchard 1955). Therefore, larvae that maintain a position in surface waters will be carried out of the estuary into the coastal ocean via the residual currents. This is the behavior seen in larvae of *Callinectes sapidus* in Delaware Bay, USA (Epifanio et al. 1984). The export process is further enhanced by female *C. sapidus* crabs migrating to the mouths of bays to spawn. This strategy, of maintaining a position high in the water column, will result in export only if there is a net seaward flow at the surface and the flushing time is shorter than the larval development period. The other ways that larvae export from estuaries can be classified as ebb-tide transport. These strategies require larvae to ascend into the water column during ebb tide and reside on or near the bottom during flood tide. The first stage zoeae of *Carcinus maenas* in Canal de Mira, Portugal, reached their highest position in the water column during ebb tide and their lowest during flood tide (Queiroga et al. 1997). By maintaining a position low in the water column during flood tides, where currents were slower, larvae minimized landward transport, and by rising into the faster moving surface currents during ebb tide, they maximized seaward transport. DiBacco et al. (2001) found that first stage *Pachygrapsus crassipes* zoeae aggregated at the sediment-water interface during flood tides and near the surface of the water column during nocturnal ebb tides preventing landward transport and maximizing their export from San Diego Bay.

Larvae that export from estuaries develop in off-shore waters and then

must return to the estuary as they become competent to settle. Larvae that invade estuaries must behave in the opposite manner of larvae leaving the estuary, i.e. remain in the landward flowing bottom waters, or hold a position high in the water column during flood tides and on or near the bottom during ebb tides. Many crab megalopae have been found to utilize flood-tide transport (i.e. ascent during flood tide and descent during ebb tide) (Epifanio et al. 1984, Brookings & Epifanio 1985, Little & Epifanio 1991, Queiroga et al. 1994, Dittel & Epifanio 1990, Dittel et al. 1991, DeVries et al. 1994). Juvenile shrimp and fish also use flood-tide transport to move up the estuary to nursery habitat (Forward & Tankersley 2001).

Zooplankton have been observed to retain in estuaries in a number of ways. Larvae with developmental periods shorter than the flushing time of their estuary and that lack behaviors to expedite export will be retained. Upon hatching, some larvae maintain a position high in the water column, but as they develop they become negatively phototactic and positively geotactic (Sulkin 1984) and take a position lower in the water column. In estuaries with net seaward flows in the upper water layer and net landward flows in the lower water layer, if a large enough portion of the larval period is spent in the lower water layer the larvae may be retained in the estuary (Epifanio 1988). This was best demonstrated in the barnacle *Balanus improvisus* in the classic study by Bousfield (1955) in the Miramichi Estuary, New Brunswick. In estuaries with two-layer circulation systems, larvae may also retain by undergoing vertical

migrations centered around the depth of no net flow. An example of this vertical migration behavior is seen in the euryhaline crab, *Rhithropanopeus harrisii* (Cronin 1982). In the Conwy Estuary, United Kingdom, which is a strongly tidal, partially mixed estuary, Hough and Naylor (1991) found that the copepod *Eurytemora affinis* could be retained in the estuary by "switching" behaviors depending on its location in the estuary. In high salinity areas, the copepods would ascend during flood tides and descend during ebb tides resulting in movement up the estuary. Alternately, in low salinity areas, copepods would ascend during ebb tides and descend during flood tides resulting in movement down the estuary. In San Diego Bay, California, freshwater input is negligible during the dry season; therefore, residual flows are weak or absent. DiBacco et al (2001) found that without a distinct vertical migration pattern, larvae of *Lophopanopeus bellus* were retained in San Diego Bay.

The transport of planktonic larvae of estuarine organisms has been studied in a number of estuaries. Many of the studies have been done on the East Coast of North America in large, partially-mixed estuaries with two layer circulation; however, more recently, smaller estuaries across several continents have been examined. On the West Coast of North America, relatively few studies have looked at the dispersal strategies of estuarine invertebrates. Therefore, we investigated the advective transport of several zooplankton species in South Slough, a small, well-mixed estuary on the southern Oregon coast. For some of the species this is the first published description of their

dispersal patterns.

CHAPTER II

DESCRIPTION OF THE STUDY SITE

This study was conducted during August and September 1996 from a floating anchor station in South Slough, an arm of the Coos Bay estuary, Oregon. The anchor station was located near the mouth of the slough, which in turn is located approximately 1.6 km from the mouth of Coos Bay (43.3°N, 124.3°W; Fig. 1). Coos Bay, located on the southern coast of Oregon, is the fifth largest estuary in the Pacific Northwest. Characterized as a drowned river valley it has a surface area of ~50 square kilometers (State of Oregon Division of State Lands 1973).

With an average depth of two meters, approximately 65% of the Coos Bay estuary is intertidal (Rumrill in prep). At low tide, extensive mudflats are exposed as well as eelgrass beds of *Zostera marina.* The mudflats, eelgrass beds, and subtidal habitat in the estuary support a diverse community of marine and estuarine invertebrates. Macrofauna typical of these habitats include: burrowing shrimp, such as *Upogebia* and *Neotrypaea*; numerous species of bivalves, worms, and crabs; as well as a variety of fishes. There is also a small amount of rocky substrata found within the estuary with an associated community of invertebrates and fish.

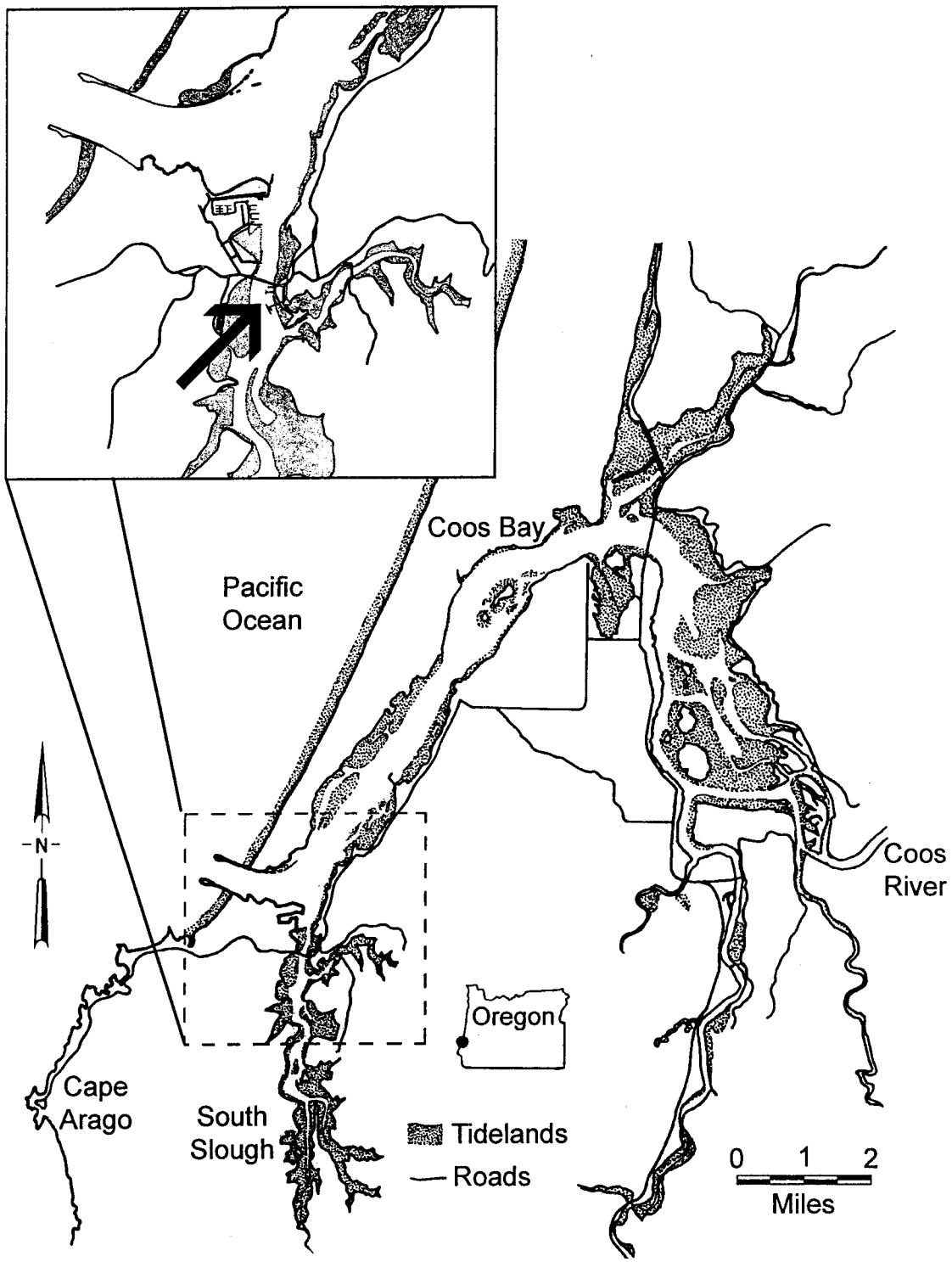

Fig. 1. Map of the Coos Bay estuary, Oregon, and location of the sampling station (indicated by arrow) in South Slough. (adapted from Roye 1979)

Freshwater input into the Coos Bay estuary is highly seasonal. Between October and May average rainfall is 140 cm, but less than 10 cm falls between June and September. Total annual rainfall (measured at the North Bend, Oregon airport) during 1996 was 214.8 cm, with 2.95 cm falling during the course of the study (and almost all of that fell during the last sampling period)(Oregon Climate Service 2001). Approximately 70% of the 1576 km^2 Coos Bay watershed drains into the Coos River (US Army Corps of Engineers 1993). Maximum freshwater flow occurs in February and minimal flow occurs in late summer (August and September), with flows of 155.7 $m^3 s^{-1}$ and 2.55 $m^3 s^{-1}$, respectively (Percy et al. 1974). A number of small creeks also contribute freshwater to Coos Bay (Fig. 1).

In the summer, circulation in the Coos Bay estuary is dominated by semidiurnal tides that have a mean excursion of 1.7 m and extremes of -0.6 and 2.8 m relative to MLLW (mean lower low water)(Oregon Dept of Trans 1983). The tidal prism is approximately 5.3 x 10^7 m^3 (Arneson 1976); therefore, approximately 77% of the water within the Coos Bay estuary is discharged during an ebb tide. The estuary is essentially well mixed throughout the year (Burt and McAlister 1959). During periods of low freshwater inflow (typical for Coos Bay during summer and early fall), well-mixed estuaries typically have a slow net seaward drift at all depths; salt moves landward against the drift by means of diffusion, enhanced by tidal mixing (Burt & McAlister 1959).

South Slough, a National Estuarine Research Reserve, is an arm of the Coos Bay estuary (Fig. 1). The slough has a surface area of 20.2 km^2 with a

watershed surface area of 193 km^2 (Rumrill in prep). It experiences limited freshwater input from a number of small creeks and streams with maximal runoff in February at 6.6 $m^3 s^{-1}$ and minimal runoff in August at 0.2 $m^3 s^{-1}$ (Pimentel 1986). The tidal prism was estimated to be $9.4 \times 10^6 m^3$ (Harris et al. 1979); hence, during an average amplitude tide approximately 48% of the water in South Slough is discharged during an ebb tide. Using a mean tidal range of 1.7 m, Pimentel (1986) calculated the flushing time of South Slough for February and August to be about one tidal cycle.

CHAPTER III

MATERIALS & METHODS

In order to investigate the physical structure of the water column and advective transport of zooplankton, we occupied an anchor station for five semi-diurnal tidal periods, spaced about a week apart, from 7 August - 14 September 1996 (Table 1, Fig. 2). Late summer dates were chosen because many of

Table 1. 1996 sampling period dates and times, maximum tidal amplitude during the sampling period, and coastal ocean conditions with respect to the upwelling-downwelling cycle.

Sampling period	Start (date / time)	End (date / time)	Maximum tidal amplitude (m)	Downwelling or upwelling
7 Aug.	7 Aug. / 01:57	8 Aug. / 06:58	2.03	upwelling
15 Aug.	15 Aug. / 07:30	16 Aug. / 07:57	2.08	upwelling
28 Aug.	28 Aug. / 06:03	29 Aug. / 07:00	2.95	downwelling
5 Sep.	5 Sep. / 00:45	6 Sep. / 01:48	1.30	downwelling
13 Sep.	13 Sep. / 06:27	14 Sep. / 07:38	1.89	downwelling

the decapod larvae are completing their larval development at these times, and second broods are just beginning to hatch (Table 2). The anchor station consisted of a boat anchored in the middle of the South Slough channel approximately 2 km from the mouth of Coos Bay. Sampling was initiated at slack low water. Conductivity, temperature, and depth were measured with a Seabird 19 CTD. A Wetstar fluorometer was attached to the CTD to measure the

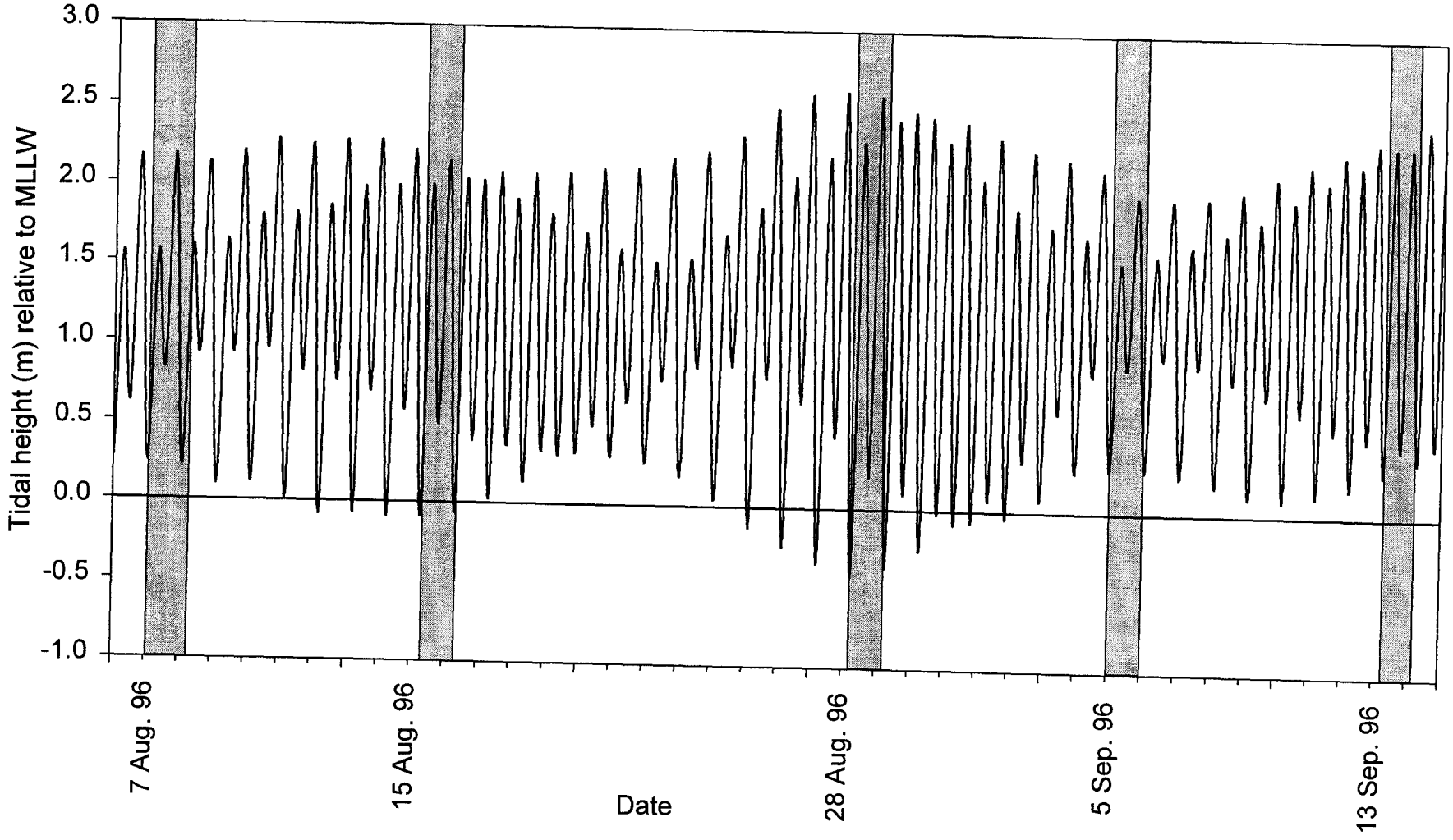

Fig. 2. Relation of sampling periods, tidal amplitudes, and the spring-neap cycle. Grey shading indicates when sampling occurred.

Table 2. Life history information of decapod species found in the vicinity of Coos Bay, Oregon.

Organism	Range	Adult habitat	Number of broods	Months broods hatch	Number of larval stages	Larval period
Neotrypaea californiensis	Alaska - Baja (a)	Estuaries (a)	3 - 4 (b)	May - Sep (b)	5 zoeae 1 megalopa (b)	6 - 8 weeks (b)
Hemigrapsus oregonensis	Alaska - Baja (a)	Estuaries but also outer coast (a)	2 (c)	May - Jul; Aug - Sep (c)	5 zoeae 1 megalopa (d)	4 - 5 weeks (d)
Lophopanopeus bellus	Alaska - California (a)	Mainly outer coast but also in lower reaches of estuaries (a)	2 (c)	May - Aug; Aug - ? (c)	4 zoeae 1 megalopa (d)	5 weeks (c)
Pachygrapsus crassipes	Oregon – Sea of Cortez (a)	Estuaries and outer coast (a)	1-2 (e)	ovigerous April - Sep (e)	5 (f) or 6 (g) zoeae 1 megalopa	3 months z1 up to meg (f)
Pinnotherid spp.	Alaska – Baja (a) (Individual species ranges may be smaller)	Commensal with estuarine organisms (a)	multiple (h)	year round (h) peaks late summer-early fall and late winter-early spring (c)	5 zoeae 1 megalpoa (h)	7 - 8 weeks (h)
Porcelain crabs	S.E. Alaska - Southern California (a)	Mainly outer coast but also in lower reaches of estuaries (a)	2 (c)	May - mid Aug; Aug - early Oct (c)	2 zoeae 1 megalopa (i)	5 - 6 weeks (i)
Emerita analoga	Oregon - Chile (a)	Outer coast (a)	?	July - Aug (j)	5 zoeae 1 megalopa (j)	4 months (k)

(a) Jensen (1995); (b) McCrow (1972); (c) Strathmann (1987); (d) Hart (1935); (e) Morris et al. (1980);
(f) Schlotterbeck (1976); (g) DiBacco (2001); (h) Lough (1975); (i) Gonor and Gonor (1973);
(j) Johnson and Lewis (1942); (k) Johnson (1939)

concentrations of chlorophyll *a*, and a NE Sensortec A/S UCM-60 acoustic current meter measured horizontal current velocity. The instrument package (CTD, fluorometer, and current meter) recorded measurements at 12 s intervals. The instrument probes were suspended from the boat at ~0.7 m depth (relative to the water's surface) except during vertical profiles that were conducted at about hourly intervals. During a vertical profile, the instrument package was first brought up to the surface and then lowered to within 5 cm above the bottom. As the instrument package was lowered through the water column, it was stopped about every 30 cm and usually held at this depth for 30 seconds, but sometimes up to a minute or more.

Zooplankton was sampled with a 333 micron mesh net (mouth dimensions of 1 x 0.3 m). Styrofoam floats along the upper edge of the net mouth and weights along the bottom edge ensured that the plane of the mouth was perpendicular to the flow of water. A rotary flow meter mounted in the center of the net mouth was used to calculate volume of water filtered. Approximately once an hour, neuston and near-bottom tows were conducted consecutively. Thirty pounds of weight was added to the lower edge of the net in order to sink it to the bottom for the near bottom samples. Samples were collected by allowing the water to pass through the net (which was approximately 35 meters downstream of the boat) for 5 to 10 min depending on the velocity of the tidal currents. The objective was to filter about 50 m^3 of water per sample. The actual

volume filtered ranged from 4 to 99 m^3, with a mean of ~40 m^3 and a median of ~37 m^3. Samples were preserved in ~7% buffered formalin.

Zooplankton were enumerated in the laboratory using a dissecting microscope. The entire sample was examined for species of interest (Table 3); however, if more than three hundred individuals of a given species were encountered in the first half of the sample, a 5 ml Stemple pipette was used to sub-sample. Aliquots were taken from a known volume until approximately two hundred organisms had been counted. Larvae were identified according to Shanks (2001) (decapods and barnacles), Wrobel and Mills (1998) (gelatinous organisms), and Matarese et al. (1989) (larval fish). Not all organisms were counted for all sampling periods; Table 3 shows whether an organism was present and counted, absent, or not counted.

Table 3. Organisms enumerated in samples collected from South Slough during five sampling periods. A = absent, P = present, NC = not counted.

Organism	Stage	7 Aug.	15 Aug.	28 Aug.	5 Sep.	13 Sep.
DECAPODS						
Cancer spp.	z1-z5	A	A	A	A	A
	meg	P	P	P	P	P
Emerita analoga	z1	P	P	NC	NC	P
	z2-z5	A	A	NC	NC	A
	meg	A	A	A	NC	A
Hemigrapsus oregonensis	z1 & z2	NC	P	P	P	P
	z3	NC	P	P	P	P
	z4 & z5	NC	P	P	P	P
	meg	P	P	A	NC	P
Lophopanopeus bellus	z1 & z2	P	P	NC	NC	P
	z3	A	A	NC	NC	P
	z4	A	A	NC	NC	P
	meg	P	P	A	NC	A
Majid spp.	z1	P	P	P	NC	P
	z2	A	P	P	NC	A
	meg	A	P	A	NC	A
Neotrypaea californiensis	z1 & z2	P	P	P	P	P
	z3	A	A	A	A	A
	z4 & z5	A	A	A	A	A
	meg	A	P	A	A	A
Pachygrapsus crassipes	z1	P	P	NC	NC	P
	z2-z5	A	A	NC	NC	A
	meg	A	A	A	NC	A
Pagurus spp.	z1 & z2	NC	P	NC	NC	P
	z3	NC	P	NC	NC	P
	z4	NC	A	NC	NC	P
	meg	P	P	P	NC	A
Pinnotherid spp.	z1 & z2	P	NC	P	P	P
	z3	P	NC	P	P	P
	z4 & z5	P	NC	P	P	P
	meg	A	A	A	NC	P
Porcelain spp.	z1	P	P	P	P	P
	z2	P	P	P	P	P
	meg	P	P	A	NC	A
NON-DECAPODS						
Clytia gregaria		NC	P	P	P	P
Aequorea spp.		NC	P	P	P	P
Pleurobrachia bachei		NC	P	P	P	P
Chaetognath spp.		NC	P	P	P	P
Barnacle Cyprids		NC	P	P	P	P
Larval Fish	~ 3 mm	NC	P	P	P	A

CHAPTER IV

RESULTS & DISCUSSION

Physical Forcing within the South Slough Estuary

Circulation in the South Slough estuary was tidally driven during the summer sampling period. Measurements of the physical variables showed little variability over the depth of the water column, indicating that the water was well-mixed. Estuarine water temperature, salinity, and velocity, however, varied with the tides. Consistent patterns in the time-series of estuarine water parameters were apparent.

The depth of the water column at the anchor station ranged from ~1.5 to ~5 m (Figs. 8-12a). Data from hourly CTD casts indicate that the water column was well-mixed during all five sampling periods. Temperature gradients greater than 1 °C or salinity gradients greater than 0.5 psu, over the depth of the water column, were rare (Figs. 3 and 4).

Plots of the individual vertical casts illustrate that the velocity varied only slightly over the depth of the water column. Within a vertical cast, it was typical for the velocity to vary 0.05 to 0.2 m s^{-1}; however, there was no consistent relationship between horizontal velocity and depth within the water column (Figs. 5-7). Of the 107 vertical profiles conducted during the five sampling periods,

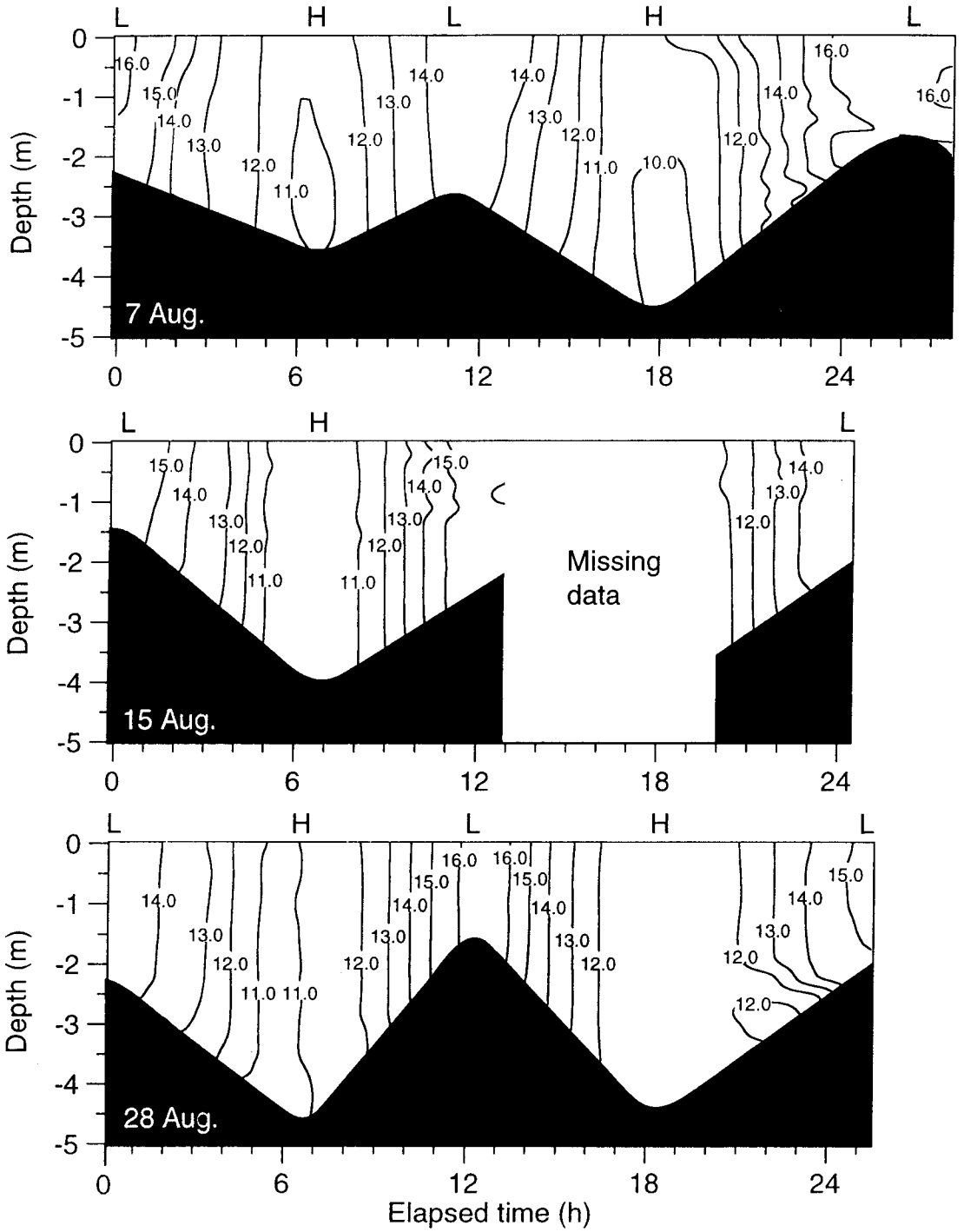

Fig. 3. Time series of hourly vertical temperature profiles for the five sampling periods. Contour intervals are 1 C. Sampling dates are indicated in the bottom left corner of the graphs. Black areas are approximations of the bottom. Since sampling was conducted from an anchor station, as the tide flooded and ebbed, water column depth increased and decreased, respectively. Along the top of the graphs, H indicates high slack tide, and L indicates low slack tide.

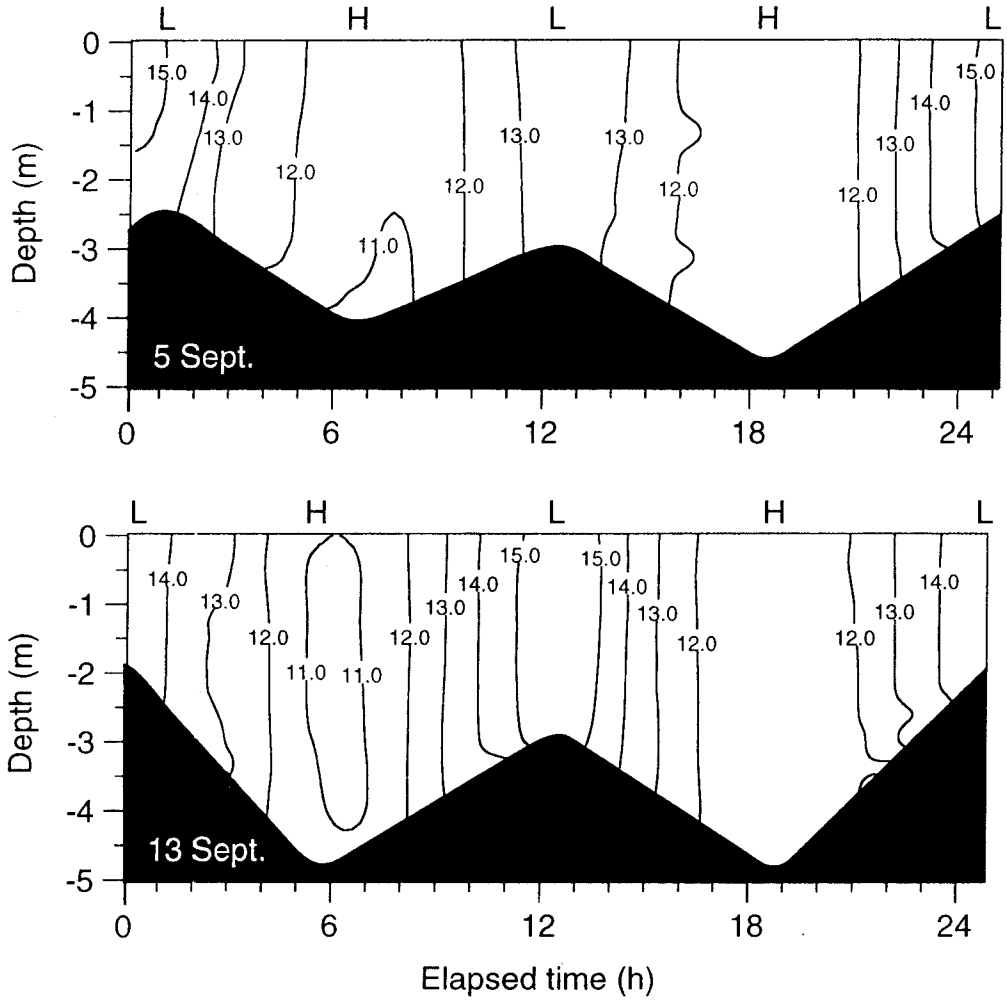
L
H
L
H
L
Depth (m)
0
-1
-2
-3
-4
-5
15.0
14.0
13.0
12.0
11.0
5 Sept.
0
6
12
18
24
13 Sept.
Elapsed time (h)

Fig. 3. Cont.

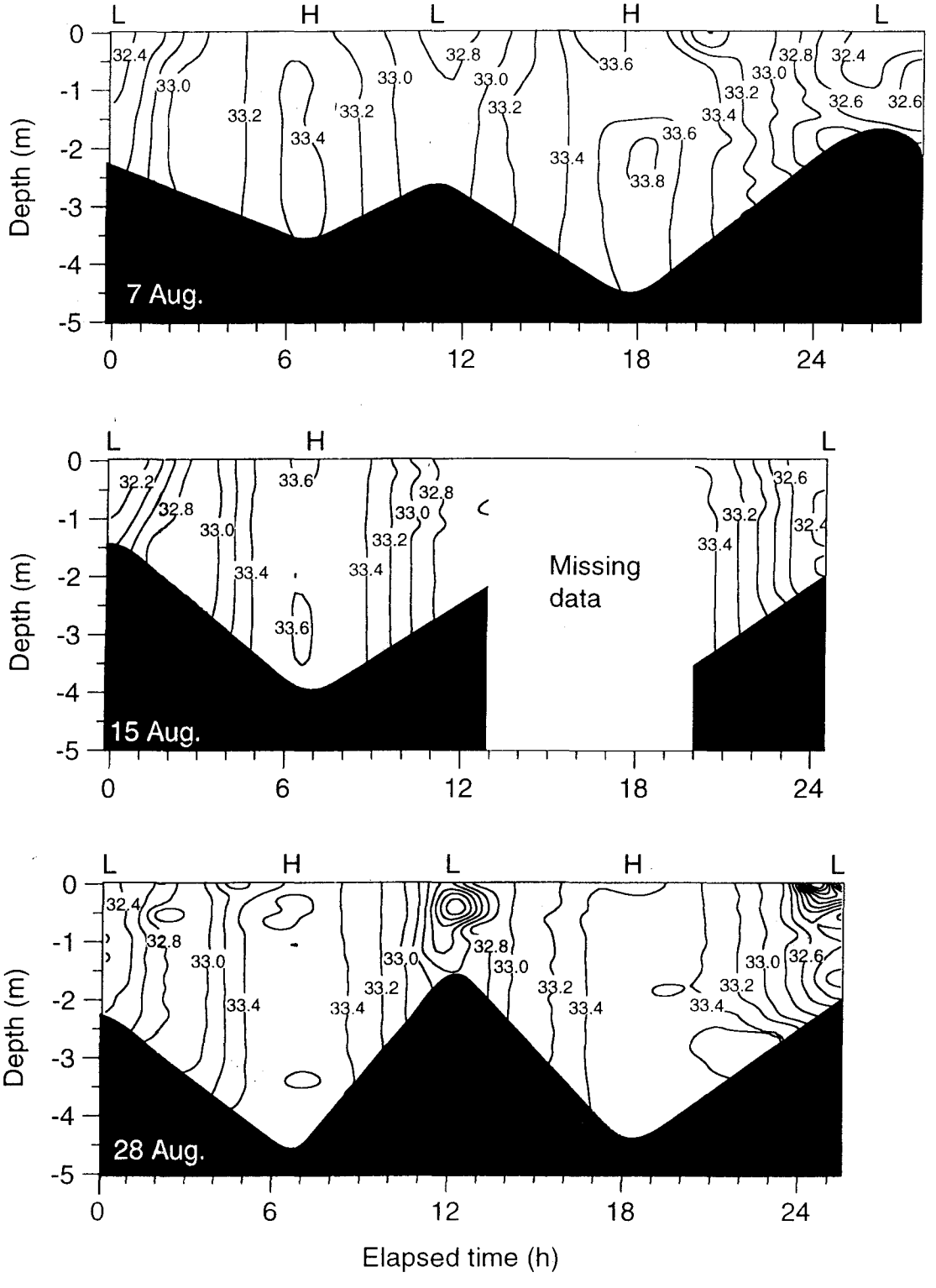

Fig. 4. Time series of hourly vertical salinity profiles. Contour intervals are 0.2 psu. Further details as in figure 3.

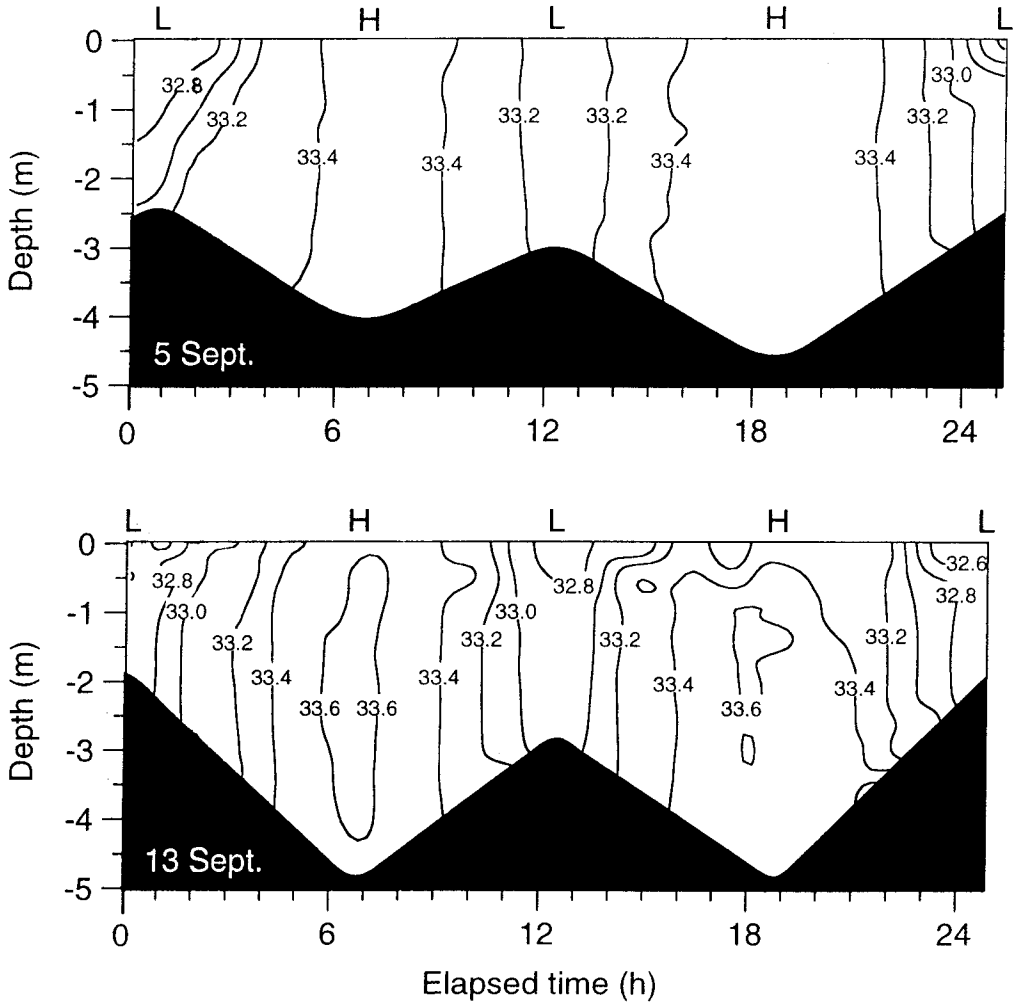
L
H
L
H
L
0
-1
-2
-3
-4
-5
Depth (m)
32.8
33.2
33.4
33.4
33.2
33.2
33.4
33.4
33.2
33.0
5 Sept.
0
6
12
18
24
L
H
L
H
L
32.8
33.0
33.2
33.4
33.6
33.6
33.4
33.2
33.0
32.8
33.2
33.4
33.6
33.4
33.2
32.8
32.6
13 Sept.
Elapsed time (h)

Fig. 4. Cont.

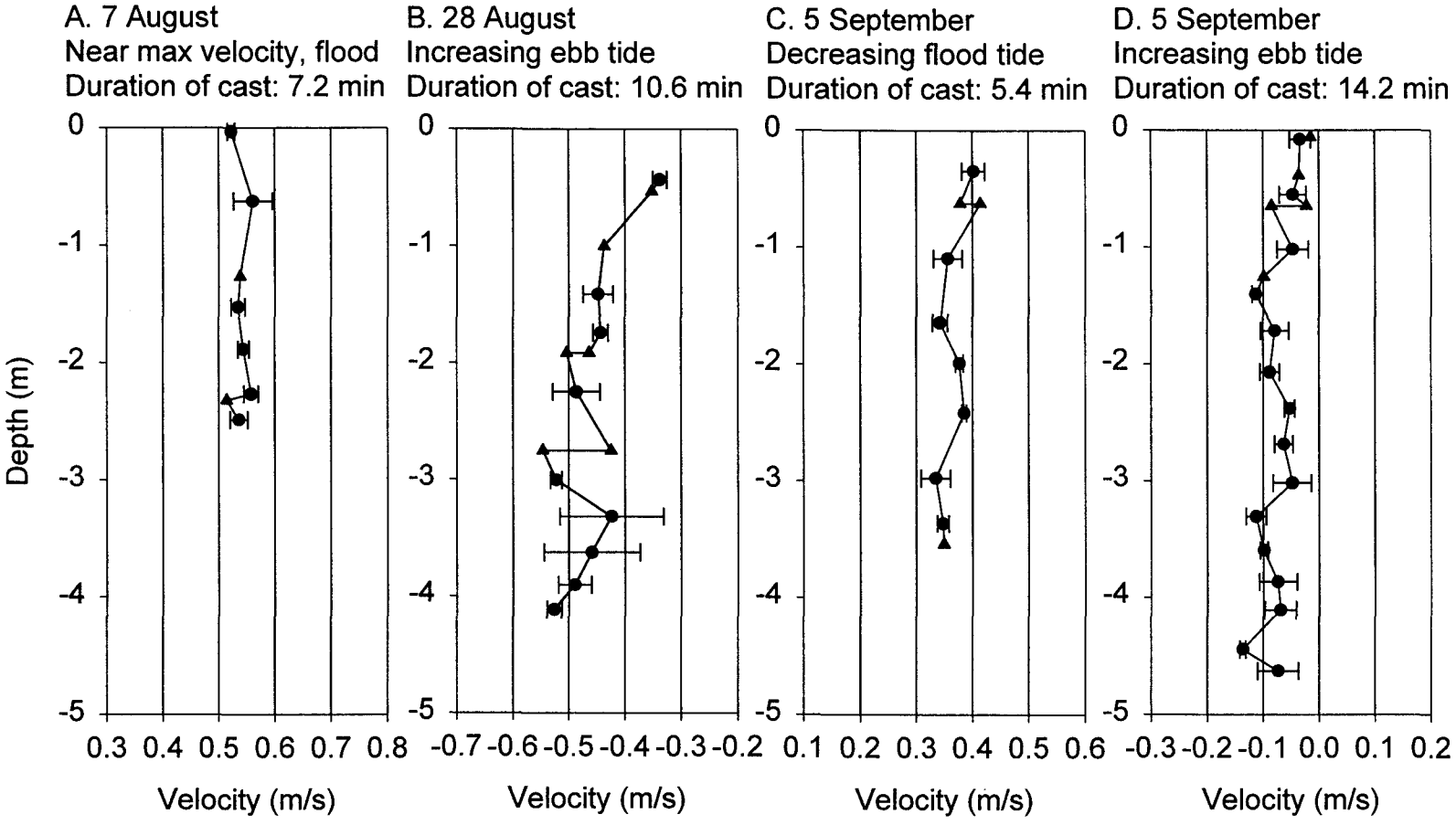

Fig. 5. Examples of vertical profiles of velocity showing variation over depth. At the top of each graph is the date the cast was made, the stage of the tide, and the length of time it took to conduct the cast. Plots are of mean values and the 95% confidence interval; triangles are used when <3 measurement were taken at a depth.

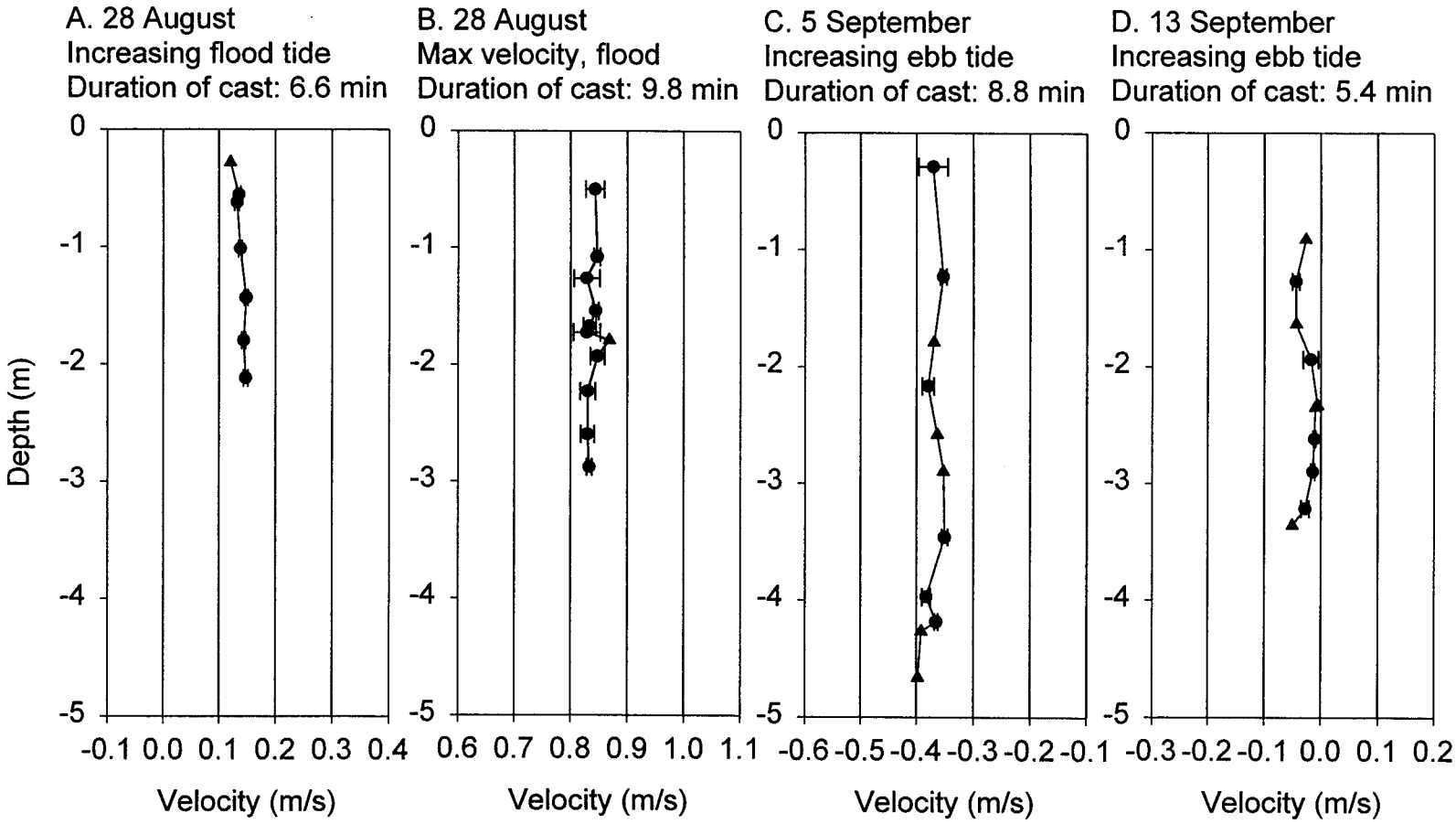

Fig. 6. Examples of vertical profiles of velocity showing the smallest variation over depth. At the top of each graph is the date the cast was made, the stage of the tide, and the length of time it took to conduct the cast. Plots are of mean values and the 95% confidence interval; triangles are used when <3 measurement were taken at that depth.

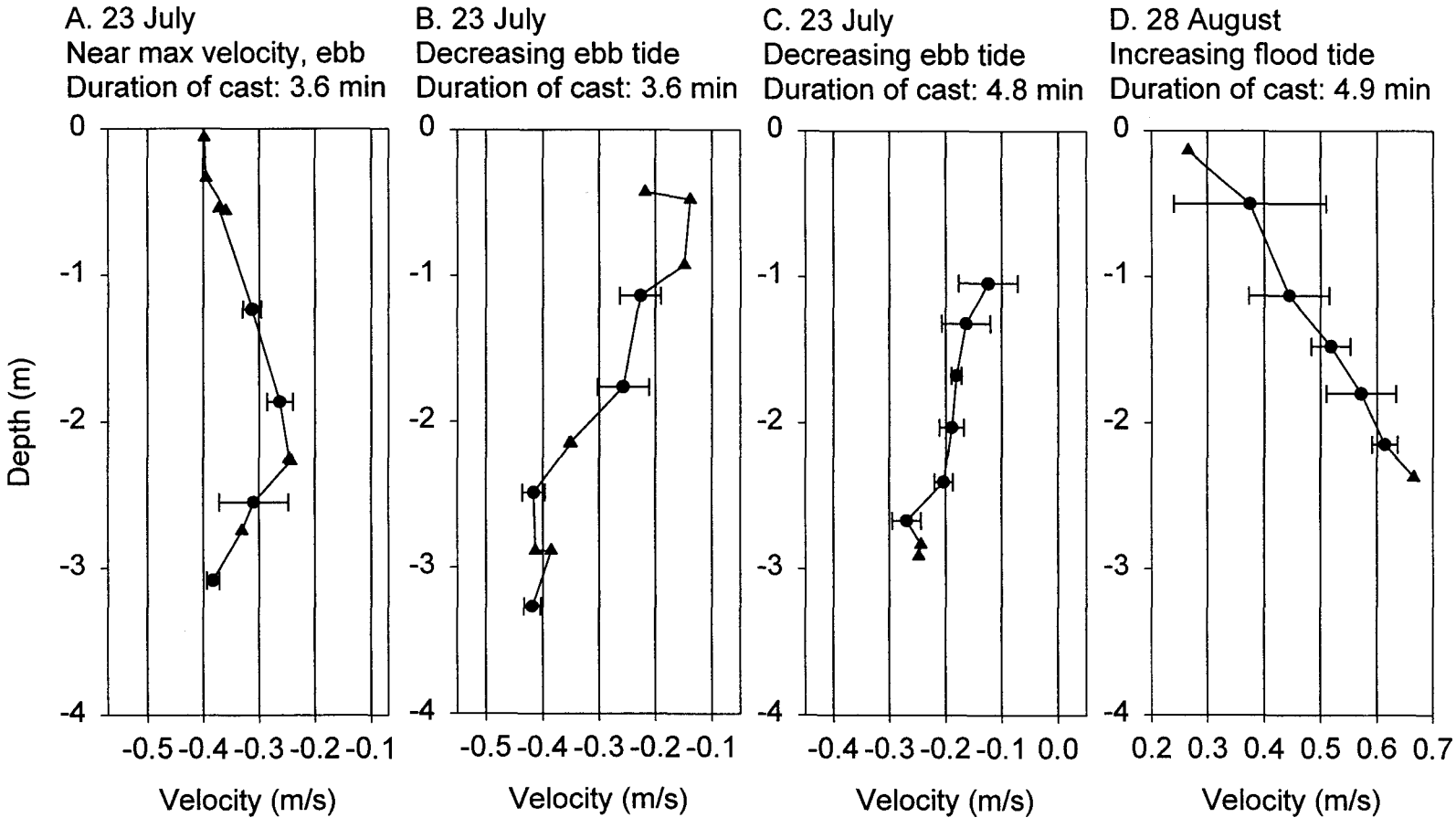

Fig. 7. Examples of vertical profiles of velocity showing the largest variation over depth. At the top of each graph is the date the cast was made, the stage of the tide, and the length of time it took to conduct the cast. Plots are of mean values and the 95% confidence interval; triangles are used when <3 measurements were taken at a depth.

65% had velocities that varied more than 0.05 m s^{-1} but less than 0.2 m s^{-1} (Fig. 5). In 19% of the vertical profiles, differences in velocity over the depth of the water column were less than 0.05 m s^{-1} (Fig. 6). The remaining 16% of the vertical profiles had velocities that varied 0.2 m s^{-1} or more (Fig. 7). We did not observe decreased velocities near the bottom; however, the deepest measurements recorded were ~5 cm above the estuary floor.

Although the water column temperature, salinity, and density were typically homogenous during each individual cast, the physical characteristics of the water at the anchor station were more variable over a tidal cycle. The difference in the values of the physical variables between consecutive slack periods largely depended on the difference in the tidal amplitude between the high and low tides. The smallest change in temperature between consecutive slack tides was ~1 °C as seen on 5 September between low high and high low tide (Table 4), and the largest change in temperature observed between consecutive slack tides was ~7 °C as seen on 7 August between high high and low low tide (Table 4). Because the study was conducted during the summer when freshwater input was at its annual minimum, the range of salinities observed was small; values varied between 0.28 and 2.9 psu between consecutive slack tides (Table 4). Density values varied from 0.6 to 3.36 sigma-t (Table 4).

Despite variation related to the spring-neap cycle, consistent patterns were evident in the physical variables over a tidal cycle. At low tide, the

Table 4: Slack tide values and the change (Δ) in value from the previous slack tide for tidal height (relative to MLLW), temperature, salinity, and density, for the five sampling periods.

7 August	Tidal height		Temperature		Salinity		Density	
	(m)	Δ	(°C)	Δ	(psu)	Δ	(σt)	Δ
Start			16.11		32.32		23.66	
Low high	1.599		10.75	5.36	33.44	1.12	25.59	1.93
High low	0.924	0.675	15.04	4.29	32.76	0.68	24.28	1.31
High high	2.135	1.211	10.18	4.86	33.87	1.11	26.04	1.76
Low low	0.109	2.026	17.06	6.88	32.28	1.59	23.42	2.62

15 August	Tidal height		Temperature		Salinity		Density	
	(m)	Δ	(°C)	Δ	(psu)	Δ	(σt)	Δ
Low low	-0.043		15.94		32.20		23.60	
High high	2.037	2.08	10.87	5.07	33.8	1.6	25.86	2.26
High low	0.406	1.631	16.03	5.16	32.67	1.13	23.95	1.91
Low high	2.031	1.625	Missing data		Missing data		Missing data	
Low low	0.036	1.995	15.08		32.27		23.85	

28 August	Tidal height		Temperature		Salinity		Density	
	(m)	Δ	(°C)	Δ	(psu)	Δ	(σt)	Δ
High low	0.227		15.04		32.16		23.77	
High high	2.588	2.361	10.94	4.1	33.49	1.33	25.61	1.84
Low low	-0.360	2.948	16.48	5.54	30.59	2.9	22.25	3.36
Low high	2.434	2.794	11.17	5.31	33.47	2.88	25.56	3.31
High low	0.109	2.325	15.24	4.07	31.71	1.76	23.58	1.98

5 September	Tidal height		Temperature		Salinity		Density	
	(m)	Δ	(°C)	Δ	(psu)	Δ	(σt)	Δ
Low low	0.278		15.04		32.8		24.26	
Low high	1.574	1.296	11.47	3.57	33.42	0.62	25.46	1.2
High low	0.911	0.663	12.55	1.08	33.14	0.28	24.86	0.6
High high	1.989	1.078	11.02	1.53	33.56	0.42	25.65	0.79
End			15.28	4.26	32.89	0.67	24.28	1.37

13 September	Tidal height		Temperature		Salinity		Density	
	(m)	Δ	(°C)	Δ	(psu)	Δ	(σt)	Δ
Start			14.60		32.71		24.30	
High high	2.325		11.68	2.92	33.50	0.79	25.45	1.15
High low	0.436	1.889	15.59	3.91	32.88	0.62	24.21	1.24
High high	2.324	1.888	11.20	4.39	33.57	0.69	25.63	1.42
End			14.74	3.54	32.57	1	24.16	1.47

temperature of the water at the anchor station was relatively warm and the salinity and density were relatively low. Temperature at low tide ranged from 12.55-17.06 °C, salinity ranged from 30.59-33.14 psu, and density ranged from 22.25-24.86 sigma-t (Table 4). The extent of the values generally depended on the spring-neap cycle. For example, during spring tides, when low tides were the lowest, the water tended to be the warmest and salinity and density tended to be lowest.

As the tide turned and began to rise, the water that most recently ebbed past the station and toward the estuary mouth, flooded back past the anchor station. As flood tide advanced, temperature decreased while salinity, density, and velocity increased (Figs. 8-12).

Approximately 1.5 to 2 hours into the flood tide, water characterized by increasing (or constant) temperature and decreasing (or constant) salinity and density values passed the station. This mass of water is interpreted as water from the main stem of the Coos Bay estuary, and is labeled Coos Bay water in figure 12. This mass of water passed by the station in ~1 to 2 hours.

Following the Coos Bay water, as velocity was typically reaching its maximum, temperature decreased and salinity and density increased relatively rapidly. This water was a mix of estuary water that had been expelled into the ocean during the ebb tide, and coastal ocean water. Eventually the rates at which temperature, salinity, and density were changing slowed as the water composition became more oceanic. Often lines of flotsam, suggesting

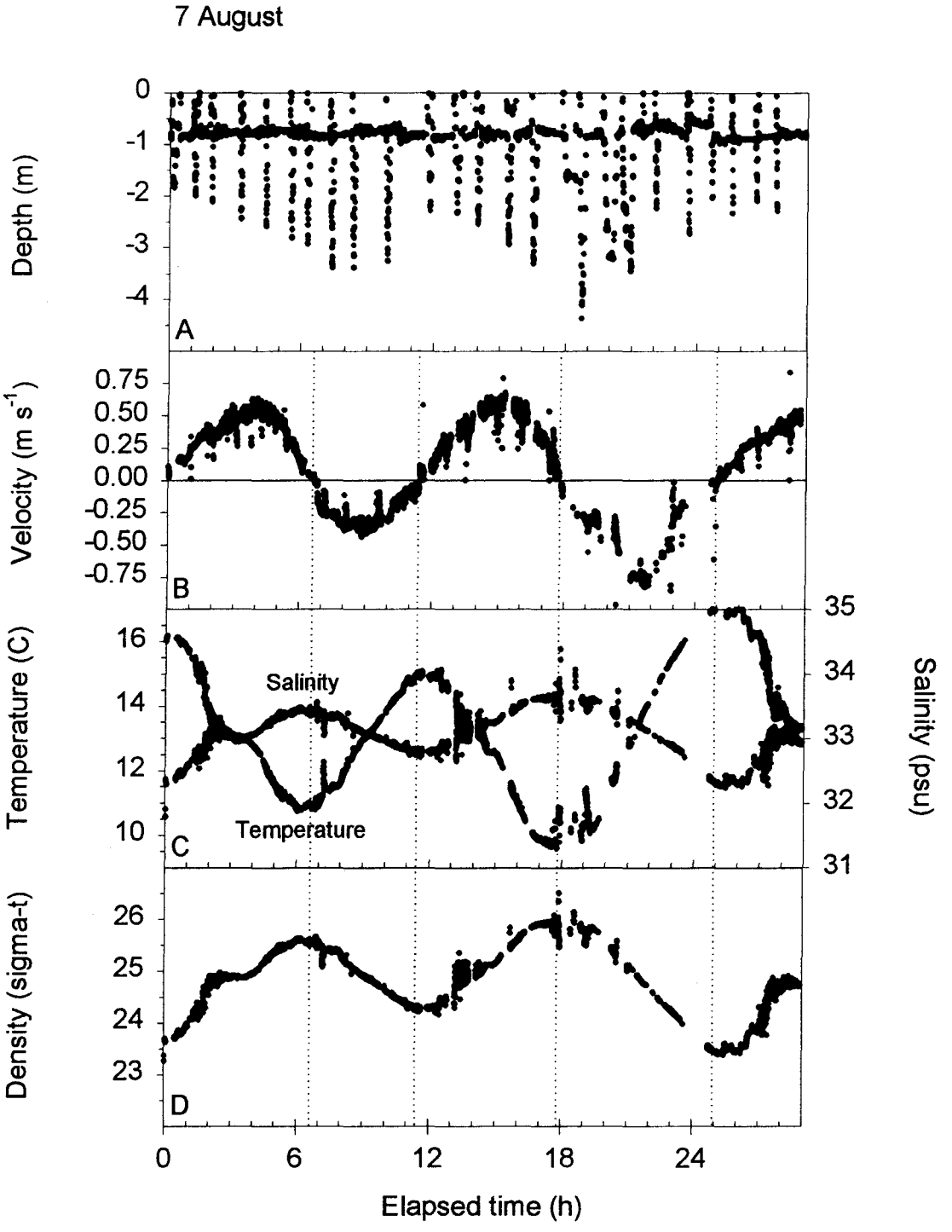

Fig. 8. Time series of physical variables for the 7 August sampling period. Except in graph A, vertical profiles have been removed. Dotted vertical lines indicate slack water. A) Position of the instrument package (CTD, current meter and fluorometer). B) Velocity. Positive values indicate flooding water, and negative values indicate ebbing water. C) Temperature and salinity. D) Density anomaly.

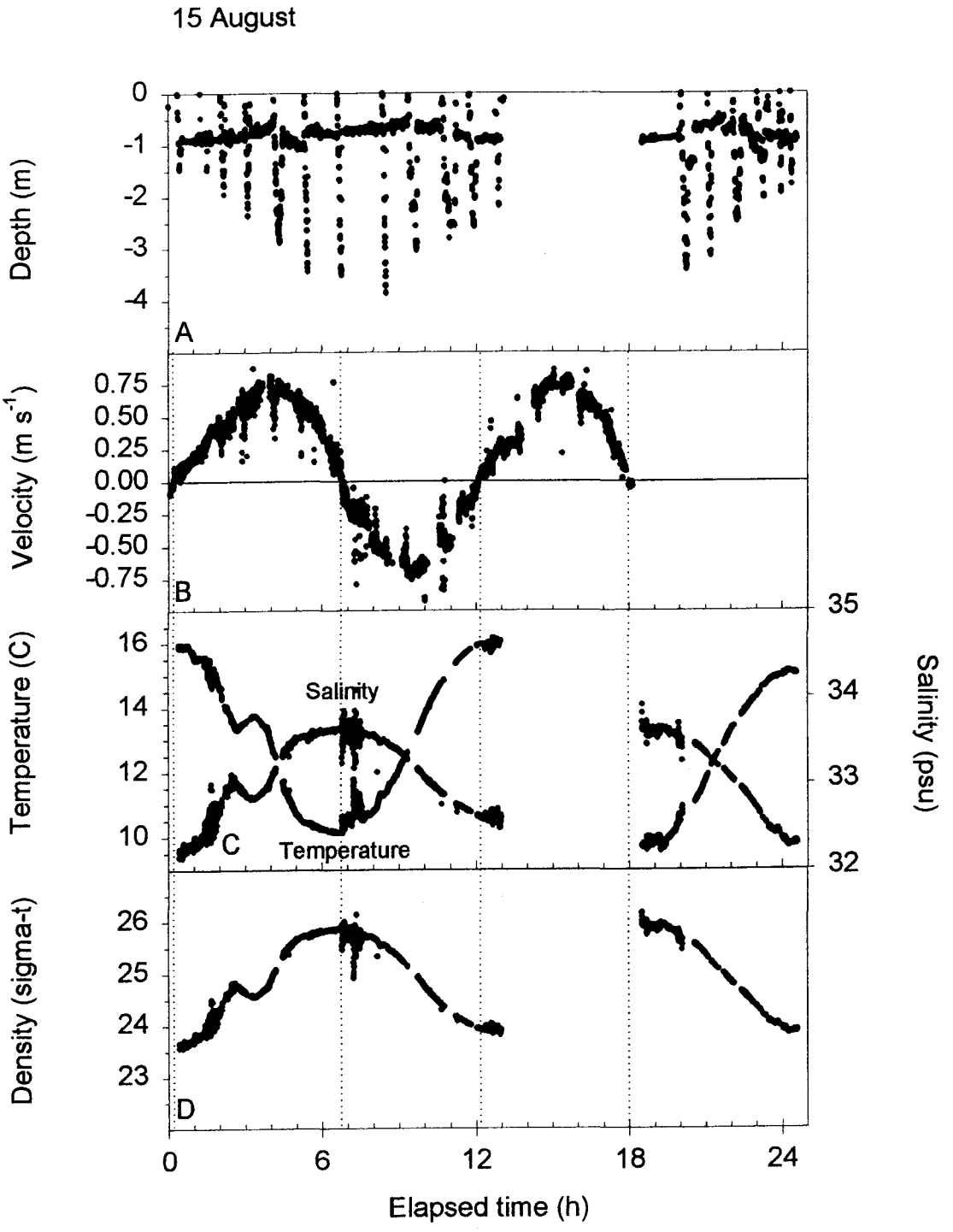

Fig. 9. Time series of physical variables for the 15 August sampling period. Further details as in figure 8.

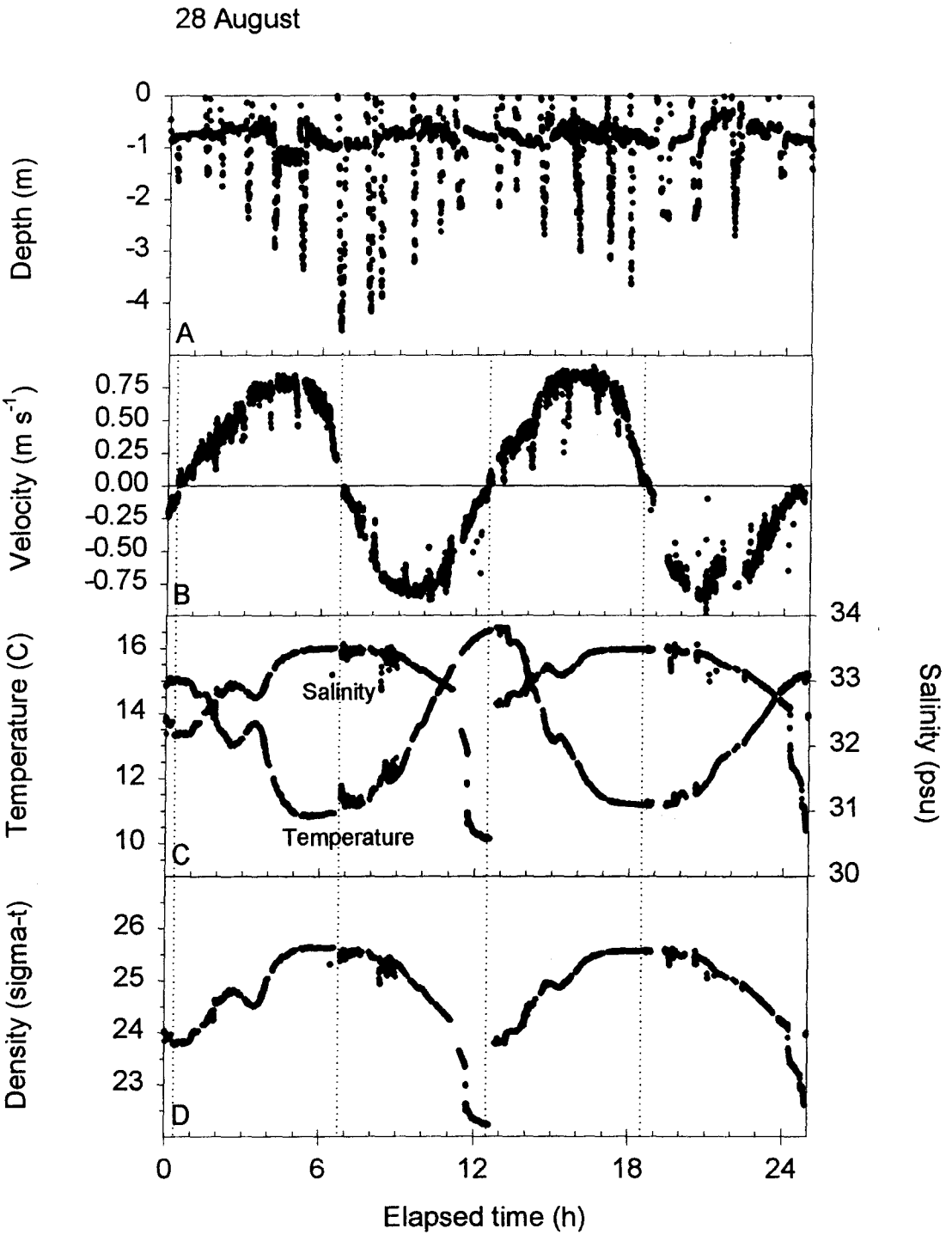

Fig. 10. Time series of physical variables for the 28 August sampling period. Further details as in figure 8.

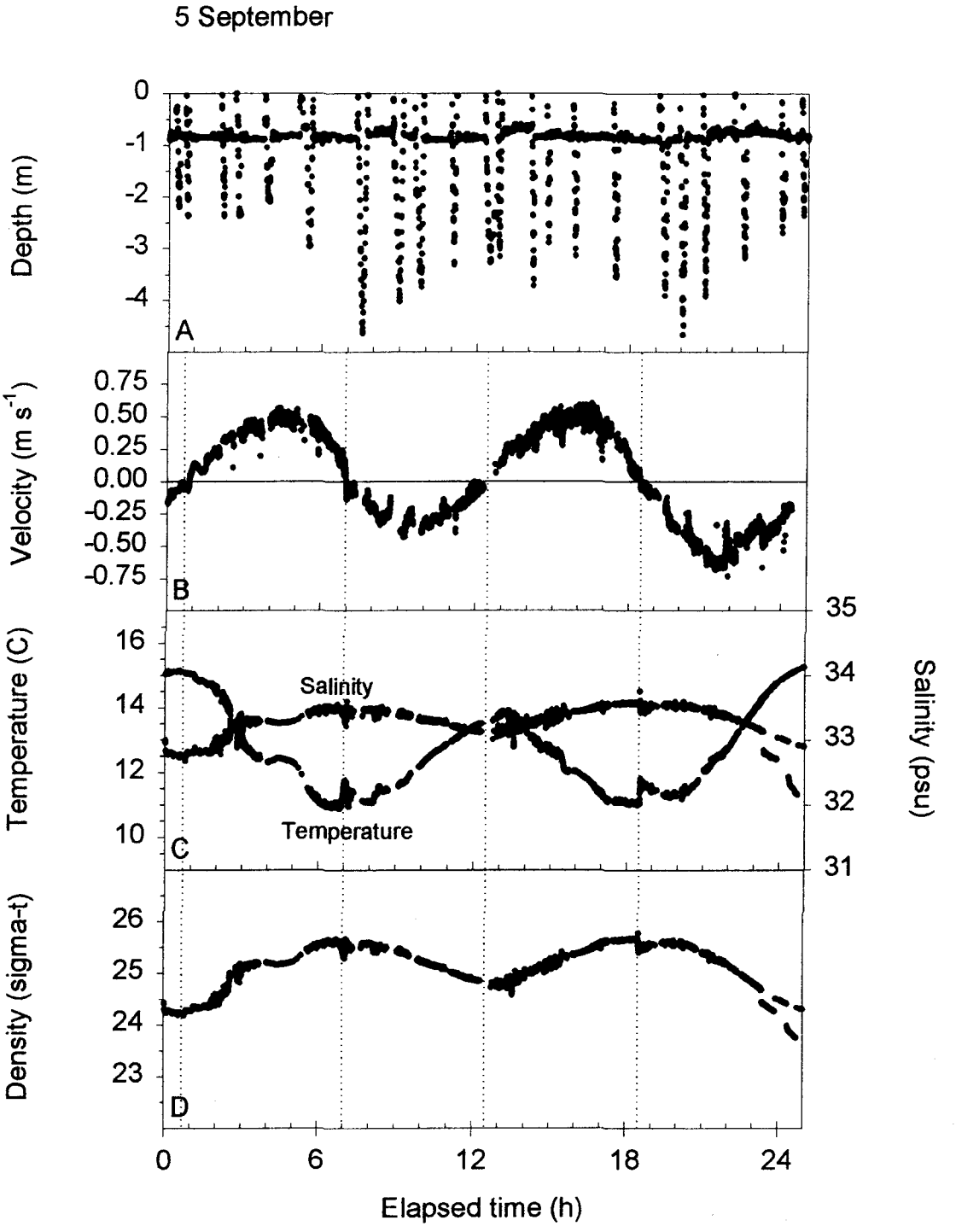

Fig. 11. Time series of physical variables for the 5 September sampling period. Further details as in figure 8.

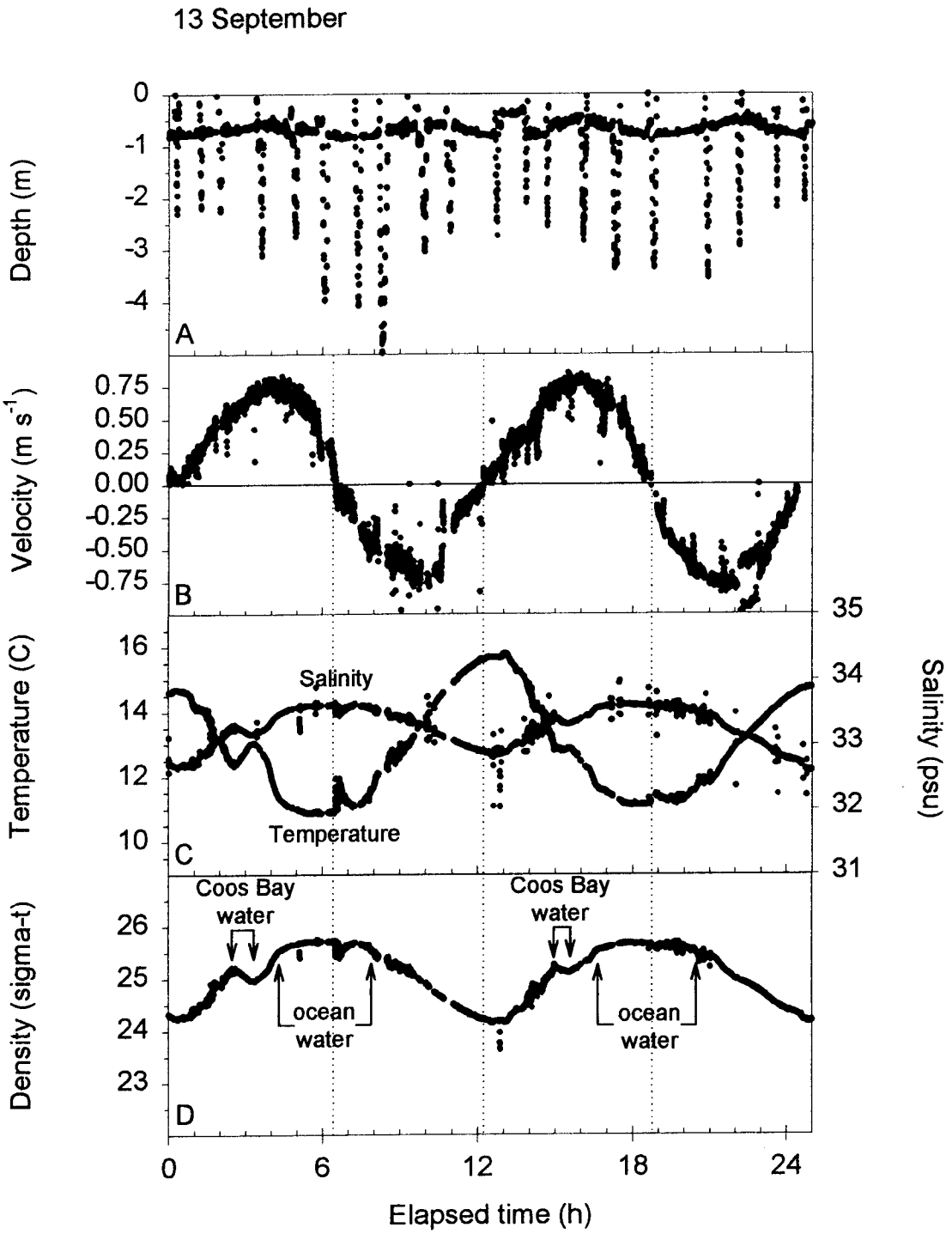

Fig. 12. Time series of physical variables for the 13 September sampling period. Further details as in figure 8.

convergent flow, preceded the coastal ocean water.

For the last 1 to 2 hours of flood tide, as velocity decreased, coastal ocean water (the coldest, highest salinity, most dense water encountered) passed the anchor station (labeled as ocean water in Fig. 12). During this time there was little change in temperature, salinity, and density. Temperatures at high tide ranged from 10.18 to 11.68 °C, salinity ranged from 33.15 to 33.87 psu, and density ranged from 25.21 to 26.04 sigma-t.

The values of the estuarine water parameters observed at high tide not only reflected differences in the spring-neap cycle, but also in the upwelling-downwelling cycle in the coastal ocean. The coldest, highest salinity, densest waters were seen during spring tides that coincided with upwelling favorable periods. Upwelling occurs when northwest winds push the Ekman layer offshore, and colder, higher salinity waters from below upwell to compensate for the displaced surface waters; the upwelled waters are in turn advected into the estuary during flood tide. When winds cease (or blow from the south), the warmer less dense waters, previously held offshore, relax (or are pushed) back against the coast. Though these waters are warm in comparison to upwelled waters, they are still colder than estuarine waters. The 7 and 15 August sampling periods took place during upwelling favorable periods, while the 28 August, 5 September, and 13 September sampling periods took place during downwelling favorable periods (Roegner and Shanks, 2001).

As the tide turned from flood to ebb, the coastal ocean water that most

recently entered the slough retreated. As ebb tide progressed and velocity increased, temperature increased while salinity and density decreased. The mass of Coos Bay water was no longer distinct.

Though the pattern in the time-series of estuarine water parameters described above was evident during most sampling periods for both portions of the semi-diurnal tidal cycle, during neap tides some features were absent during the smallest tidal amplitude changes. On 7 August and 5 September, ocean water failed to arrive at the anchor station during the shift from the low low tide to low high tide (Figs. 8 and 11). On 5 September the Coos Bay water mass was not apparent during the shift from the high low tide to high high tide (Fig. 11).

In summary, during the summer near the mouth of South Slough the water column was vertically well mixed. Horizontal current velocity also varied little with depth. The waters that passed by the station during flood tide can be identified as being estuarine or oceanic, while the waters that passed the station during ebb have been mixed during their passage through the slough and form a roughly constant gradient. Circulation in estuaries is complex and is influenced by factors such as water density, tides, wind stress, and bathemetry. Yet, consistent patterns in the physical variables at the anchor station were evident and appeared to be highly influenced by the mixed semidiurnal tides. Because of its close proximity to the mouth of the estuary, the study site was inundated with coastal ocean water during most high tides. Therefore processes affecting the nearshore, like the upwelling-downwelling cycle, impact the estuary.

Zooplankton Abundance Patterns

A total of 199,530 decapod larvae, 3,670 barnacle cyprids, 32,107 gelatinous organisms, and 1,562 larval fish were enumerated. All of the zooplankton species counted during the five sampling periods as well as their average and maximum concentrations are listed in Table 5. The most abundant organisms enumerated were typically early stage zoeae of the estuarine decapods Pinnotherid spp., *Hemigrapsus oregonensis*, and *Neotrypaea californiensis*, and the hydromedusae, *Clytia gregaria*. Very few megalopae were collected. The least abundant organisms, when they were caught at all, were mid and late stage zoeae (excepting Pinnotherid spp.).

Based on zooplankton abundance patterns, dispersal strategies can be inferred; thus, the estuarine zooplankton have been classified as either exporting or retaining. There were also decapod larvae, barnacle cyprids, hydromedusae, and other zooplankton that imported into the estuary from the coastal ocean. The following data and interpretations are therefore divided into three sections: export, retention, and import. For some of the organisms, interpretation of the data is uncertain because the abundances were low and/or they were present or counted in only one or two of the sampling periods. Despite this, they have been included and placed in the section that is most consistent with the data. Majid spp. larvae, Cancer spp. larvae, and *Pagurus* spp. larvae, due to low abundances and inconsistent patterns will not be discussed any further.

Table 5. Average and maximum concentrations of all zooplankton enumerated from the five sampling periods.

7 Aug. Organism	Average concentration (number m^{-3})	Maximum concentration (number m^{-3})
Pinnotherid spp. z1 & z2	29.23	208.83
Neotrypaea californiensis z1	5.18	33.24
Pachygrapsus crassipes z1	0.48	1.68
Emerita analoga z1	0.43	3.38
Pinnotherid spp. z3	0.16	0.80
Majid spp. z1	0.14	0.85
Pinnotherid spp. z4 & z5	0.074	0.37
Lophopanopeus bellus z1	0.072	0.44
Porcelain spp. z1	0.017	0.31
Hemigrapsus nudus megalopae	0.013	0.31
Hemigrapsus oregonensis megalopae	0.011	0.14
Cancer spp. megalopae	0.0081	0.14
Lophopanopeus bellus megalopae	0.0059	0.071
Porcelain spp. megalopae	0.0033	0.061
Pagurus spp. megalopae	0.0025	0.042
Porcelain spp. z2	0.00094	0.031

15 Aug. Organism	Average concentration (number m^{-3})	Maximum concentration (number m^{-3})
Hemigrapsus oregonensis z1 & z2	21.24	333.99
Clytia gregaria	9.78	159.28
Neotrypaea californiensis z1	6.89	49.20
Pagurus spp. z1 & z2	2.30	4.80
Pleurobrachia bachei	1.63	20.16
Balanus glandula cyprids	1.53	7.33
Larval fish	1.48	25.24
Pachygrapsus crassipes z1	0.50	2.14
Emerita analoga z1	0.45	3.38
Majid spp. z1	0.27	1.30
Balanus crenatus cyprids	0.26	2.12
Semibalanus cariosus cyprids	0.12	1.80
Porcelain spp. z1	0.12	0.93
Lophopanopeus bellus z1	0.095	1.11
Hemigrapsus oregonensis z3	0.069	0.39
Aequorea spp.	0.058	0.47

15 Aug. (cont.) Organism	Average concentration (number m^{-3})	Maximum concentration (number m^{-3})
Pollicipes polymerus cyprids	0.053	0.51
Chthamalus dalli cyprids	0.044	0.41
Chaetognath spp.	0.042	0.40
Balanus nubilus cyprids	0.033	0.16
Pagurus spp. megalopae	0.030	0.15
Hemigrapsus oregonensis z4 & z5	0.015	0.19
Balanus improvisus cyprids	0.010	0.19
Lepas spp. cyprids	0.0053	0.051
Porcelain spp. z2	0.0039	0.052
Cancer spp. megalopae	0.0021	0.051
Majid spp. megalopae	0.0019	0.025
Porcelain spp. megalopae	0.0014	0.020
Neotrypaea californensis megalopae	0.00073	0.026
Lophopanopeus bellus megalopae	0.00055	0.020
Hemigrapsus oregonensis megalopae	0.00043	0.016
Majid spp. z2	0.00037	0.013
Neotrypaea californiensis z2	0.00037	0.013
Pagurus spp. z3	0.00018	0.013

28 Aug. Organism	Average concentration (number m^{-3})	Maximum concentration (number m^{-3})
Pinnotherid spp. z1	7.33	59.22
Clytia gregaria	5.41	40.55
Hemigrapsus oregonensis z1	4.58	98.85
Porcelain spp. z1 & z2	0.97	7.61
Neotrypaea californiensis z1	0.78	6.01
Larval fish	0.24	2.16
Pleurobrachia bachei	0.21	1.13
Cancer spp. megalopae	0.15	3.08
Hemigrapsus oregonensis z2	0.15	2.28
Pinnotherid spp. z2	0.13	1.12
Pinnotherid spp. z3	0.093	0.46
Aequorea spp.	0.069	1.72
Cyprids	0.058	1.00
Hemigrapsus oregonensis z3	0.025	0.23
Majid spp. zoeae	0.018	0.41
Pinnotherid spp. z4	0.015	0.18
Chaetognath spp.	0.013	0.13

28 Aug. (cont.) Organism	Average concentration (number m^{-3})	Maximum concentration (number m^{-3})
Hemigrapsus oregonensis z4	0.0030	0.046
Pagurus spp. megalopae	0.0030	0.023
Pinnotherid spp. z5	0.0012	0.015

5 Sep. Organism	Average concentration (number m^{-3})	Maximum concentration (number m^{-3})
Pinnotherid spp. z1	51.27	570.81
Hemigrapsus oregonensis z1	10.02	141.11
Clytia gregaria	8.47	66.91
Neotrypaea californiensis z1	5.49	108.38
Pinnotherid spp. z2	3.28	25.31
Pinnotherid spp. z3	1.20	6.93
Porcelain spp. z1 & z2	0.52	5.03
Pinnotherid spp. z4	0.52	1.73
Pleurobrachia bachei	0.37	2.98
Pinnotherid spp. z5	0.21	1.69
Larval fish	0.15	1.12
Non-*Cancer* megalopae	0.082	0.44
Aequorea spp.	0.056	0.44
Chaetognath spp.	0.038	0.46
Hemigrapsus oregonensis z2	0.035	0.34
Cancer spp. megalopae	0.029	0.27
Cyprids	0.029	0.30
Hemigrapsus oregonensis z3	0.021	0.41
Hemigrapsus oregonensis z5	0.0015	0.022
Hemigrapsus oregonensis z4	0.00090	0.025

13 Sep. Organism	Average concentration (number m^{-3})	Maximum concentration (number m^{-3})
Pinnotherid spp. z1	29.84	145.07
Pinnotherid sp. A z1	7.30	112.55
Hemigrapsus oregonensis z1 & z2	5.37	27.72
Clytia gregaria	4.23	24.30
Pinnotherid spp. z2	4.13	20.77
Neotrypaea californiensis z1	2.41	21.91
Porcelain spp. z1	1.96	6.82
Pinnotherid sp. A z2	1.93	47.69
Pinnotherid spp. z3	1.50	10.14
Lophopanopeus bellus z1	1.46	20.57
Pinnotherid spp. z4	0.78	5.30
Pinnotherid spp. z5	0.73	3.97
Pleurobrachia bachei	0.64	3.66
Pagurus spp. z1 & z2	0.56	2.54
Emerita analoga z1	0.42	2.30
Pachygrapsus crassipes z1	0.28	1.44
Balanus glandula cyprids	0.22	2.19
Chaetognath spp.	0.21	2.19
Semibalanus cariosus cyprids	0.20	1.11
Balanus nubilus cyprids	0.18	0.97
Majid spp. z1	0.16	0.62
Pinnotherid sp. A z3	0.089	1.37
Porcelain spp. z2	0.086	0.38
Hemigrapsus oregonensis z3	0.065	0.40
Balanus crenatus cyprids	0.061	0.93
Pinnotherid spp. megalopae	0.055	0.30
Pagurus spp. z3	0.027	0.19
Hemigrapsus oregonensis z4 & z5	0.025	0.15
Cancer spp. megalopae	0.020	0.21
Pinnotherid sp. A z4	0.018	0.12
Pollicipes polymerus cyprids	0.015	0.12
Chthamalus dalli cyprids	0.014	0.11
Pinnotherid sp. A z5	0.0090	0.070
Lophopanopeus bellus z2	0.0070	0.12
Hemigrapsus spp. megalopae	0.0067	0.066
Aequorea spp.	0.0034	0.053
Pagurus spp. z4	0.0031	0.034
Lophopanopeus bellus z3 & z4	0.0020	0.041

Export

If larvae export from an estuary and develop offshore, later to return to the estuary to settle, only early stage larvae and the last larval stage would be found in estuarine waters. Four of the decapod species enumerated have abundance patterns that suggest that their larvae are exported from the bay: *Neotrypaea californiensis, Hemigrapsus oregonensis, Lophopanopeus bellus*, and *Pachygrapsus crassipes*.

Neotrypaea californiensis

Neotrypaea californiensis is a burrowing thalassinid shrimp. Adults are found in bays and estuaries in the middle to low intertidal zones in sand and muddy sand (Jensen 1995). They produce three to four broods per year that hatch May through September (McCrow 1972). *Neotrypaea californiensis* molts through five zoeal stages and one megalopal stage, spending approximately six to eight weeks in the plankton (McCrow 1972) (Table 2).

Of the 22,959 *N. californiensis* larvae caught during the five sampling periods, 99.6% of them were first stage zoeae (hereafter referred to as z1), the remaining larvae were second stage zoeae (z2), third stage zoeae (z3) and megalopae (Table 6). No stage four or five zoeae were caught. The fact that most larvae caught were early stages and that the middle stage larvae were absent in estuarine waters suggests that *N. californiensis* larvae were exported from the estuary. Our findings are consistent with those of Johnson and Goner

Table 6. Percentage of each stage comprising the total catch for a given species. Parenthetical numbers indicate the number of sampling dates organisms were counted. X indicates when a species does not have that stage.

Organism		z1	z2	z3	z4	z5	meg
Neotrypaea californiensis	average	99.62 (5)	0.35 (5)	0.0087 (5)	0 (5)	0 (5)	0.0087 (5)
	range	100 – 94.88	4.98 – 0	0.13 – 0	0	0	0.021 – 0
Hemigrapsus oregonensis	average	97.66 (4)	1.65 (4)	0.53 (4)	0.12 (4)	0.0045 (4)	0.018 (4)
	range	99.38 – 96.41	3.03 – 0.35	1.31 – 0.21	0.50 – 0.015	0.031 – 0	0.10 – 0
Lophopanopeus bellus	average	99.29 (3)	grouped with z1	0.35 (3)	0.11 (3)	X	0.23 (4)
	range	99.47 – 95.08		0.39 – 0	0.13 – 0	X	4.91 – 0
Pachygrapsus crassipes	average	100 (3)	0 (3)	0 (3)	0 (3)	0 (3)	0 (4)
	range	100	0	0	0	0	0
Pinnotherid spp.	average	88.25 (4)	6.63 (4)	2.56 (4)	1.34 (4)	1.12 (4)	0.084 (3)
	range	98.30 – 79.81	11.31 – 0.99	4.08 – 0.46	2.31 – 0.17	2.28 – 0.016	0.20 – 0
Porcelain spp.	average	95.30 (3)	4.47 (3)	X	X	X	0.23 (3)
	range	95.57 – 63.63	9.09 – 0	X	X	X	27.27 – 0
Emerita analoga	average	100 (3)	0 (3)	0 (3)	0 (3)	0 (3)	0 (4)
	range	100	0	0	0	0	0

(1982). Their study, conducted in the Salmon River Estuary, Oregon, found that 88% of z1 *N. californiensis* larvae were exported during an ebb tide. McCrow (1972, p 43), in a study conducted in Yaquina Bay, Oregon also found a "total lack of older stages" in the bay. However, all *N. californiensis* larval stages were found 1-3 miles offshore with larval densities up to two orders of magnitude greater than those found in the bay; larvae were rare further than 3 miles offshore (McCrow 1972).

High concentrations of z1 *N. californiensis* consistently occurred in the surface samples during nocturnal ebb tides and in bottom flood samples that followed a nocturnal ebb tide (Fig. 13). This suggests that *N. californiensis* zoeae were vertically migrating to hasten their export from the estuary. The best illustration of this is seen on 7 August, figure 13. Zoeae were concentrated at the surface during the nocturnal ebb tide, yet when the tide turned and flooded back in, the zoeae were concentrated near the bottom. Whether it was day or night, peaks in zoeal abundance occurred near the bottom during flood tides that followed a nocturnal ebb tide (Fig. 13). Zoeae were rarely caught during daytime ebb tides and the flood tides that followed. These data suggest that the zoeae were selectively entering the water column to enhance their transport out of the estuary. At the anchor station current speeds near the bottom were appreciable. If larvae are to prevent transport in an "undesired" direction, they must swim into the benthic boundary layer, or even into the sediment. There is only one study that suggests that decapod zoeae might reside on the bottom to avoid transport.

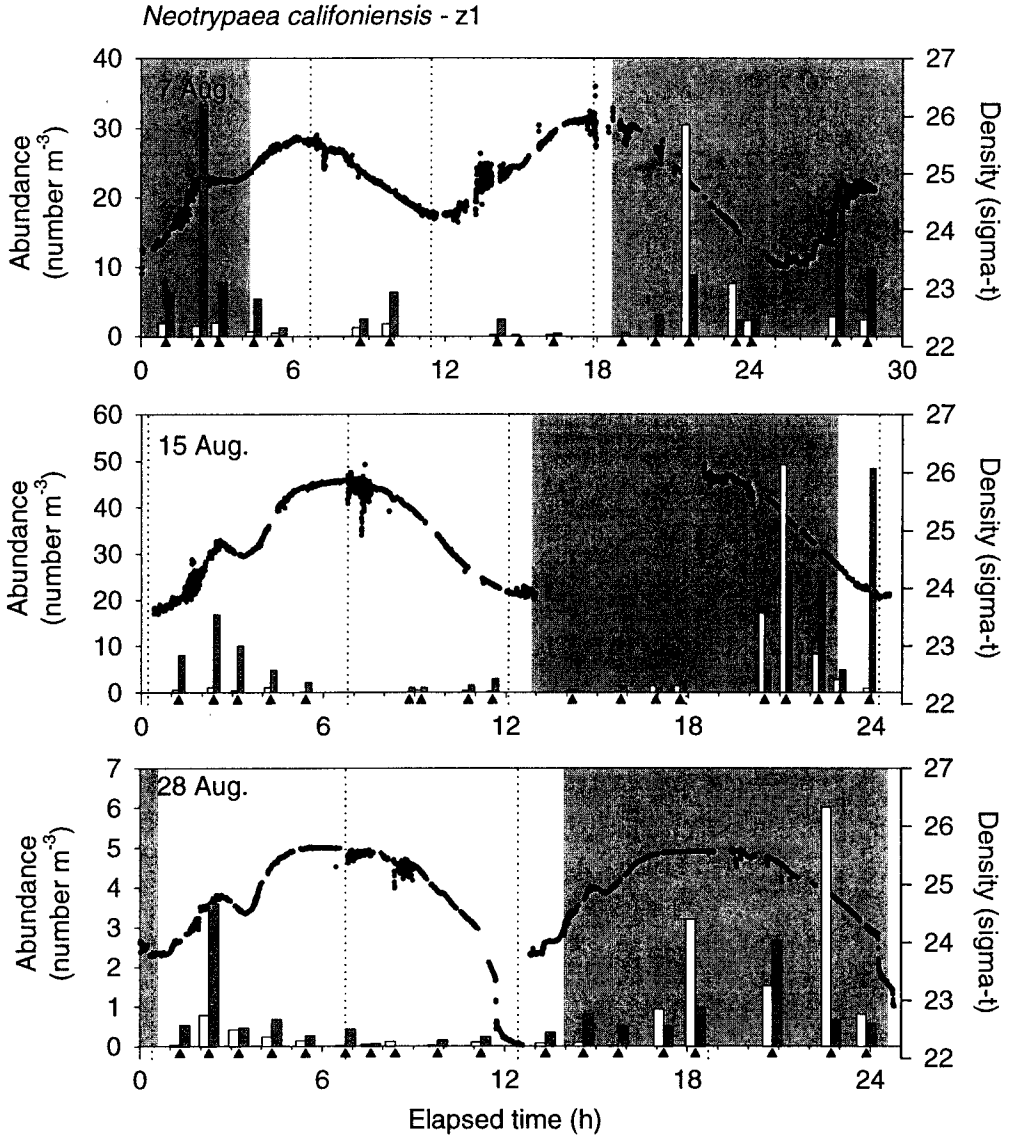

Fig. 13. Abundance (number of individuals per m^3) of first stage zoeae of the burrowing shrimp, *Neotrypaea californiensis*, at the South Slough anchor station over five sampling periods. Unshaded bars represent surface zooplankton samples, and the shaded bars represent near bottom zooplankton samples. Water density is also plotted to identify the water masses in which the organisms are found. Gray background shading indicates night. Dotted vertical lines indicate slack water. Triangles along the bottom axis indicate the time at which the zooplankton samples were collected.

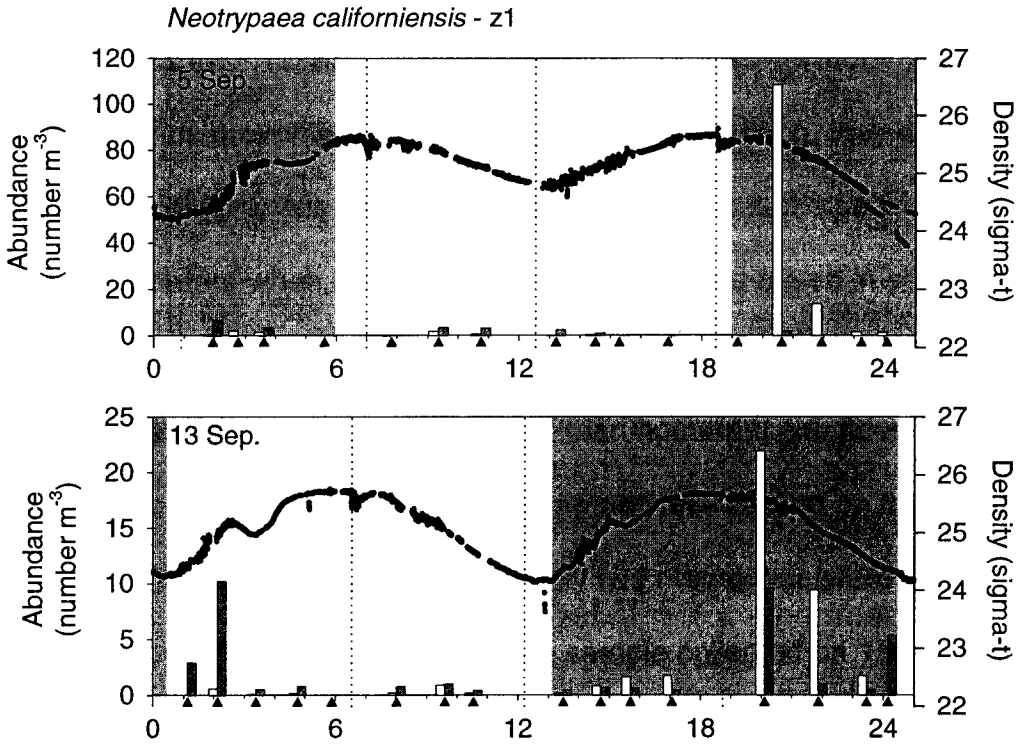
Neotrypaea californiensis - z1
5 Sep
13 Sep.
Abundance (number m-3)
Density (sigma-t)
0
6
12
18
24

Fig. 13. Cont.

Samples collected in the field by DiBacco et al. (2001) suggest that a significant proportion of z1 *P. crassipes* are resting on the sediment-water interface during flood tides, thus preventing landward transport. In addition, they observed that first stage *Pachygrapsus crassipes* zoeae burrowed into the sediment to a depth of two centimeters when hatched in the laboratory and raised in still water in aquariums with coarse sand bottoms. The near absence of *N. californiensis* zoeae from samples taken at times other than nocturnal ebb tides and the following flood tide suggests that the zoeae may be residing on the bottom or possibly burrowing into the sediment. Only two megalopae were caught during the study, both of them were in the same sample collected on 15 Aug., at the surface, at night, one hour before high tide. The low abundances of megalopae caught during this study will be addressed in the concluding chapter.

Hemigrapsus oregonensis

Hemigrapsus oregonensis is a grapsid crab found in mudbank burrows in estuaries and throughout the intertidal among rocks on mud or gravel bottoms (Jensen 1995). They produce two broods per year. In Puget Sound, Washington, the first broods hatch early May through late July; second broods are produced almost immediately and typically hatch by late September (Strathmann 1987). *Hemigrapsus oregonensis* molts through five zoeal stages and one megalopal stage, spending approximately four to five weeks in the plankton (Hart 1935) (Table 2).

Of the 43,513 *H. oregonensis* larvae caught during four sampling periods, 97.66% of them were z1, 1.65% were z2, and the remaining ~0.7% were z3-megalopae (Table 6). The sharp decline in abundance of third to fifth stage zoeae suggests that *H. oregonensis* larvae are exported from the estuary, develop in the coastal ocean, and return to the estuary as megalopae. This is also supported by the fact that the small number of later stage zoeae (z3-z5) that were caught tended to be most abundant in ocean water (Fig. 14). In a study in Elkhorn Slough, California, Hsueh (1991) also concluded that H. oregonensis zoeae transported offshore, based on the scarcity of second to fifth stage zoeae in horizontal plankton tows taken biweekly at four stations over a 14 month period.

The abundance patterns of *H. oregonensis* were similar to *N. californiensis* in that peaks in abundance of early zoeae often occurred at the surface, at night, during ebb tides, and at the bottom during flood tides that followed nocturnal ebb tides (Fig. 15). However, there were also differences. The higher proportion of second stage *H. orgonensis* zoeae suggests that export was not as rapid as it was for *N. californiensis*. Some of the largest peaks in abundance of z1 larvae were at the bottom, near slack low tide (Fig. 15); *H. oregonensis* z1 larvae were also caught in low abundances during daytime ebb tides and the flood tides that followed, whereas N. californiensis were virtually absent during these times (Fig. 15 compared to Fig. 13). Also, later stage *H. oregonensis* larvae were caught in oceanic samples (Fig. 14). These data

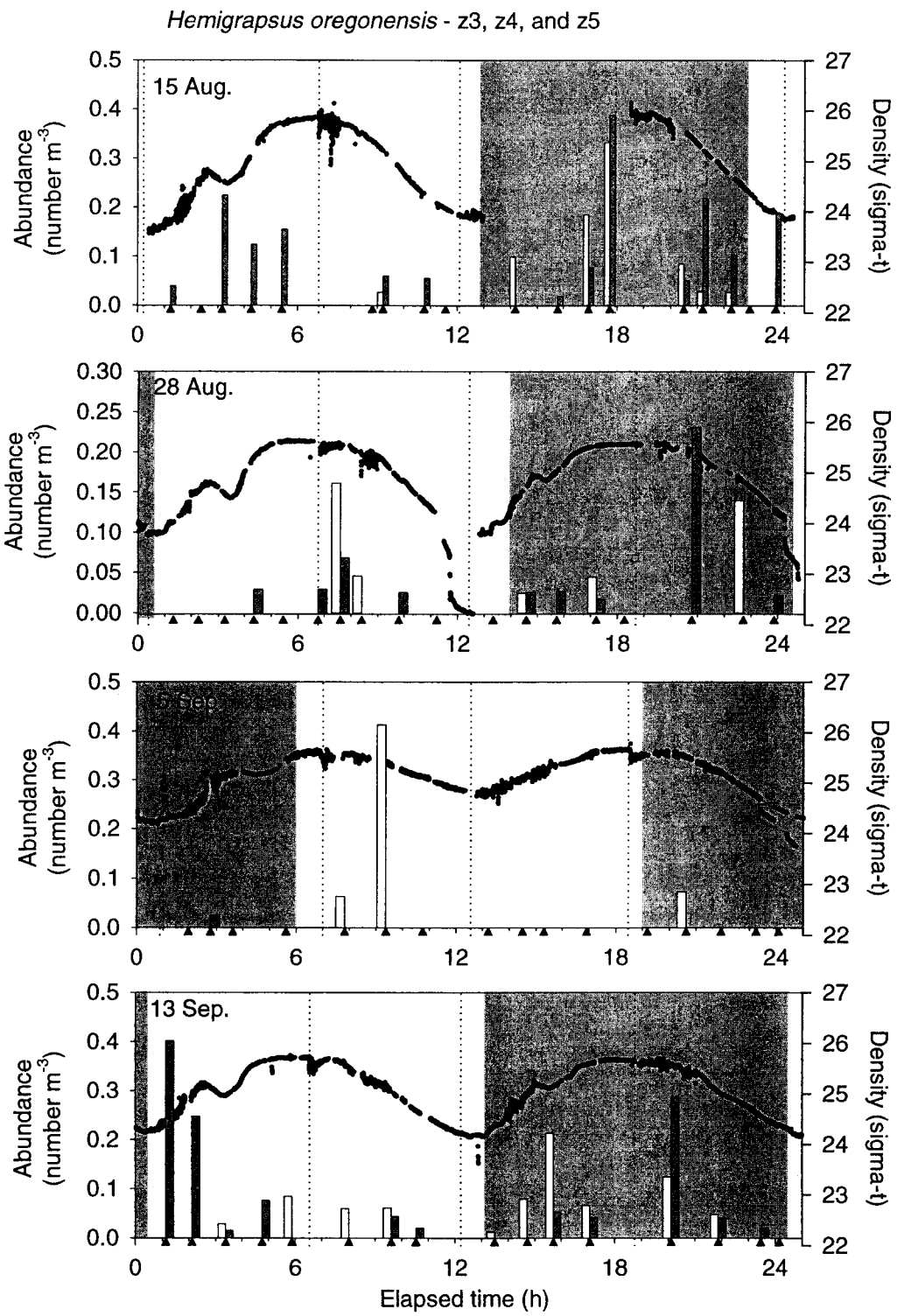

Fig. 14. Abundance (number of individuals per m^3) of later stage zoeae of the brachyuran crab, *Hemigrapsus oregonensis*, at the South Slough anchor station over four sampling periods. Unshaded bars represent surface zooplankton samples, and the shaded bars represent near bottom zooplankton samples. Water density is also plotted to identify the water masses in which the organisms are found. Gray background shading indicates night. Dotted vertical lines indicate slack water. Triangles along the bottom axis indicate the time at which the zooplankton samples were collected.

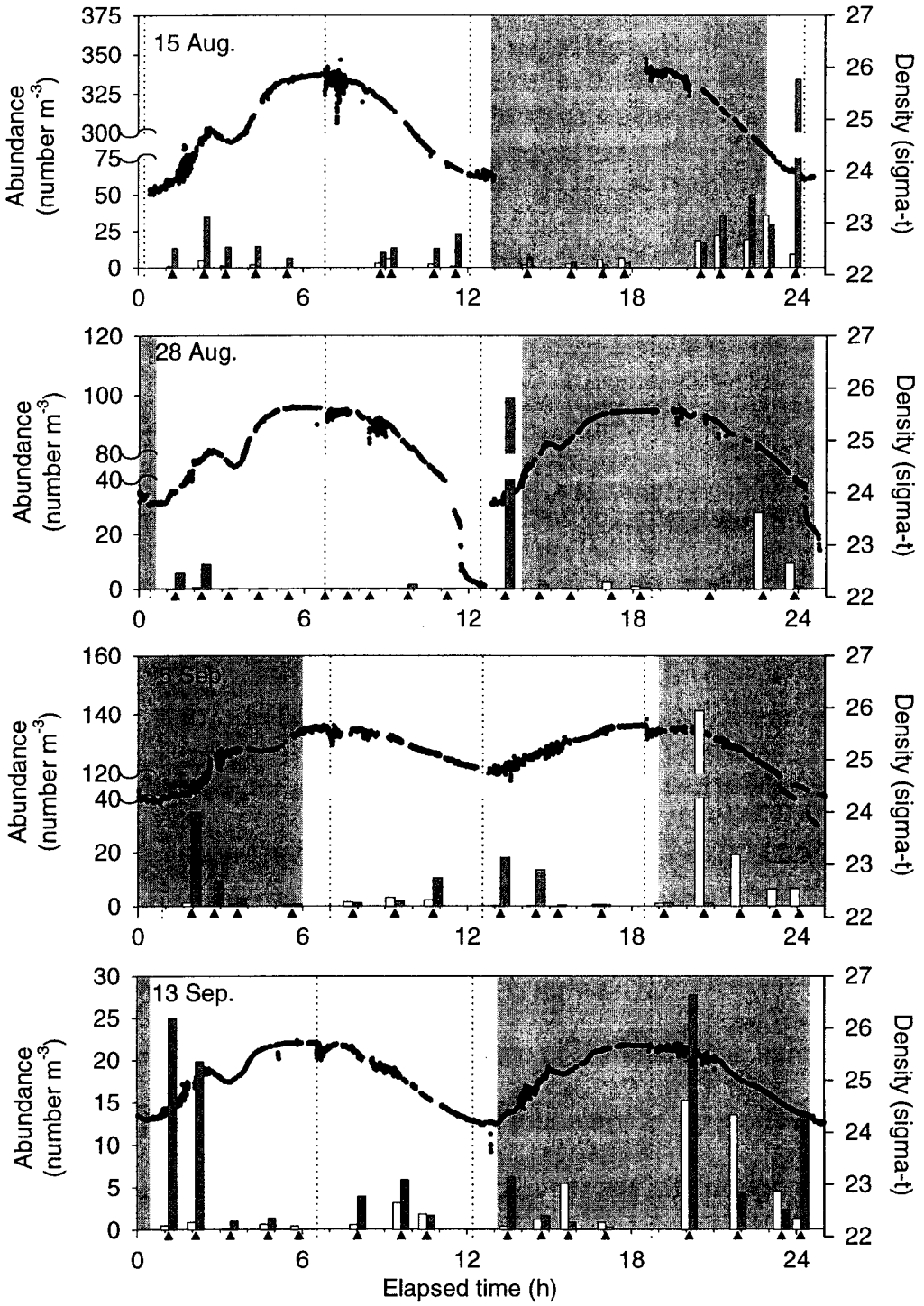

Fig. 15. Abundance (number of individuals per m^3) of first stage zoeae of the brachyuran crab, *Hemigrapsus oregonensis*, at the South Slough anchor station over four sampling periods. Unshaded bars represent surface zooplankton samples, and the shaded bars represent near bottom zooplankton samples. Water density is also plotted to identify the water masses in which the organisms are found. Gray background shading indicates night. Dotted vertical lines indicate slack water. Triangles along the bottom axis indicate the time at which the zooplankton samples were collected.

suggest that *H. oregonensis* zoeae were behaving differently than *N. californiensis* zoeae. The presence of late stage zoeae in oceanic samples, albeit in low numbers, suggests that *H. oregonensis* larvae may have been staying closer to shore. *H. oregonensis* megalopae, when they were caught, were mainly at the surface during flood tides (Fig. 16).

Lophopanopeus bellus

Lophopanopeus bellus is a xanthid crab found in the low intertidal and subtidal under rocks on sand or gravel (Jensen 1995), and also in the low intertidal areas of estuaries under rocks where there is some tidal current (Strathmann 1987). In Puget Sound, Washington, 60-70 percent of females produce two broods per year, the first hatching beginning in May, peaking in June, and the second hatches in the fall (Strathmann 1987). *Lophopanopeus bellus* molts through four zoeal stages and one megalopal stage, spending approximately five weeks in the plankton (Table 2).

A total of 1,692 *L. bellus* zoeae were counted in three sampling periods and four megalopae were found in two of four sampling periods examined. Over 99% of the larvae counted were z1 and z2, very few z3 through megalopae were caught (Table 6). Over 91% of the larvae were caught on 13 September, and this is the only sampling period when later stage zoeae were caught. During this sampling period, z1 and z2 larvae were most abundant at the surface, at night, during ebb tide (Fig. 17), while z3 and z4 larvae were found near the bottom,

H. oregonensis megalopae

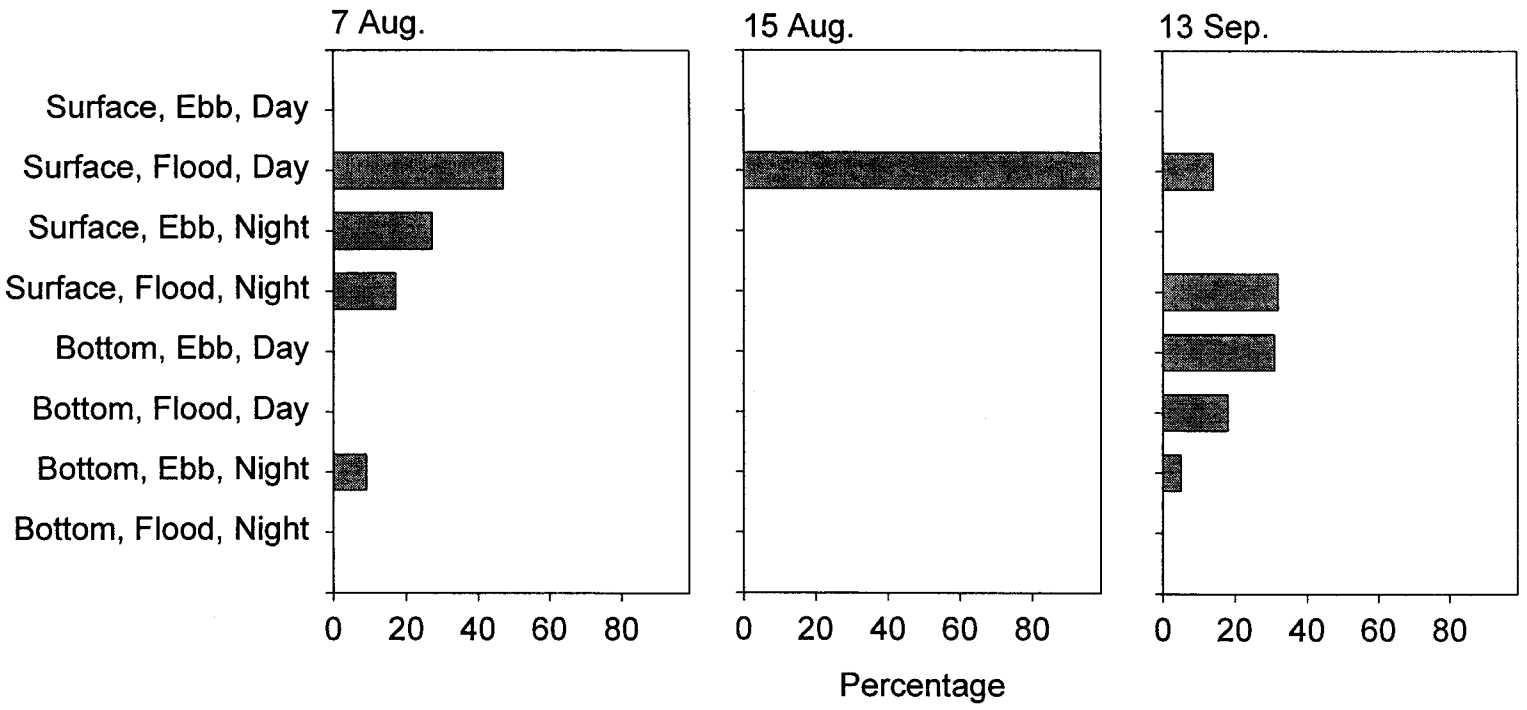

Fig. 16. Distribution of *H. oregonensis* megalopae for three sampling periods.

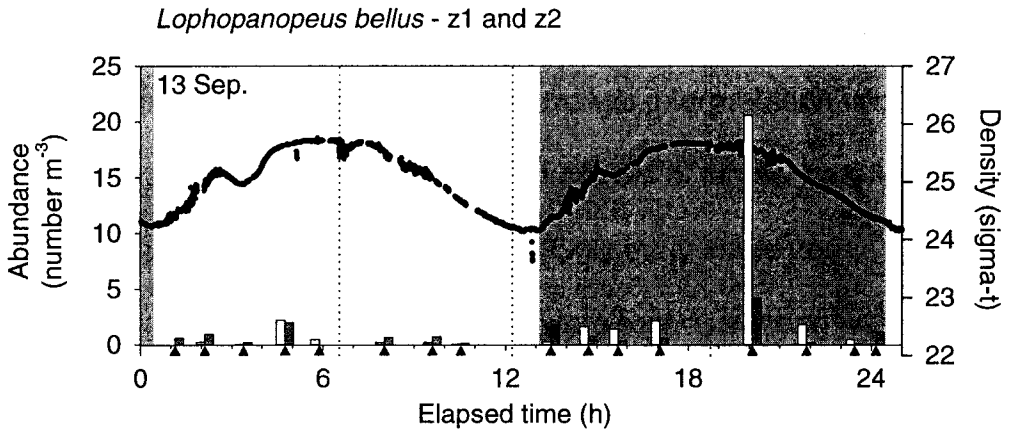

Fig. 17. Abundance (number of individuals per m^3) of early stage zoeae of the brachyuran crab, *Lophopanopeus bellus*, at the South Slough anchor station on 13 September. Unshaded bars represent surface zooplankton samples, and the shaded bars represent near bottom zooplankton samples. Water density is also plotted to identify the water masses in which the organisms are found. Gray background shading indicates night. Dotted vertical lines indicate slack water. Triangles along the bottom axis indicate the time at which the zooplankton samples were collected.

associated with ocean water, and primarily at night (data not shown). During the other two sampling dates no discernible pattern was apparent most likely due to low larval abundances.

The low number of larvae caught makes interpretation uncertain, but the one sampling date when relatively high numbers of larvae were collected suggests that the larvae were exported. Only early stage zoeae were found in estuarine waters while late stage zoeae were found in ocean waters. And like *N. californiensis* and *H. orgonensis*, early stage zoeae were found at the surface, at night, during early ebb. DiBacco et al. (2001) found that in San Diego Bay, which has little to no non-tidal residual flow in the dry season, *L. bellus* larvae did not exhibit a distinct vertical migration behavior and as a result were retained. Well mixed estuaries with low inflow, like South Slough, typically have a slow net drift outward at all depths, with a back-and-forth tidal movement superimposed upon the slow drift (Burt and McAlister 1959). In South Slough, with an exchange ratio of 0.48 and approximate summer flushing times of one tidal cycle (Pimentel 1986), it is unlikely that larvae without behavioral adaptations would be retained in the estuary. Even in Coos Bay, with an exchange ratio of 0.78 and approximate summer flushing times of 10 days for the lower half and 23 days for the upper half of the bay (Arneson 1976), it is unlikely that larvae without behaviors that aid in retention would be retained. Like the late stage zoeae, the megalopae all were found at the bottom at night.

Pachygrapsus crassipes

Pachygrapsus crassipes is a grapsid crab found in the upper and middle intertidal of rocky shores and estuaries (Jensen 1995). They produce one to two broods per year. Females are reported to be ovigerous from April through September (Morris et al. 1980). While Schlotterbeck (1976) reports that there are five zoeal stages, more recently DiBacco (2001) reports six zoeal stages that required between 68 and 108 days to develop (at 18 to 20°C).

A total of 1,535 *P. crassipes* larvae were counted in three sampling periods. All of the larvae caught were z1. This suggests that the zoeae are exported from the estuary. This is consistent with the findings of Hsueh (1991) and DiBacco et al. (2001).

Stage one zoeae were abundant during nocturnal ebb tides, and at the bottom during flood tides that followed nocturnal ebb tides. However, it was common for zoeae to be present at concentrations of about half that of peak concentrations in both surface and bottom estuarine samples (Fig. 18). There is some indication that zoeae may be vertically migrating to hasten export, but low abundances make for dubious interpretations. Low abundances of zoeae may be due to a small population of *P. crassipes* in South Slough, and/or the sampling periods did not coincide with larval spawning and zoeae exported shortly after hatching.

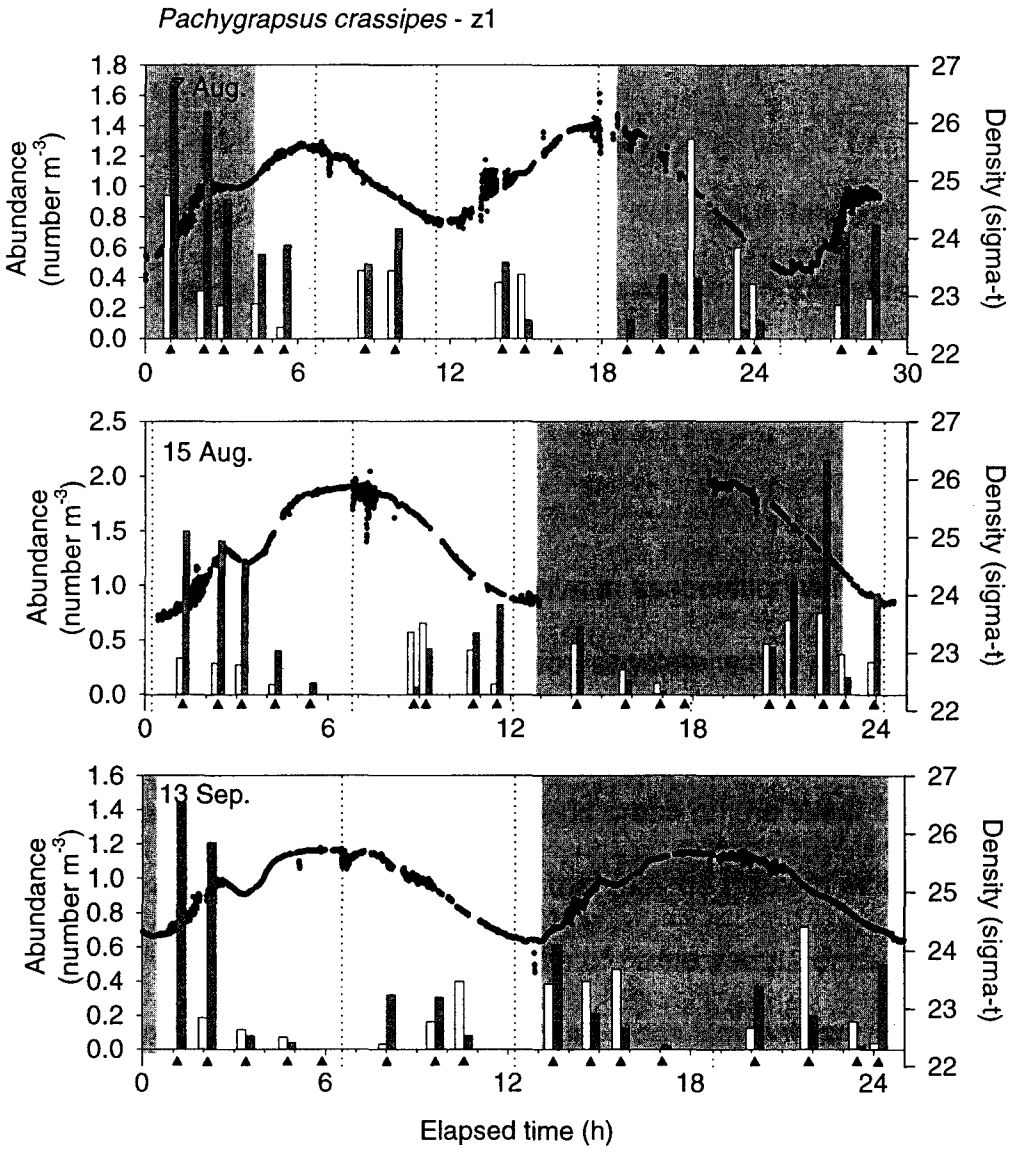

Fig. 18. Abundance (number of individuals per m^3) of first stage zoeae of the brachyuran crab, *Pachygrapsus crassipes*, at the South Slough anchor station over three sampling periods. Unshaded bars represent surface zooplankton samples, and the shaded bars represent near bottom zooplankton samples. Water density is also plotted to identify the water masses in which the organisms are found. Gray background shading indicates night. Dotted vertical lines indicate slack water. Triangles along the bottom axis indicate the time at which the zooplankton samples were collected.

Retention

If larvae retain in an estuary, all larval stages would be found in estuarine waters. Two zooplankton groups enumerated have abundance patterns that suggest that their larvae were retained in the estuary: pinnotherids and larval fish.

Pinnotherid spp.

Pinnotherids are small crabs that live in association with a variety of invertebrate hosts. Each species tends to associate with a specific host, though some pinnotherid species are less specific, and juveniles are even less so. Based on the reported ranges of pinnotherid crabs on the West Coast of North America there are potentially 10 species that may be present in the vicinity of Coos Bay. I've personally observed adults of *Fabia subquadrata, Pinnixa littoralis, Pinnixa faba, Pinnixa tubicola* in the Coos Bay estuary. I have also searched for *Scleroplax granulata*, which lives in the burrows of *N. californiensis*, but have not found them. Of all 10 species, only *Fabia subquadrata* is reported to live in association with an outer coast host, the rest have been found associated with primarily estuarine hosts. Pinnotherids tend to have multiple broods per year that hatch year round with peaks in late summer-early fall and late winter-early spring (Strathmann 1987). They typically molt through four to five zoeal stages and one megalopal stage spending approximately 7-8 weeks in the plankton (Table 2). Descriptions of the larvae for only three of the species

are available. None of the larvae collected in this study fit the descriptions of *Fabia subquadrata* (Lough 1975) or *Pinnotheres taylori* (Hart 1935). Adult *Pinnixa littoralis* and *Pinnixa faba* are commonly found in the gaper clam, *Tresus capax*, in Coos Bay and South Slough (personal observation). Lough (1975) describes the larvae of *P. littoralis*, but Pearce (1966) reports that the larvae of *P. littoralis* and *P. faba* are indistinguishable. Therefore, all pinnotherid crab larvae were lumped together.

A total of 113,258 pinnotherid larvae were counted during four sampling periods. All zoeal stages were caught on all sampling dates, but megalopae were only caught on 13 September. All larval stages were collected (Table 6) predominately from estuarine waters (Figs. 19-21). This suggests that the larvae are retained. Strangely, the highest concentrations of z1 pinnotherid larvae tended to be in surface samples collected during nocturnal ebb tides and often in bottom flood samples that followed nocturnal ebb tides (Fig. 19), as was seen in *H. oregoensis* and *N. californiensis* larvae (Figs. 15 and 13 respectively), both of which export. Possibly these are all newly hatched zoeae. Many decapod larvae are negatively geotactic when they first hatch. In addition, regardless of where larvae develop, many species have evolved to spawn during nocturnal ebb tides, perhaps to avoid visually hunting planktivorous fishes (Morgan 1995). However, z1 pinnotherid larvae were also found at the surface during nocturnal flood tides (Fig. 19). Later stage zoeae (z3-z5) were found mainly in estuarine waters, but they were also found in incoming ocean water (Figs. 20 and 21). The

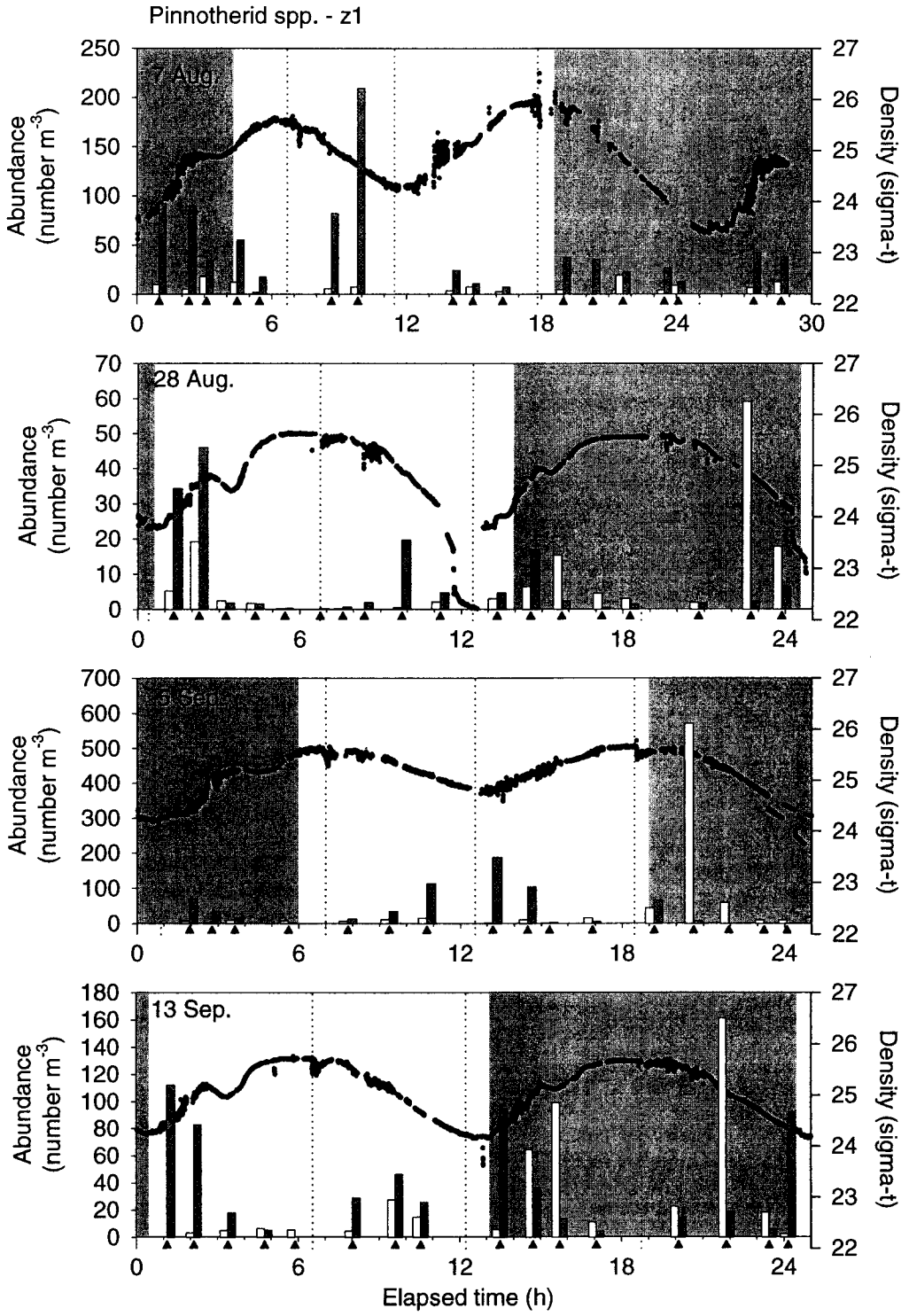

Fig. 19. Abundance (number of individuals per m^3) of first stage zoeae of the commensal crabs, Pinnotherid spp., at the South Slough anchor station over four sampling periods. Unshaded bars represent surface zooplankton samples, and the shaded bars represent near bottom zooplankton samples. Water density is also plotted to identify the water masses in which the organisms are found. Gray background shading indicates night. Dotted vertical lines indicate slack water. Triangles along the bottom axis indicate the time at which the zooplankton samples were collected.

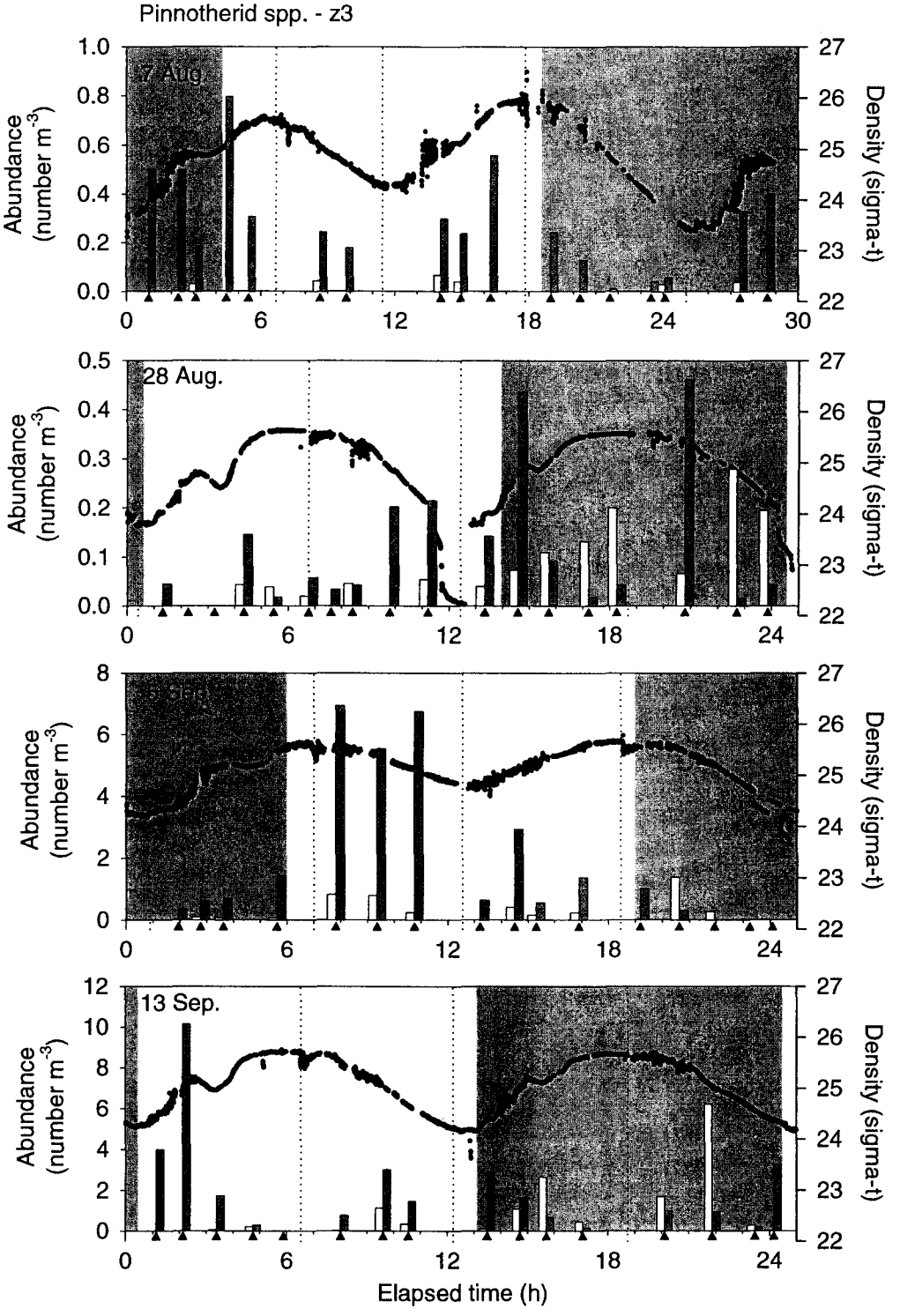

Fig. 20. Abundance (number of individuals per m^3) of third stage zoeae of the commensal crabs, Pinnotherid spp., at the South Slough anchor station over four sampling periods. Unshaded bars represent surface zooplankton samples, and the shaded bars represent near bottom zooplankton samples. Water density is also plotted to identify the water masses in which the organisms are found. Gray background shading indicates night. Dotted vertical lines indicate slack water. Triangles along the bottom axis indicate the time at which the zooplankton samples were collected.

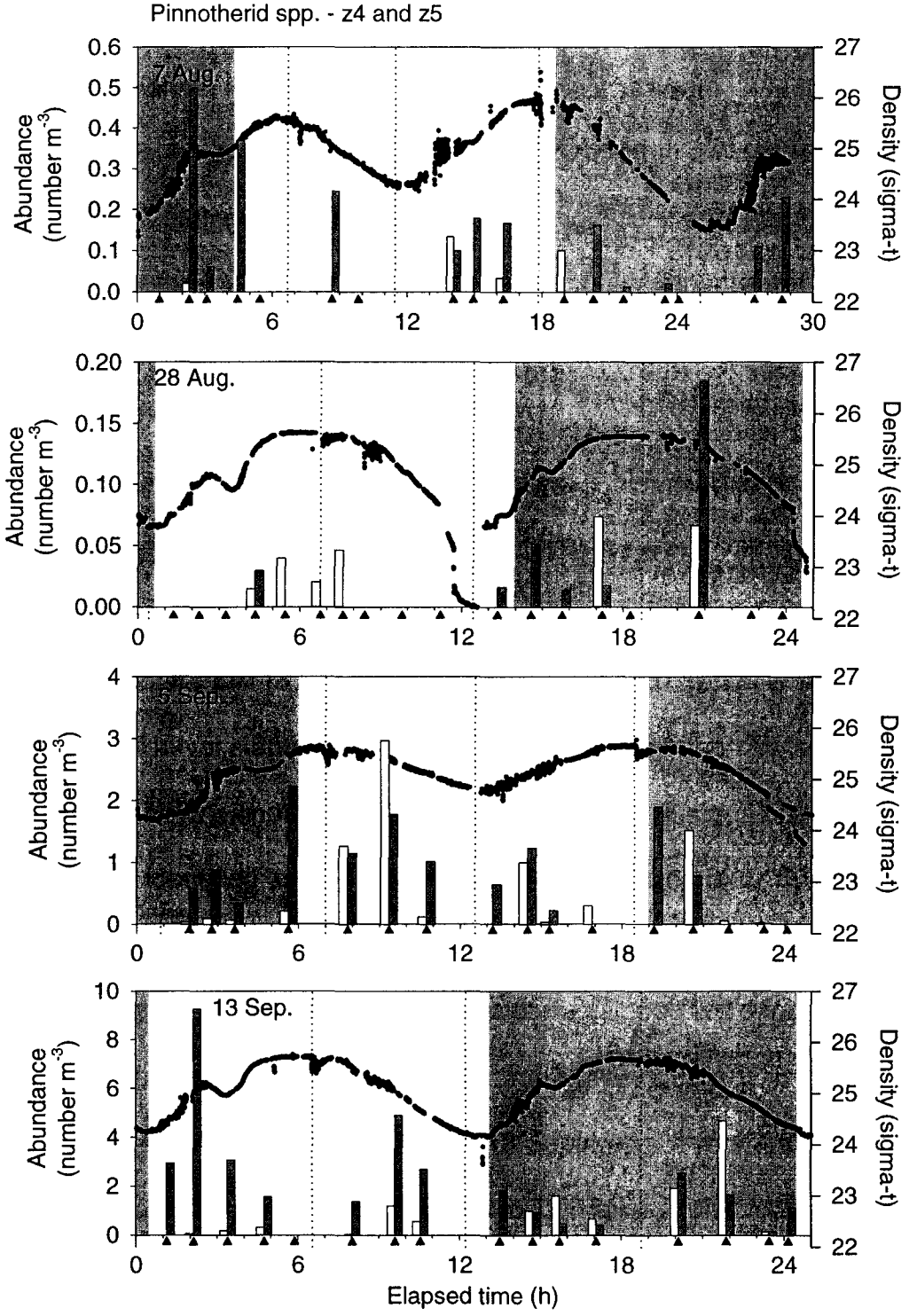

Fig. 21. Abundance (number of individuals per m^3) of fourth and fifth stage zoeae of the commensal crabs, Pinnotherid spp., at the South Slough anchor station over four sampling periods. Unshaded bars represent surface zooplankton samples, and the shaded bars represent near bottom zooplankton samples. Water density is also plotted to identify the water masses in which the organisms are found. Gray background shading indicates night. Dotted vertical lines indicate slack water. Triangles along the bottom axis indicate the time at which the zooplankton samples were collected.

presence of larvae in oceanic samples suggests that some larvae "leak" out of the estuary, but their behaviors result in their return to the estuary. Another possible explanation is that the distribution of host species extend out of the estuary; therefore, larvae may be spawned in the waters adjacent to the estuary mouth. However, the presence or absence of host species in that area is not known.

Examination of individual sampling periods reveals that peaks in abundance of the different larval stages occur in the same water masses (Figs. 22-24), suggesting that they behave similarly throughout development. This is most apparent for the 13 September sampling period (Fig. 24) when the largest number of all larval stages were caught. This was also the only sampling period examined to have pinnotherid megalopae. A total of 96 megalopae were counted and identified as five different species. Species B, C, D, and F were mostly found at night (Fig. 25). Most of the megalopae were caught in estuarine waters; however, relatively large numbers of megalopae were found in incoming ocean waters.

While counting the samples from 13 September it was apparent that one pinnotherid species was smaller and had longer spines relative to its body size. This species, which will be referred to as pinnotherid sp. A, was counted separately. Of the 7,632 pinnotherid sp. A larvae counted, 84.89% were z1, 13.27% were z2, 1.2% were z3, 0.35% were z4, and 0.28% were z5. Again, the fact that all larval stages were found in estuarine waters suggests that

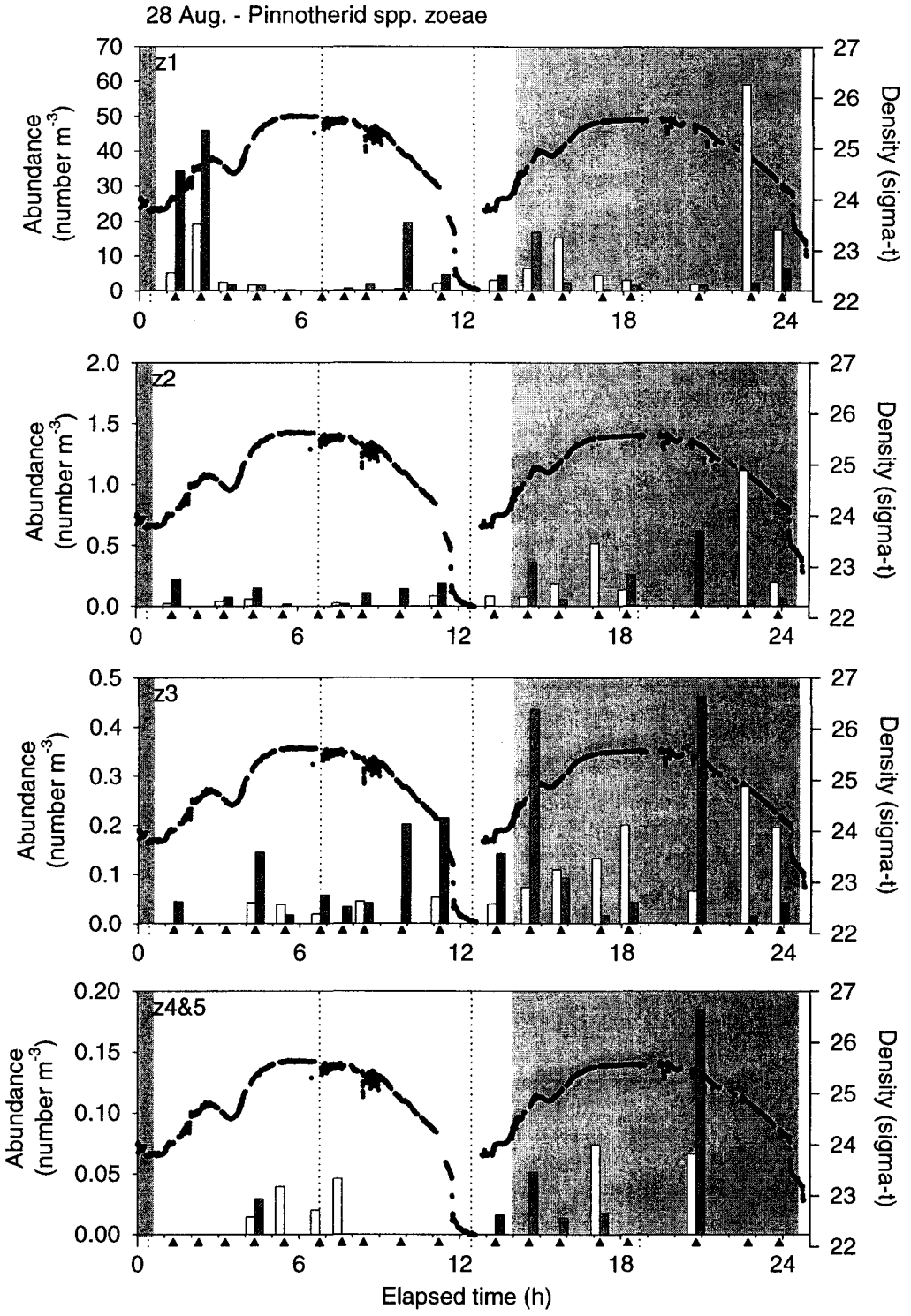

Fig. 22. Abundance (number of individuals per m^3) of the five zoeal stages of the commensal crabs, Pinnotherid spp., at the anchor station on 28 August. Unshaded bars represent surface zooplankton samples, and the shaded bars represent near bottom zooplankton samples. Water density is also plotted to identify the water masses in which the organisms are found. Gray background shading indicates night. Triangles along the bottom axis indicate the time at which the zooplankton samples were collected.

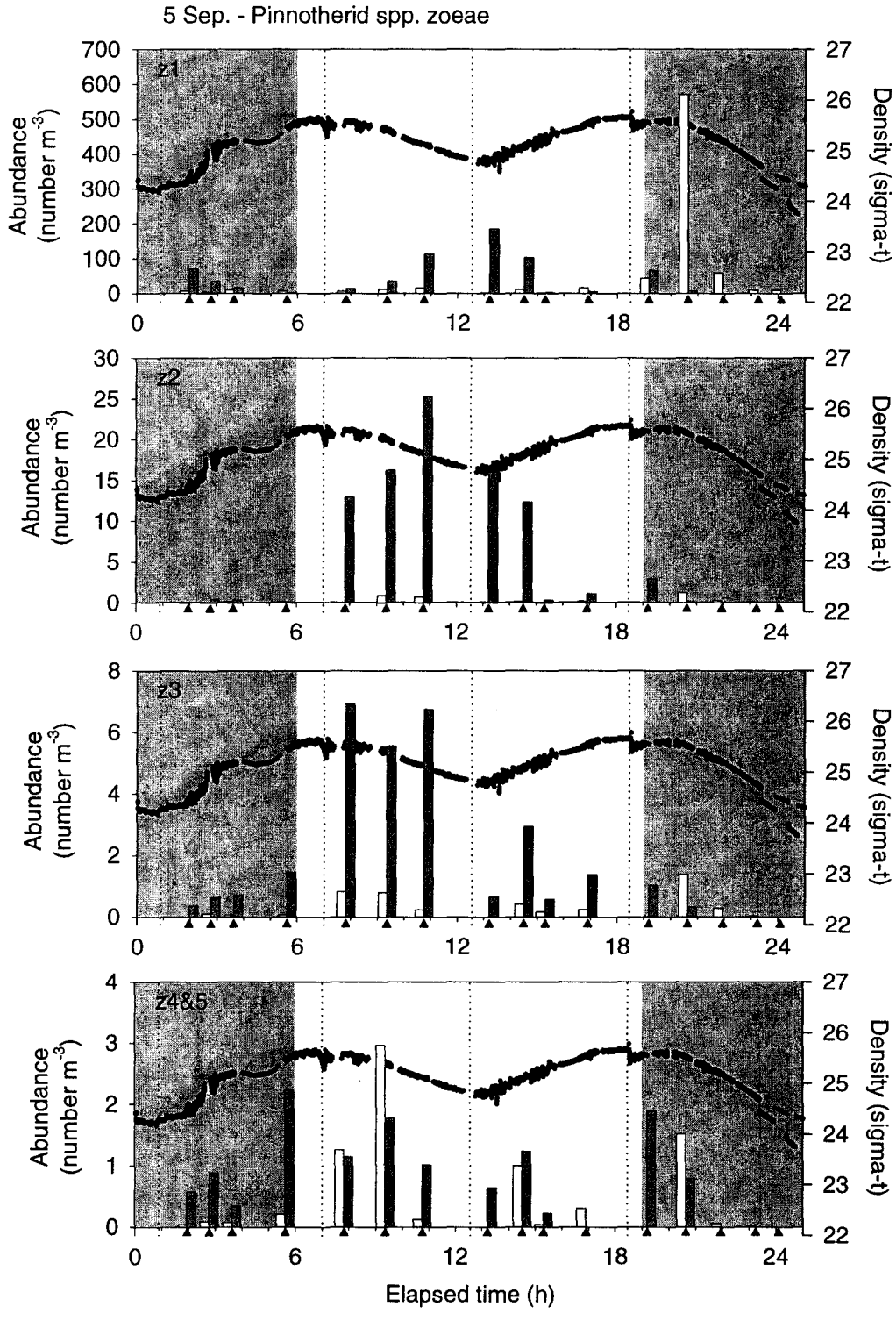

Fig. 23. Abundance (number of individuals per m^3) of the five zoeal stages of the commensal crabs, Pinnotherid spp., at the anchor station on 5 September. Unshaded bars represent surface zooplankton samples, and the shaded bars represent near bottom zooplankton samples. Water density is also plotted to identify the water masses in which the organisms are found. Gray background shading indicates night. Triangles along the bottom axis indicate the time at which the zooplankton samples were collected.

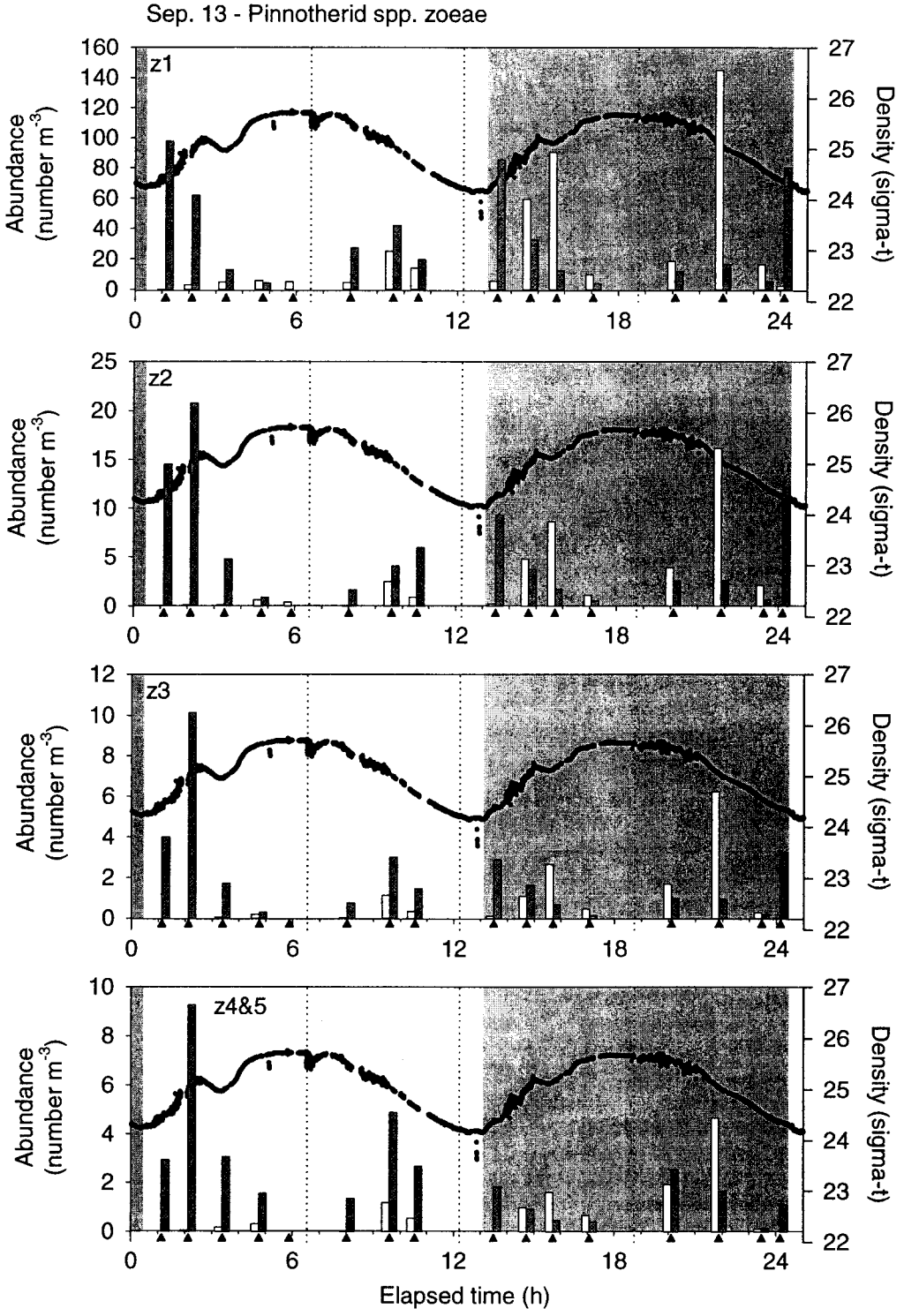

Fig. 24. Abundance (number of individuals per m^3) of the five zoeal stages of the commensal crabs, Pinnotherid spp., at the anchor station on 13 September. Unshaded bars represent surface zooplankton samples, and the shaded bars represent near bottom zooplankton samples. Water density is also plotted to identify the water masses in which the organisms are found. Gray background shading indicates night. Triangles along the bottom axis indicate the time at which the zooplankton samples were collected.

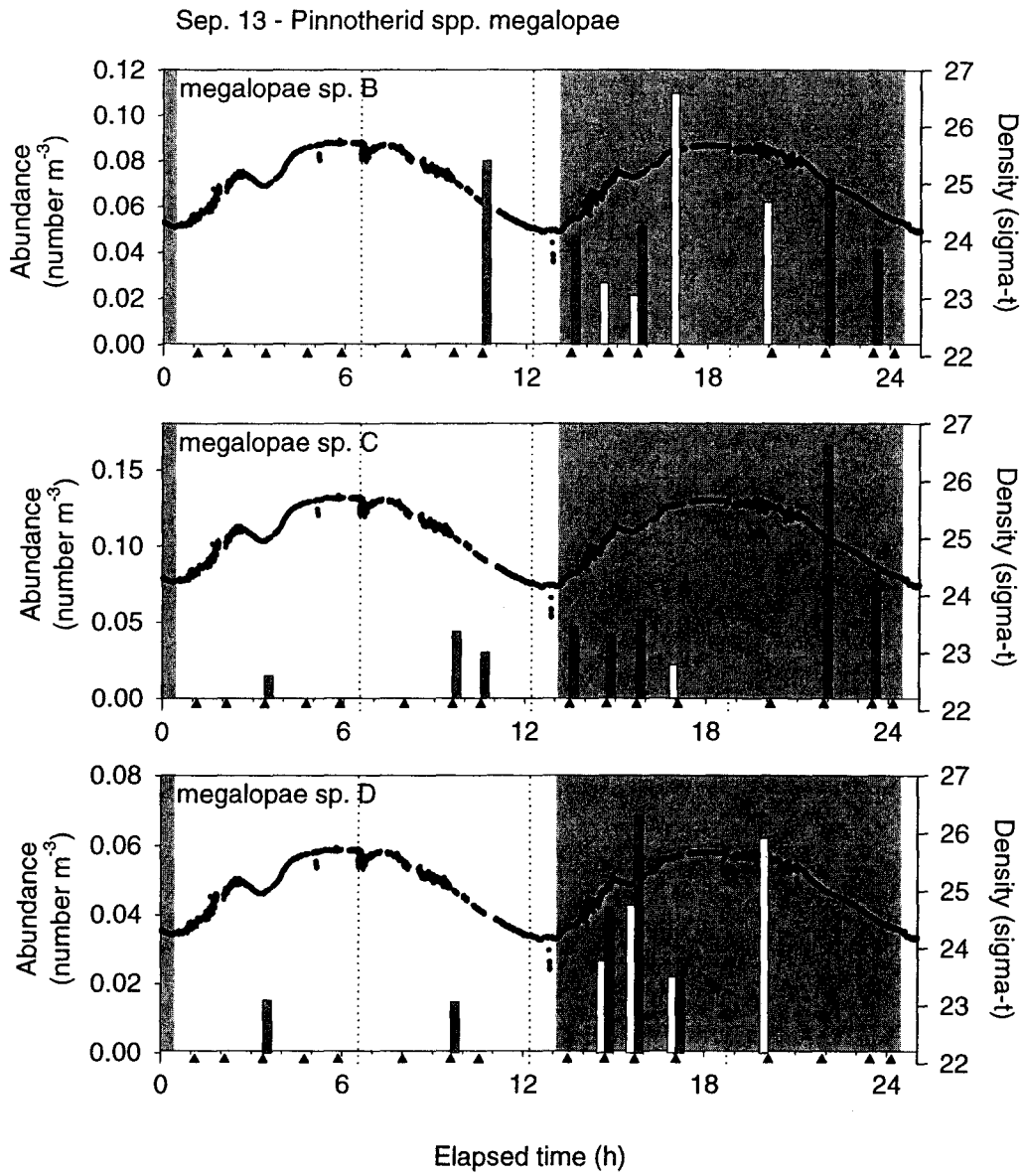

Fig. 25. Abundance (number of individuals per m^3) of megalopae of the commensal crabs, Pinnotherid spp., at the anchor station on 13 September. Unshaded bars represent surface zooplankton samples, and the shaded bars represent near bottom zooplankton samples. Water density is also plotted to identify the water masses in which the organisms are found. Gray background shading indicates night. Triangles along the bottom axis indicate the time at which the zooplankton samples were collected.

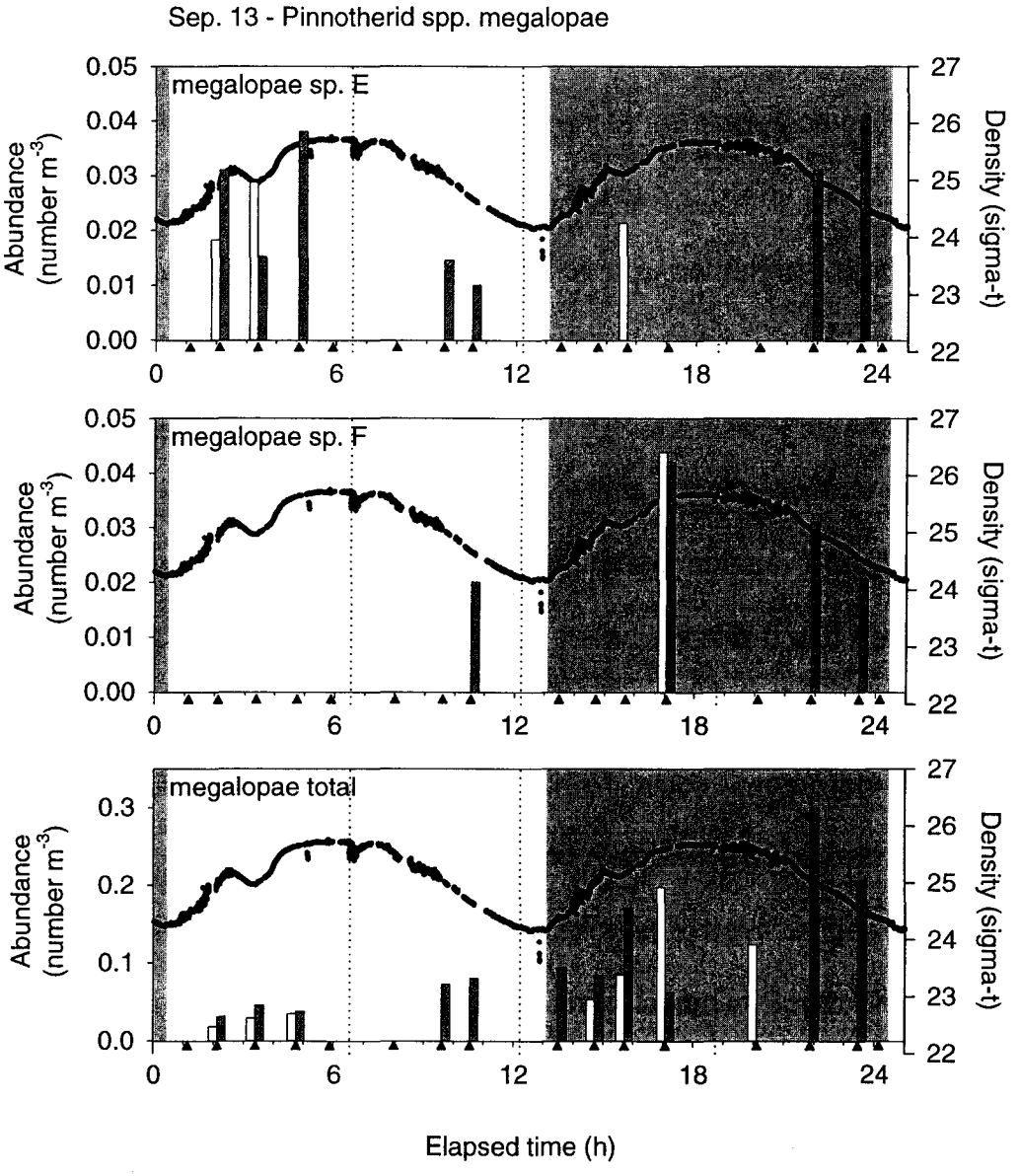
Sep. 13 - Pinnotherid spp. megalopae
megalopae sp. E
megalopae sp. F
megalopae total
Abundance (number m-3)
Density (sigma-t)
Elapsed time (h)
0.05
0.04
0.03
0.02
0.01
0.00
0.3
0.2
0.1
0.0
0
6
12
18
24
27
26
25
24
23
22

Fig. 25. Cont.

pinnotherid sp. A larvae were retained in the estuary. Like the other pinnotherid species, peaks in abundance of the different larval stages co-occurred (Fig. 26), suggesting that the different larval stages behave similarly. The larvae were mainly caught at the bottom in the lowest density estuarine waters sampled (Fig. 26). It is interesting to note that these larvae have the longest spines relative to their body size of the pinnotherids found in this study (personal observation). Morgan (1989, 1990) has found that larvae that remain in estuaries tend to be better defended by being larger and having longer spines. Lough (1975) commented that pinnotherid larvae have especially sharp and rigid spines.

The presence of all larval stages in estuarine waters suggests that the pinnotherid larvae are retained. Hsueh (1991) also found all larval stages of the pinnotherid crabs, *Pinnixa franciscana* and *Pinnixa weymouthi* in Elkhorn Slough, California. Neither of these species are reported to have ranges that extend into Oregon. How exactly pinnotherid larvae are retained in South Slough is unclear. The vast majority of studies that have looked at zooplankton retention have been done in stratified estuaries with two-layer circulation. Because the slough is well mixed and has low freshwater inflow, it is likely that there is a net seaward drift at all depths. On top of that, flushing times are on the order of one tidal cycle and approximately 48% of the slough water is discharged on an average ebb tide. Therefore strategies used by zooplankton in two layer systems would not work in South Slough. Tidally timed migrations resulting in ascent during flood tides and residence on the bottom or in the benthic boundary layer during ebb tides could

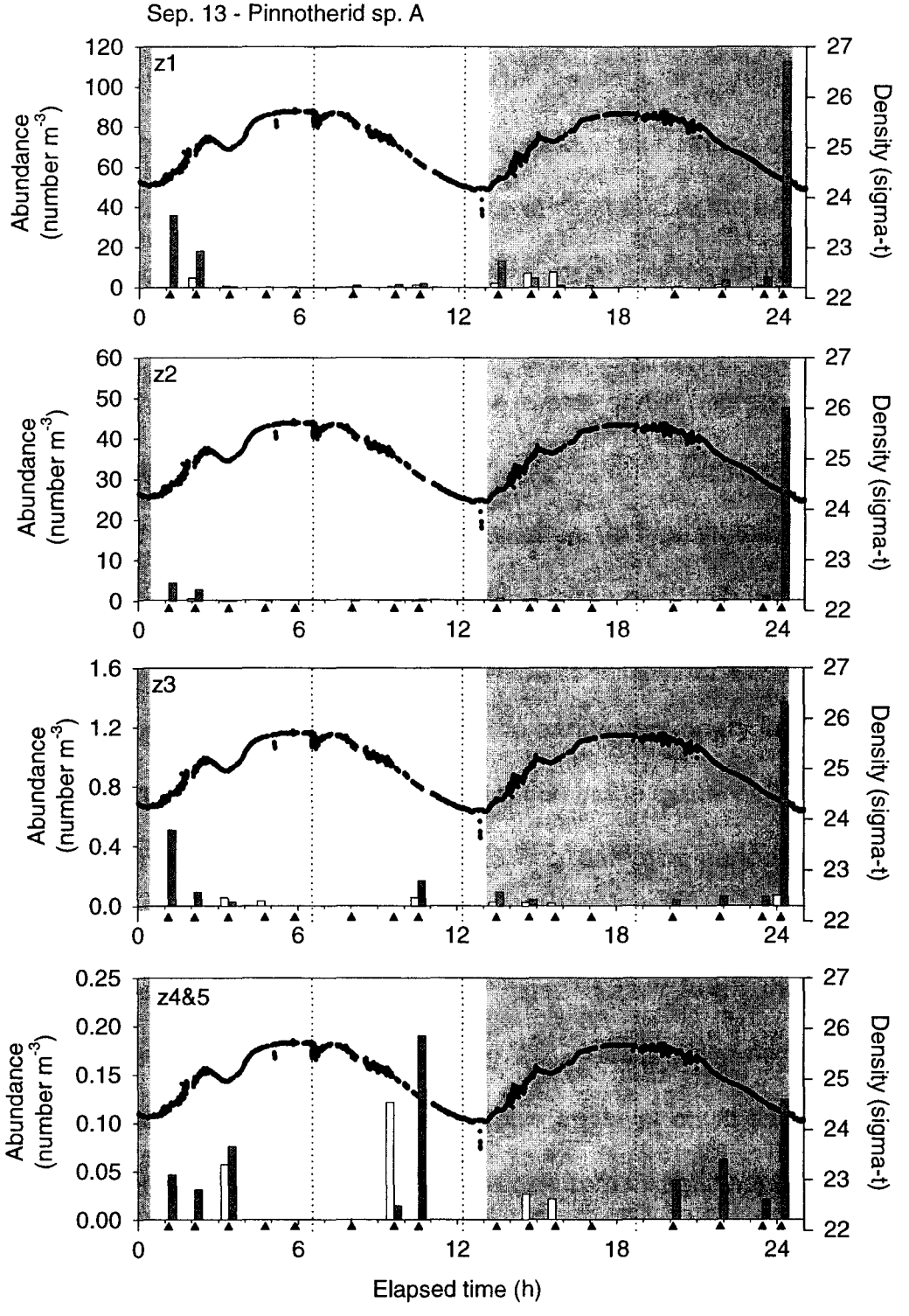

Fig. 26. Abundance (number of individuals per m^3) of the five zoeal stages of the commensal crab, Pinnotherid sp. A, at the anchor station on 13 September. Unshaded bars represent surface zooplankton samples, and the shaded bars represent near bottom zooplankton samples. Water density is also plotted to identify the water masses in which the organisms are found. Gray background shading indicates night. Triangles along the bottom axis indicate the time at which the zooplankton samples were collected.

result in retention, but does not appear to be the case for pinnotherid larvae in South Slough. Some days first through third stage pinnotherid spp. zoeae tended to be more abundant at the surface at night and at the bottom during the day, while forth and fifth stage zoeae were more evenly distributed (but their numbers were often low). Without a better understanding of the circulation in South Slough it is difficult to determine the effects of diel migrations on dispersal. Vertical migration behavior as was seen in the copepod *Eurytemora affinis* (Hough and Naylor 1991) could lead to retention. In high salinity areas the zoeae could ascend during flood tides and descend to the benthic boundary layer (or onto the bottom) during ebb tides; alternately, in low salinity areas zoeae could ascend during ebb tides and descend to the benthic boundary layer (or onto the bottom) during flood tides, resulting in retention in the estuary. There does seem to be some evidence for this during the 28 Aug. sampling period (Fig. 22), but not during any of the other sampling dates. On 7 Aug. almost all pinnotherid spp. larvae were collected in bottom samples (Figs. 19-21, 7 Aug.), this was also the case for pinnotherid sp. A on 13 Sep. (Fig. 26). Tidally timed migrations between the near bottom waters and the benthic boundary layer could easily lead to retention and at the same time reduce the risk from visually hunting planktivores. It appears that the mechanism for retention in pinnotherid larvae is complex. It is also confounded by the lumping together of several species. A more thorough and intensive sampling protocol will be necessary to understand the mechanisms involved in their retention.

Larval Fish

The larval fish caught during this study were all approximately 3 mm long and were extremely similar in appearance. Larvae taken randomly from multiple samples in each of the four sampling periods that larval fish were present all keyed out as *Clevelandia ios* based on morphological characteristics and the number of caudal and precaudal vertebrae. *Clevelandia ios*, the arrow goby, belongs to the family Gobiidae. Gobies are small sedentary fishes that frequently rest on the bottom partially buried in sand. Adult *C. iosi* live in sheltered bays and estuaries and are very tolerant of extreme conditions of temperature and salinity. When threatened or during low tides, adults take shelter in the burrows of ghost shrimps (such as *Neotrypaea californiensis*) and mud shrimps. In California, arrow gobies spawn December to August. Eggs, laid in groups, sink and are non-adhesive. Eggs, at ~15°C, hatch in 10 to 12 days, and produce pelagic larvae 2.7-3.8 mm long. They grow rapidly reaching 7 mm in 10 days. There is no parental care of young (Hart 1973).

A total of 1,562 larval fish were counted in four sampling periods. Peaks in larval fish abundance were consistently in the lowest salinity estuarine waters sampled. Larvae were rare in Coos Bay and ocean waters. They were caught almost exclusively in bottom samples and mainly during the day (Fig. 27). These data suggest that the larvae are retained in the estuary. Larval fish longer than ~3 mm were not caught, perhaps because larger fish were able to avoid the net. How the larvae are retained is unclear. One possibility is that the larval fish are

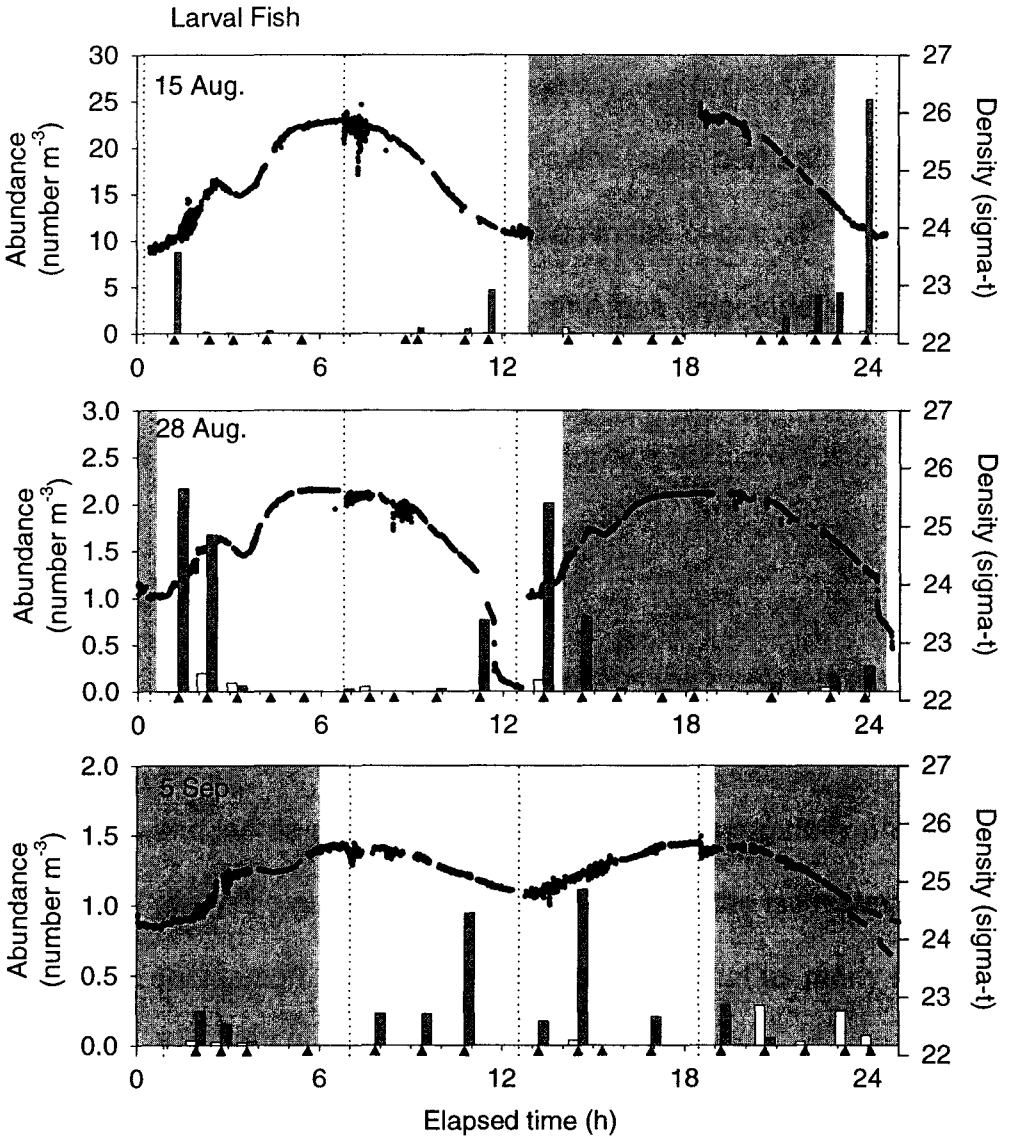

Fig. 27. Abundance (number of individuals per m^3) of larval fish at the South Slough anchor station over three sampling periods. Unshaded bars represent surface zooplankton samples, and the shaded bars represent near bottom zooplankton samples. Water density is also plotted to identify the water masses in which the organisms are found. Gray background shading indicates night. Dotted vertical lines indicate slack water. Triangles along the bottom axis indicate the time at which the zooplankton samples were collected.

resting on the bottom during ebb and flood when velocities are high and are coming up off the bottom during daytime slack tides, perhaps to feed. A similar type of vertical migration behavior was seen in the copepod *Pseudodiaptomus hessei* in the Sundays River estuary, South Africa (Wooldridge and Erasmus 1980). The copepods would retain in the estuary by avoiding flood and ebb surface currents, but migrated toward the surface during times of slack water.

Import

Though the focus of my investigation was the transport of planktonic larvae of estuarine organisms, while processing the zooplankton samples, holoplankton and larvae of coastal invertebrates were regularly present in the samples and often in high abundance. Because so little is known about the transport of zooplankton in South Slough, I decided that as many species, as time permitted, should be included in the study. Therefore all crab larvae, barnacle cyprids, and gelatinous zooplankton were counted, though not for all sampling periods (Table 3).

The zooplankters that imported typically live on the outer coast as adults, but some can tolerate living in the lower portions of estuaries. Estuarine zooplankton are spawned in the estuary, whereas larvae importing to the estuary originated outside of the estuary. Zooplankton were classified as imported if peaks in abundance occurred in incoming ocean waters. Without behavioral adaptations it is unlikely that zooplakton coming into the estuary with ocean

waters near the end of flood tide would remain in the estuary during the following ebb tide. Though some zooplankters may be entrained due to tidal mixing the majority are most likely expelled.

Porcelain spp.

There are four species of porcelain crabs found in the vicinity of the Coos Bay: *Petrolisthes cinctipes*, *Petrolisthes eriomerus*, *Pachycheles pubescens*, and *Pachycheles rudis*. It is time consuming to identify their larvae to the genus level, and identification to the species level requires dissection; therefore, the larvae were grouped together. Porcelain crabs live in rocky intertidal and subtidal areas. The *Petrolisthes* species are also known to live in the interstices of well developed mussels beds and around submerged jetties and rip-rap (Morris et al. 1980). They produce two broods per year, the first hatching in May through mid August and the second August through early October (Strathmann 1987). Porcelain crabs molt through two zoeal stages and one megalopal stage spending approximately five to six weeks in the plankton (Gonor and Gonor 1973)(Table 2).

A total of 4,965 porcelain crab larvae were counted in five sampling periods. Larvae were identified to stage for three of the sampling periods; for those three dates 95.30% of the larvae were z1, 4.47% were z2, and 0.23% were megalopae (Table 6). Peaks in zoeal abundance occurred in ocean waters, although zoeae were common in estuarine waters (Fig. 28). The zoeae

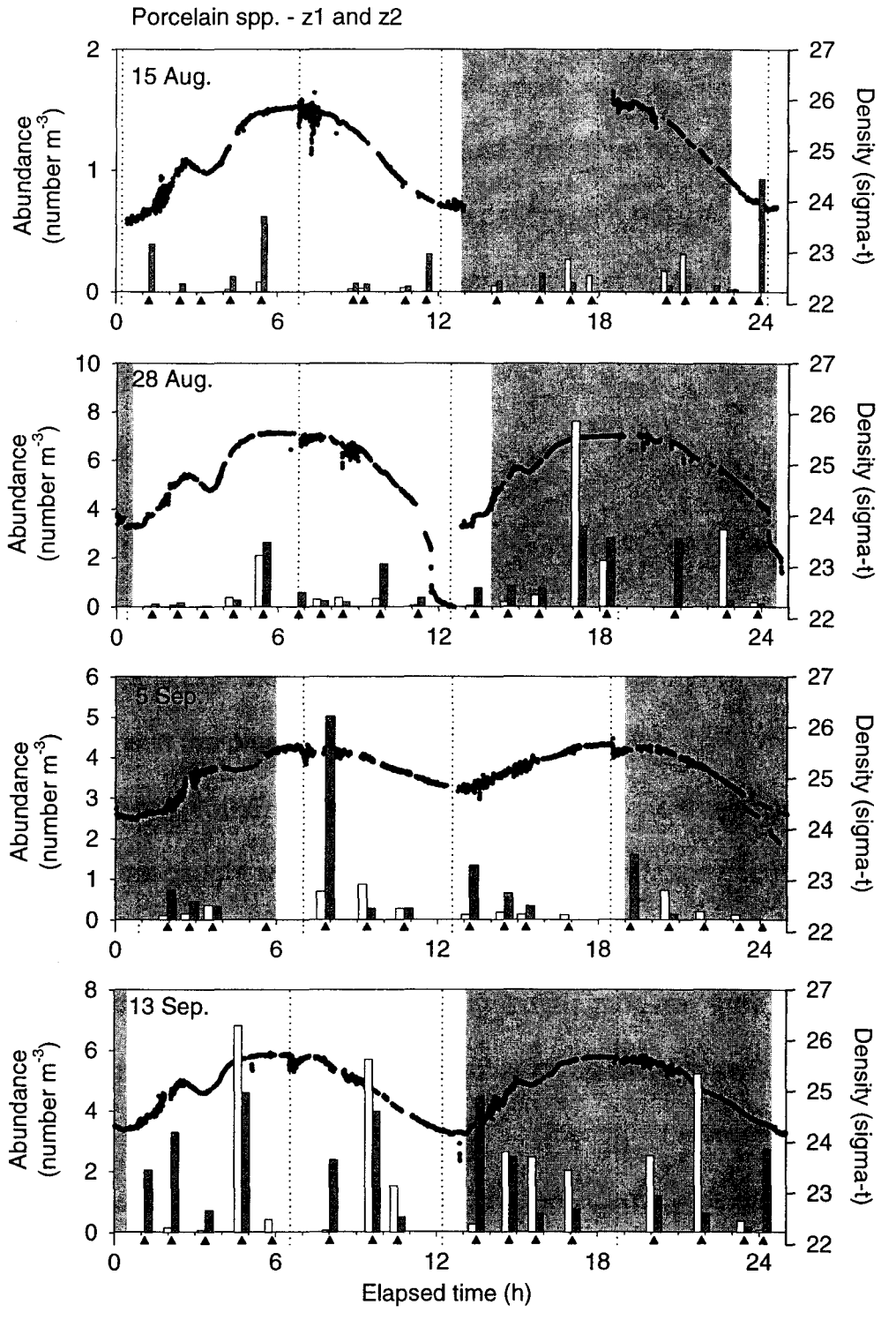

Fig. 28. Abundance (number of individuals per m^3) of first and second stage zoeae of porcelain crabs at the South Slough anchor station over four sampling periods. Unshaded bars represent surface zooplankton samples, and the shaded bars represent near bottom zooplankton samples. Water density is also plotted to identify the water masses in which the organisms are found. Gray background shading indicates night. Dotted vertical lines indicate slack water. Triangles along the bottom axis indicate the time at which the zooplankton samples were collected.

were found both day and night, at the surface and bottom (Fig. 28). Six megalopae were caught, three on 7 August, and three on 15 August. There was no consistency in when megalopae were caught with regards to time of day, water mass, or stage of tide. Porcelain larvae do not appear to vertically migrate to regulate their transport within the estuary.

Emerita analoga

Emerita analoga, the Pacific sand crab, lives on sandy beaches in the surf zone (Jensen 1995). Larvae hatch July through August. They molt through five zoeal stages and one megalopal stage (Johnson and Lewis 1942), spending up to four months in the plankton (Johnson 1939).

A total of 1,160 *E. analoga* larvae were counted in three sampling periods. All of the larvae caught were z1. Peaks in larval abundance occurred in ocean waters (Fig. 29). Larvae tended to be more abundant at night, and appeared to be evenly distributed vertically; when caught during the day they were mainly in bottom samples (Fig. 29). There is no habitat for *E. analoga* in South Slough; therefore, their transport into the slough is "accidental". Larvae that have not evolved to develop in brackish waters will experience physiological stress in salinities lower than typical ocean salinities; thus, larvae entrained in estuarine waters for too long a period may die.

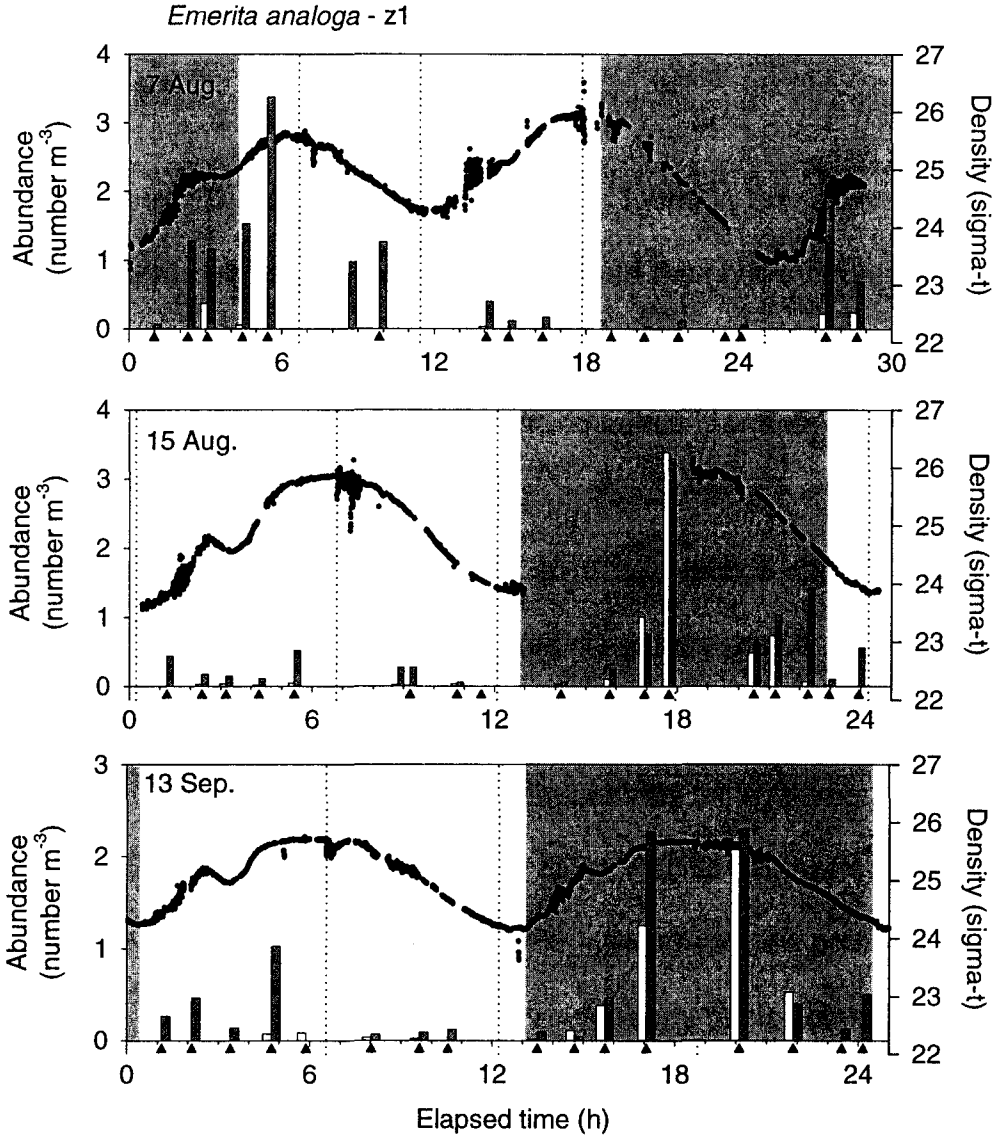

Fig. 29. Abundance (number of individuals per m^3) of first stage zoeae of the anomuran crab, *Emerita analoga*, at the South Slough anchor station over three sampling periods. Unshaded bars represent surface zooplankton samples, and the shaded bars represent near bottom zooplankton samples. Water density is also plotted to identify the water masses in which the organisms are found. Gray background shading indicates night. Dotted vertical lines indicate slack water. Triangles along the bottom axis indicate the time at which the zooplankton samples were collected.

Barnacle Cyprids

Excepting *Balanus improvisus,* which is found in the upper reaches of estuaries, barnacles in the Pacific Northwest are mainly distributed on the outer coast. However, most species can inhabit the lower reaches of bays and estuaries where hard substrate is present. *Balanus glandula, B. nubilus,* and *Semibalanus cariosis* are all found in the Charleston boat basin near the mouth of South Slough (personal observation). In most barnacle species the larval period lasts two to four weeks, during which time they molt through six naupliar stages and one cyprid stage. The cyprid is the last larval stage, it is non-feeding, and it is responsible for seeking out suitable habitat for settlement. For the barnacle species that have been studied in the Pacific Northwest, peak settlement is typically in the spring. However, most species produce multiple broods, thus lower levels of settlement through early fall is common (Strathmann 1987).

3,670 barnacle cyprids were caught during four sampling periods. Except for the 15 August sampling period, cyprid concentrations in the water column were low with maximum concentrations of less than 3 m^{-3}. Approximately 76% of the cyprids were caught on 15 August, ~2% were caught on 28 August, less than 1% were caught on 5 September, and ~21% were caught 13 September. On 15 August and 13 September the cyprids were identified to the species level. *Balanus glandula* was the most abundant species on these two dates. The species composition of the catch is shown in Table 7.

Table 7. Percentage of each species of barnacle comprising the catch for a given day.

Organism	15 Aug.	13 Sep.
Balanus crenatus	12.42	8.82
Balanus glandula	74.52	31.88
Balanus improvisus	0.51	0
Balanus nubilus	1.60	25.97
Chthamalus dalli	2.14	2.06
Lepas spp.	0.26	0
Pollicipes polymerus	2.57	2.20
Semibalanus cariosus	5.98	29.07

Peaks in cyprid abundance were often at the surface in incoming ocean water (Fig. 30). After such peaks, during the subsequent ebb tide, cyprids were abundant in bottom samples or were not caught at all. These data suggest that cyprids were imported from the coastal ocean and were then sinking or swimming downward in search of settlement habitat. Vertical migration behavior has been observed in cyprids by Bousfield (1955), who found that barnacle cyprids in the Miramichi estuary, New Brunswick, achieved upstream transport not only by maintaining a position in the landward flowing bottom waters, but also augmented this transport by being higher in the water column during flood than during ebb. Cyprids were found at the surface in incoming ocean waters, both day and night; suggesting that over the shelf cyprids maintain a position in surface waters, but upon entering the estuary their behavior changes.

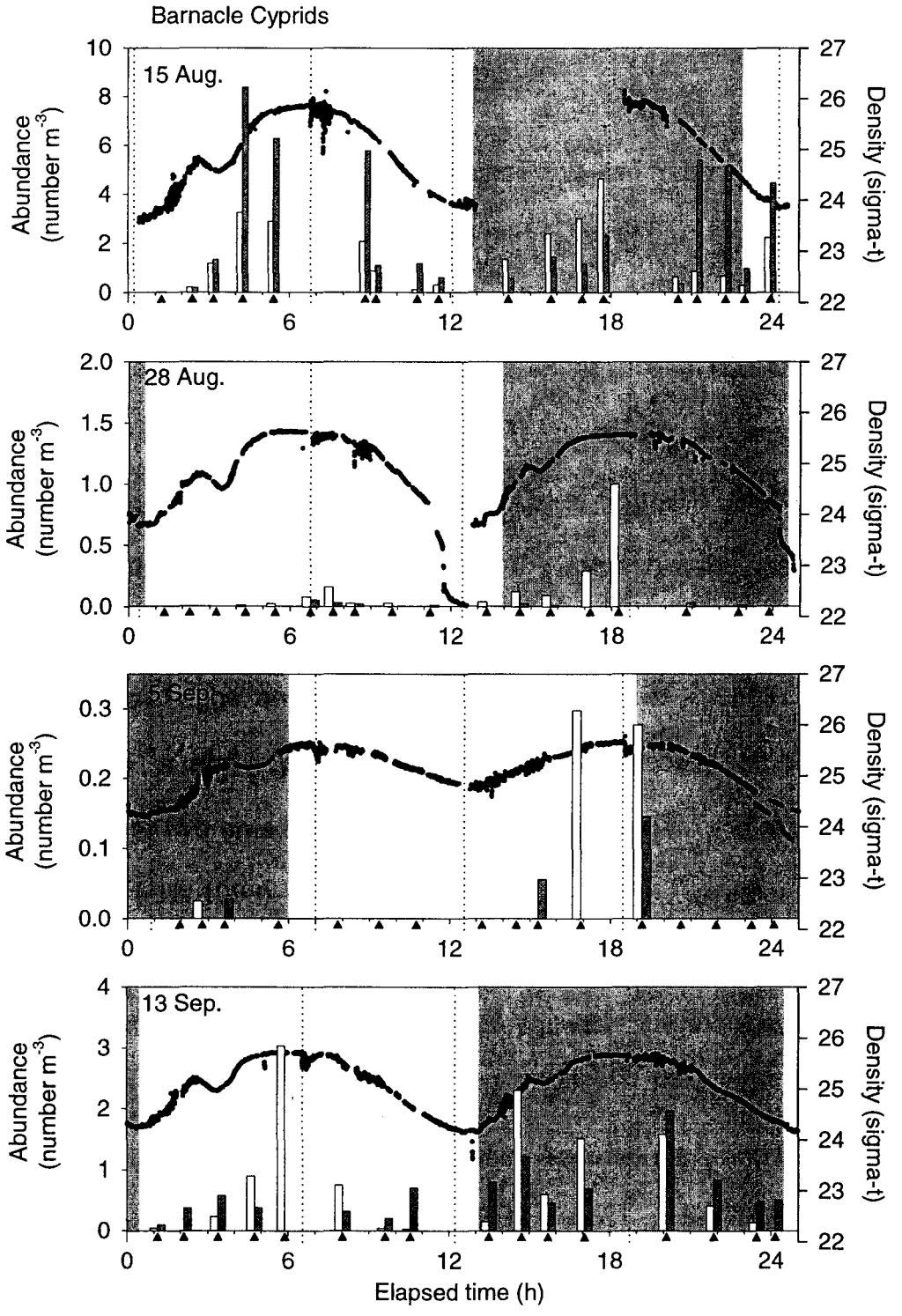

Fig. 30. Abundance (number of individuals per m^3) of barnacle cyprids at the South Slough anchor station over four sampling periods. Unshaded bars represent surface zooplankton samples, and the shaded bars represent near bottom zooplankton samples. Water density is also plotted to identify the water masses in which the organisms are found. Gray background shading indicates night. Dotted vertical lines indicate slack water. Triangles along the bottom axis indicate the time at which zooplankton samples were collected.

Gelatinous Zooplankton and Chaetognaths

Clytia gregaria, Pleurobrachia bachei, and *Aequorea* sp. were the most common gelatinous organisms collected during the study. *Clytia* is one of the most abundant small hydromedusae in the Pacific Northwest. Its hydroid form is an inconspicuous member of the fouling community. Medusae are released from spring until early fall (Wrobel and Mills 1998). *Clytia* spp. are reported to feed on copepods, eggs of euphausiids and copepods, and small crustacean and noncrustacean larvae (Lucas et al. 1995). *Pleurobrachia*, the sea gooseberry, is a nearly spherical ctenophore. It is reported to feed on copepods, larval fish, various types of eggs, and other small plankton (Wrobel and Mills 1998). *Aequorea* sp., a relatively large hydromedusae, eats mostly soft-bodied prey including other hydromedusae, ctenophores, polychaetes, and appendicularians (Wrobel and Mills 1998). Chaetognaths were all lumped together. They are primarily oceanic, but some estuarine species are known. They are voracious predators eating larval fishes and small zooplankton; there are even reports of cannibalism.

Clytia gregaria, Pleurobrachia bachei, Aequorea sp., and chaetognaths were all most abundant at the surface and in ocean waters (Figs. 31-33, *Aequorea* spp. not graphed). *Clytia gregaria* and *P. bachei* were more abundant at night (Figs. 31 & 32), which suggests that they were undergoing diel vertical migrations. Diel vertical migrations have been observed in *P. bachei* by Hirota (1974) and in *Pleurobrachia pileus* by Rowe (1971). Hirota (1974) suggests that

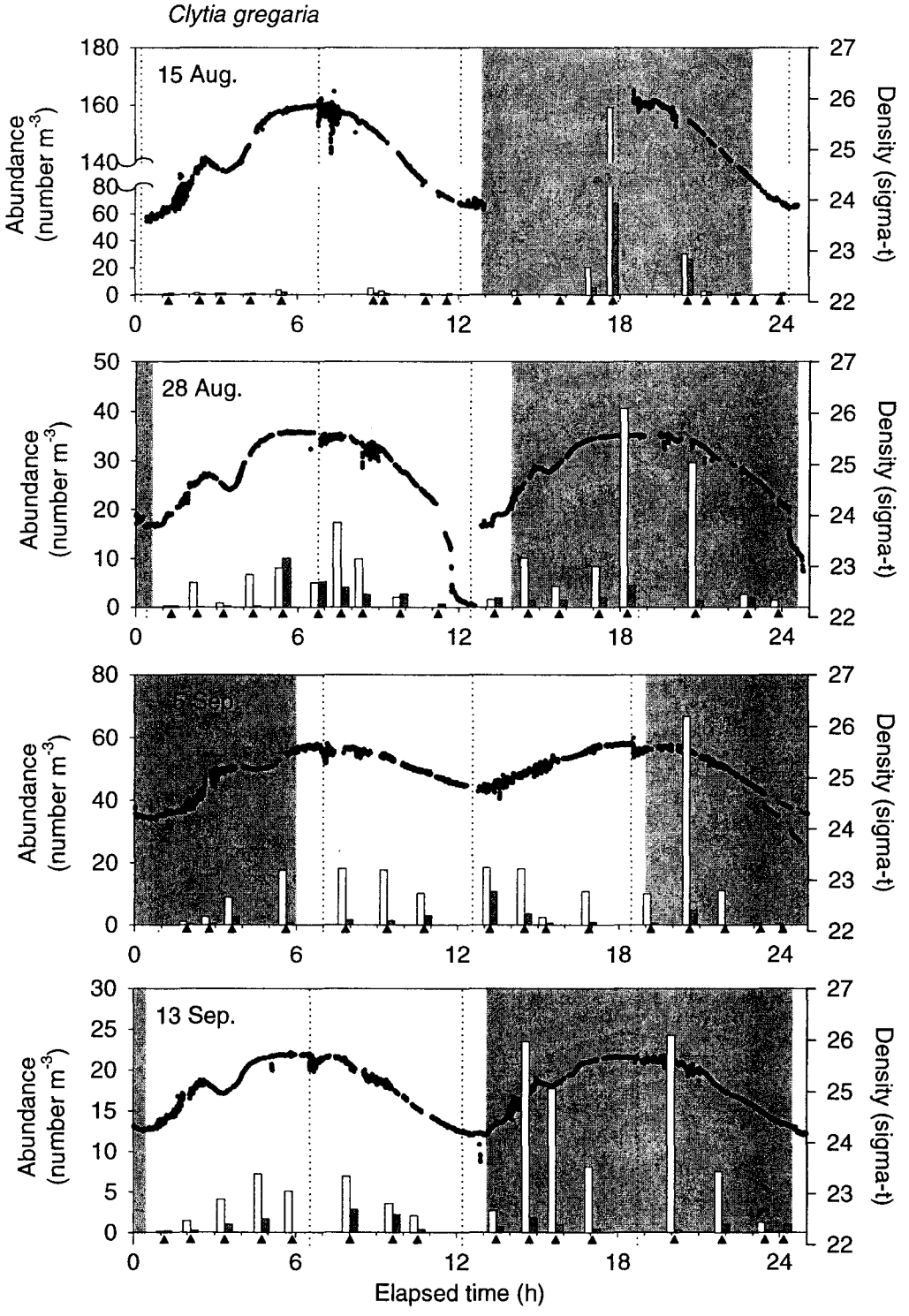

Fig. 31. Abundance (number of individuals per m^3) of the hydromedusae, *Clytia gregaria*, at the South Slough anchor station over four sampling periods. Unshaded bars represent surface zooplankton samples, and the shaded bars represent near bottom zooplankton samples. Water density is also plotted to identify the water masses in which the organisms are found. Gray background shading indicates night. Dotted vertical lines indicate slack water. Triangles along the bottom axis indicate the time at which zooplankton samples were collected.

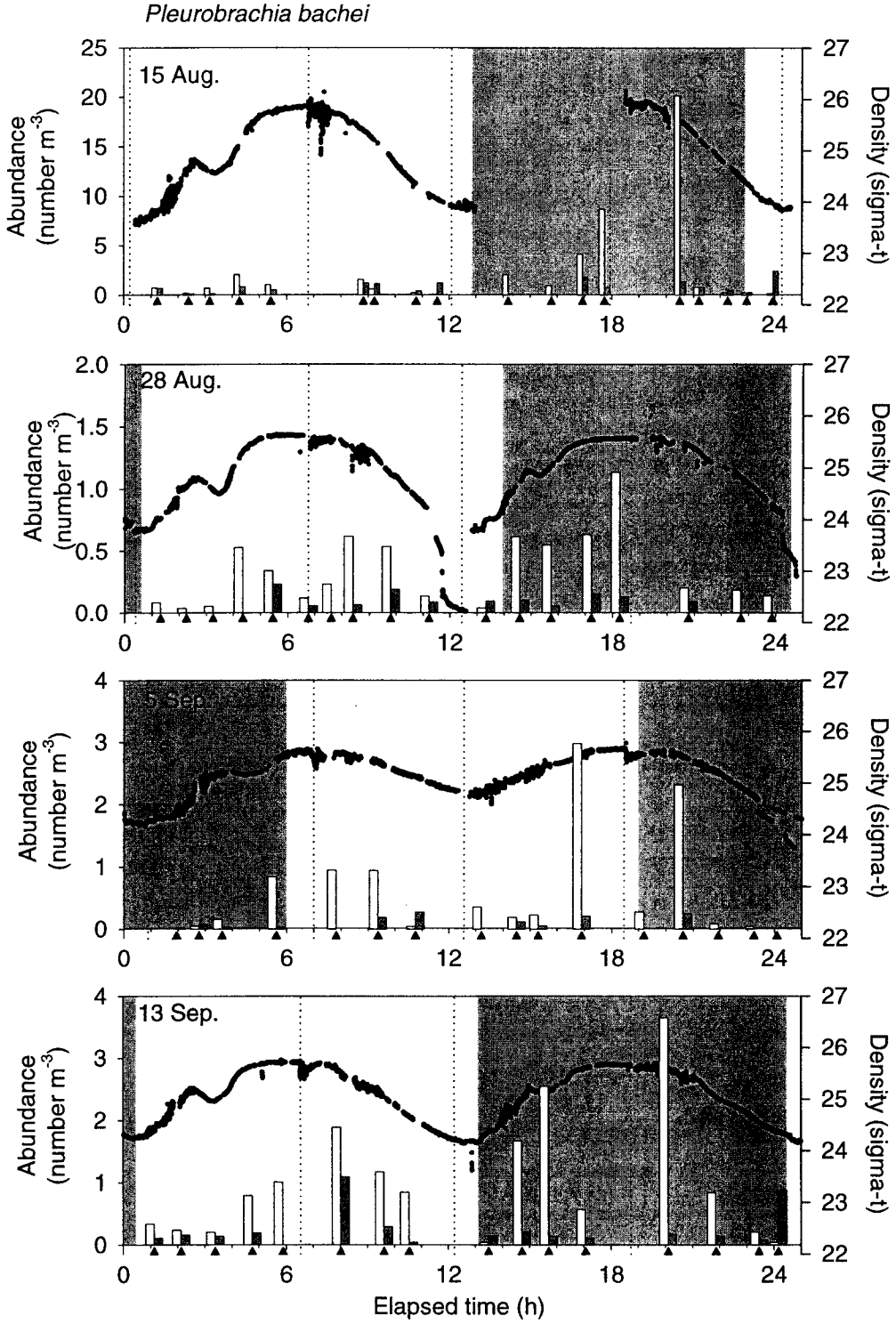

Fig. 32. Abundance (number of individuals per m^3) of the ctenophore, *Pleurobrachia bachei*, at the South Slough anchor station over four sampling periods. Unshaded bars represent surface zooplankton samples, and the shaded bars represent near bottom zooplankton samples. Water density is also plotted to identify the water masses in which the organisms are found. Gray background shading indicates night. Dotted vertical lines indicate slack water. Triangles along the bottom axis indicate the time at which the zooplankton sapmples were collected.

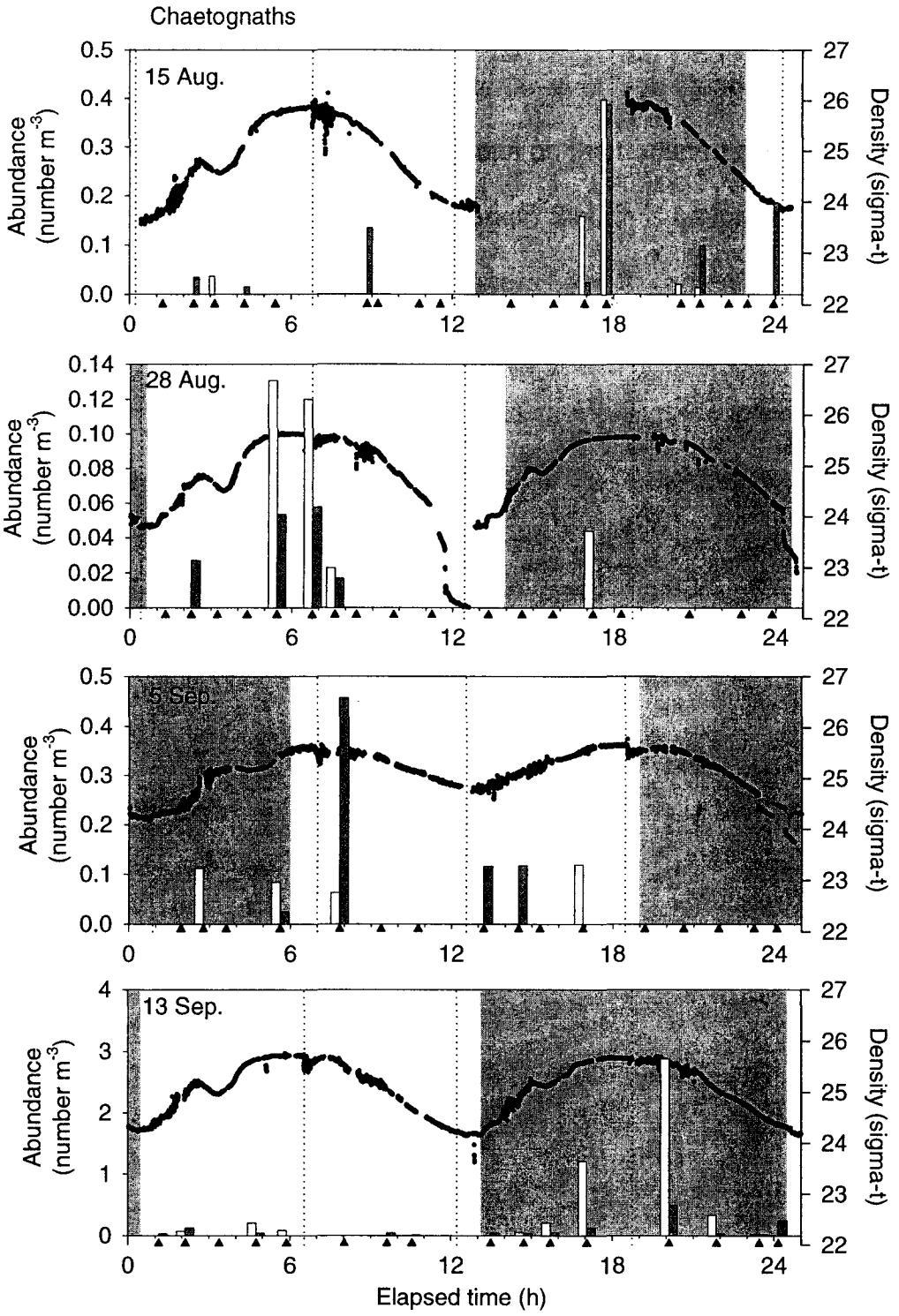

Fig. 33. Abundance (number of individuals per m^3) of chaetognaths at the South Slough anchor station over four sampling periods. Unshaded bars represent surface zooplankton samples, and the shaded bars represent near bottom zooplankton samples. Water density is also plotted to identify the water masses in which the organisms are found. Gray background shading indicates night. Dotted vertical lines indicate slack water. Triangles along the bottom axis indicate the time at which the zooplankton sapmples were collected.

the vertical migrations may lead to maintenance of high ctenophore abundances close to shore. The effect of diel migrations on the transport of *P. bachei* and *C. gregaria* off the coast of Oregon and in South Slough is beyond the scope of this paper. Because many gelatinous consumers have the potential for high ingestion rates (Alldredge 1984), the high densities of gelatinous zooplankton in South Slough, sometimes in excess of 160 individuals per cubic meter, may have profound effects on the population dynamics of their planktonic prey.

CHAPTER V

CONCLUSIONS

This study investigated the transport of zooplankton in South Slough, Oregon, and the role of vertical migration in the transport process. The data demonstrate that larvae of *Neotrypaea californiensis* and *Hemigrapsus oregonensis* were exported from the estuary. Early stage zoeae of these species dominated the catch in estuarine waters. No later stage zoeae of *N. californiensis* were caught, and the few later stage zoeae of *H. oregonensis* caught were primarily in ocean waters. There is evidence that early stage zoeae of *Neotrypaea californiensis* and *Hemigrapsus oregonensis* underwent rhythmic vertical migrations that enhanced their export. Peaks in larval abundances occurred at the surface during nocturnal ebb tides and then at the bottom during the following flood tide. The data also suggest that larvae of *Lophopanopeus bellus* and *Pachygrapsus crassipes* may be exported. *N. californiensis, H. oregonensis, L. bellus,* and *P. crassipes* larvae had similar patterns of abundance and vertical distribution, but differences during day-time ebb tides and the flood tides that followed were observed. The differences in distributions may have been due to differences in the location of spawning adults, and/or differences in larval swimming behavior.

All larval stages of pinnotherid crabs were found in estuarine waters, indicating that the larvae were retained in the estuary. Larval fish, which were probably the arrow goby, *Clevelandia ios*, were found exclusively in estuarine waters, this suggests that they also were retained. How pinnotherid spp. larvae and larval fish were retained in South Slough is unclear. Almost half of the slough water is discharged on an average ebb tide, and summer flushing times are on the order of one tidal cycle (Pimentel 1986). Given that the estuary is well-mixed, and freshwater input is minimal in the summer, it is likely that there is a net seaward flow at all depths (Burt and McAlister 1959). In such conditions it is unlikely that larvae without behaviors that aid in retention would be retained. Patterns of abundance and vertical distribution of pinnotherid spp. zoeae were variable between sampling periods, only z1 larvae showed somewhat consistent patterns. However, during a sampling period, distributions of the different larval stages were often remarkably similar, suggesting that the different larval stages were behaving similarly. Therefore the data suggest that larvae swimming behavior plays a role in the retention of pinnotherids, however, a more thorough and intensive sampling design will be necessary to elucidate the mechanisms involved.

Why do some larvae export while others retain? Predation, food resources, physiological stress, and the risk of being dispersed "too far" from settlement habitat are all thought to be factors. Larvae that export are thought to benefit from lower predation risks, and lower physiological stress, while larvae

that retain are thought to benefit from higher food resources and reduced dispersal (and thus enhanced recruitment) (Strathmann 1982, McConaugha 1988). Predation risks are assumed to be lower in coastal waters because the density of planktivorous fishes decreases with increasing distance from shore (Morgan 1995); however, during my study, abundances of gelatinous zooplankton in incoming ocean waters were as high as ~160 organisms per cubic meter. Zooplankton food resources are often reported as being higher in estuaries than adjacent coastal areas (Mann 2000). Recent studies in Pacific Northwest estuaries suggest that in the summer, phytoplankton production in the estuary is low, and that coastal waters, due to wind driven upwelling, often have much higher concentrations of phytoplankton (Roegner and Shanks 2001, Roegner et al. 2002). Larval development success of some estuarine invertebrate larvae has been found to be highest in salinities approximating ocean water (Strathmann 1982, McConaugha 1988), while others develop optimally in brackish water (Costlow et al. 1966, Strathmann 1982, Gonçalves et al. 1995, Strasser & Felder 2001). Finally, just as retained larvae have behaviors that result in their retention, larvae of exported species are known to have behavioral adaptations that result in their return to the estuary (Shanks 1995). Although it seems intuitive that exporting larvae into the ocean, where currents are less predictable, would be riskier, I know of no study that has looked at recruitment success of exported versus retained larvae.

Larvae of estuarine invertebrates may be retained or exported by taking advantage of residual currents in stratified estuaries, however, the more species that are examined, the more prevalent selective tidal-stream transport (STST) is found to be. Examples exist for export and retention via STST in a wide variety of estuaries (references in Forward and Tankersley 2001). The involvement of endogenous rhythms in STST can be investigated under constant conditions in the laboratory. Unfortunately, few studies have looked at a species vertical migration behavior in both the field and in the laboratory. Even fewer studies exist looking at the same species in multiple estuaries, especially estuaries that are drastically different (with regards to size, circulation, flushing rates, turbidity, physical constituents, geographic location, etc.). But for the few species that have been intensively studied in both the lab and in multiple locations in the field, the picture that is emerging is that zoeae have endogenous rhythms that are set by local zeitgebers and are modified by exogenous factors (Cronin and Forward 1983, Zeng and Naylor 1996). Therefore larvae may be able to undergo the same dispersal strategy even in different hydrodynamic conditions.

While some estuarine larvae export to coastal waters, a variety of organisms were imported into South Slough from coastal waters. Porcelain spp. zoeae, *Emerita analoga* first stage zoeae, several species of barnacle cyprids, *Clytia gregaria*, *Pleurobrachia bachei*, *Aequorea* sp., and chaetognaths all were most abundant in incoming ocean waters. Of these organisms, only barnacle cyprids appeared to change their vertical position upon entering the estuary.

Peaks in cyprid abundance occurred at the surface, in incoming ocean waters, both day and night, but during the subsequent ebb tides, cyprids were abundant in bottom samples or were not caught at all (suggesting that they settled while in the estuary). Changes in vertical position or vertical migrations in the estuary in the other imported organisms were either not observed or the data were inconclusive.

Given that the sampling dates were chosen to coincide with the time of year when megalopae are typically recruiting, it was surprising that so few megalopae were caught with the incoming ocean waters. One possible explanation is that import of megalopae from coastal waters is pulsed, and sampling periods may have been out of phase with peaks in megalopal ingress. Data from light trap samples collected daily near the mouth of South Slough revealed species-specific variation in megalopae abundance, with variability in the number, size, duration, and timing of peaks between years (Roegner et al. in prep. a). Generally, abundances increased sharply from low background levels over 2 to 7 day periods. Additionally, cruise data from coastal waters adjacent to the Coos Bay and other Pacific Northwest estuaries suggest that megalopae are concentrated in patches (Roegner et al. in prep. b). The authors hypothesize that larval advection into the estuary depends on proximity of the larval patch in relation to the estuary mouth. Therefore it is possible that sampling dates missed peaks in megalopal ingress. There is also evidence that megalopae may import into estuaries via axial convergent fronts. In Grays Harbor, Washington,

Eggleston et al. (1998) found that mean concentrations of *Cancer magister* megalopae were significantly higher in fronts than in adjacent waters 20 to 30 m outside of the front. They propose "axial convergent fronts may serve as a type of 'larval conduit' delivery system" (Eggleston et al 1998, p 80). Axial convergent fronts regularly occur in South Slough, and were seen during this study (personal observation); however, they were not sampled. If megalopae were concentrated in axial convergent fronts in South Slough, the fact that my samples were collected outside the front could account for the low megalopae densities. The two possible explanations for low megalopal abundances presented here (episodic import and the larval conduit theory) are not mutually exclusive.

Twice a day the lower reaches of the Coos Bay estuary were inundated with coastal ocean waters. Along with the intruding waters came the community of plankton in those waters. During high tide the water and zooplankton community at the anchor station can be characterized as oceanic. Cziesla (1998) has found that the phytoplankton assemblages in South Slough were also dominated by oceanic species during high tide. What organisms import into the estuary at high tide depends on what organisms are near the mouth as the tide begins to flood. What organisms are found near the mouth of the estuary depends on coastal circulation and zooplankton behavior. Because the lower estuary is inundated with ocean waters, large scale processes that affect coastal ocean waters, such as the wind driven upwelling-downwelling cycle, also impact the estuary

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