

CROSS-SHELF TRANSPORT OF PLANKTONIC LARVAE OF INNER SHELF
BENTHIC INVERTEBRATES

by

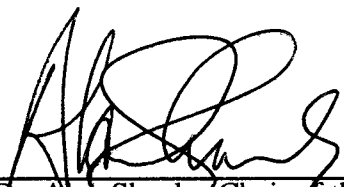
LAURA ANN BRINK

A THESIS

Presented to the Department of Biology
and the Graduate School of the University of Oregon
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Master of Science

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"Cross-Shelf Transport of Planktonic Larvae of Inner Shelf Benthic Invertebrates," a thesis prepared by Laura Ann Brink in partial fulfillment of the requirements for the Master of Science degree in the Department of Biology. This thesis has been approved and accepted by:



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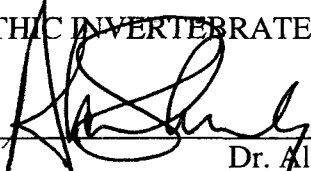
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Title: CROSS-SHELF TRANSPORT OF PLANKTONIC LARVAE OF INNER SHELF
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Approved: _____


Dr. Alan Shanks

There are two schools of thought on the affect of the physical environment in larval transport and dispersal. One is that larvae act as passive particles, being transported solely by physical means. The other idea is that through behavioral changes, larvae can alter their transport so as to improve their chances of successfully settling. Both cross-shelf and 23 hour vertical sampling of meroplanktonic larvae was conducted to investigate the hypothesis that larvae act as passive particles, being dispersed by the currents. The lengths of bivalve larvae were also measured to determine if there were ontogenetic differences in the vertical distributions of these larvae. No diel vertical migrations were observed. Most larvae appeared to be using density isopleths as a means of "monitoring" their vertical position within the water column. By swimming vertically against low density downwelling water or higher density upwelling water, larvae were able to maintain their relative positions within the water column. Larvae were often observed to remain within a certain density range over the course of the 23 hour sampling period. For some bivalve species, larger larvae were found near the bottom, possibly an indication of byssus thread drifting occurring. The relationship of larval size to vertical distribution appears to be a function of the location of the adult habitat.

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GENERAL INTRODUCTION

Although the transport of marine invertebrate larvae has received considerable attention within the last four decades (Bousfield, 1955; Shanks, 1983; Scheltema, 1986; Farrell *et al.*, 1991; Tremblay & Sinclair, 1992; Botsford *et al.*, 1994), our understanding of the relationship between prevailing oceanographic conditions and the advective and diffusive transport of meroplankton is still in its infancy. During much of this time, larval transport has been considered as primarily a stochastic process, where populations of larvae are dispersed solely by currents (Scheltema, 1971; deWolf, 1974; Banse, 1986; Levin, 1986). These authors suggest that larvae are transported passively offshore with offshore-moving waters, followed by a period of dispersion and shoreward transport back to potential settlement sites via shoreward-flowing waters. The vast majority of larvae, however, may be carried too far away from the adult habitat to ever allow for settlement and recruitment to adult populations (Jackson & Strathmann, 1981).

Offshore transport during the dispersal phase is not the only problem faced by planktonic larvae. Swimming larvae also encounter potential threats including mortality caused by predation, starvation, and encounters with unfavorable water masses (i.e., water of poor temperature or salinity regimes; Thorson, 1946; Jackson & Strathmann, 1981; Rumrill, 1990). These added risks further decimate the number of larvae in the plankton. Those larvae which are able to survive must find some way of returning to a suitable adult habitat in order to settle and metamorphose into the adult form. Relying solely on currents for transport back to the adult habitat seems much too haphazard of a process to insure that sufficient numbers of larvae will settle and recruit so as to maintain adult population numbers. Thus, a mode of transport other than simple stochastic movement by water currents seems likely.

Over the continental shelf, horizontal current velocities can range from <1 to 10 's cm sec^{-1} , while vertical current speeds are usually much slower, on the order of mm sec^{-1} (Austin, person communication). In comparison, most ciliated meroplanktonic larvae can swim horizontally at a maximum speed of only a few mm sec^{-1} , but vertical swimming/sinking speeds can range from 10 's mm sec^{-1} to cm sec^{-1} (reviewed in Chia *et al.*, 1984). Therefore, for a larva to swim horizontally against the currents seems unlikely. Because currents often change direction and speed with depth, larvae may be able to select the direction in which they are transported by moving vertically within the water column (Woodmansee, 1966; Shanks, 1986; Hill, 1991a, 1991b, 1995). For example, in order to remain within the estuaries of their spawning, oyster larvae (Wood & Hargis, 1971) and mud crab zoea (Cronin & Forward, 1982) have been found to swim up into flood tides and then swim back down to the bottom during ebb tides. For oyster larvae, this swimming behavior was believed to occur in response to increasing salinity (Wood & Hargis, 1971). In contrast, mixing events were thought to cause mud crab zoea to swim up into the flood tides (Cronin & Forward, 1982). Carriker (1951) also found that oyster larvae swam up into flood tides, but he attributed this behavioral response to increased current velocity and turbulence rather than an increase in salinity. Rothlisberg (1982) suggested that penaeid shrimp larvae make daily vertical migrations as a means of moving into different current regimes. By so doing, a larva could theoretically be displaced up to 100 km, depending upon depth and horizontal current speeds. This distance would be sufficient to transport penaeid shrimp larvae from the offshore adult habitat to their nursery grounds along the west coast of Australia and in the Gulf of Carpentaria estuary (Rothlisberg, 1982). The mechanisms by which larvae sense changes in physical variables such as salinity or velocity are unknown. But changes in a larva's vertical position in response to these water column characteristics would appear to operate as behavioral mechanisms that have important implications for horizontal transport.

The research presented in this thesis was part of a larger study funded by the Coastal Ocean Processes (CoOP) program of the National Science Foundation (1994). The CoOP study, conducted off the North Carolina coast, included scientists from the fields of biology, oceanography, and geology, and addressed four interdisciplinary questions: 1) what physical processes contribute to the evolution of the cross-shelf distribution of larvae?, 2) what are the temporal variations in the vertical distributions of larvae and how are these variations related to physical features of the environment and behaviors of the organisms?, 3) do planktonic larvae from differing adult habitats display spatial and temporal differences in their cross-shelf distributions?, and 4) is there a size difference among larvae at different depths and if so, how is this difference affected by the cross-shelf and temporal variations in larval distributions? Within the context of these questions, I have addressed three hypotheses:

- H₁: Planktonic larvae of benthic invertebrates act as passive particles that are transported and dispersed solely by physical means.
- H₂: There are no species-specific differences between the distributions of planktonic larvae from differing adult habitats.
- H₃: A larva's vertical position within the water column is unrelated to larval body size or competency to settle.

From the plethora of larvae found in inner shelf waters during the CoOP study, the bivalve, gastropod, and polychaete larvae were selected as the focus of this research. These particular groups of animals were chosen because: 1) the morphological characteristics of the larval stages have previously been described (Thorson, 1946; Sullivan, 1948; Rees, 1950; Korn, 1960; Loosanoff *et al.*, 1966; Hurst, 1967; Chanley & Andrews, 1971; Thiriot-Quievreux, 1980, 1983; Bhaud & Cazaux, 1982), 2) aspects of their adult ecology are fairly well known (Cerame-Vivas & Gray, 1966; McHugh, 1993; Perry *et al.*, 1993; McKillup *et al.*, 1995), and 3) they were abundant in the samples under

study. Furthermore, the adults are economically and ecologically important members of the East coast benthic community.

It is possible that the cross-shelf transport of marine invertebrate larvae is an active or passive process that is regulated by larval behavior, physical oceanic processes, or some combination of both. Studying the mechanisms that lead to the cross-shelf transport of benthic invertebrate larvae will help us to gain a better understanding of the early life-history stages of some of the more important East coast benthic community members.

CHAPTER I

CROSS-SHELF TRANSPORT OF MEROPLANKTONIC LARVAE

Introduction

Many studies suggest larval transport is a passive process (Scheltema, 1971; deWolf, 1974; Banse, 1986; Levin, 1986) while other studies suggest that larvae play a more active role in their dispersal (Bousfield, 1955; Wood & Hargis, 1971; Forward, 1985; Shanks, 1986). Much of the research on larval transport mechanisms has been conducted in the lab or under conditions in which ambient physical oceanographic measurements could not be taken. Because the vast majority of planktonic larvae are relatively slow swimmers and are susceptible to being swept along with currents, the role of the physical oceanographic environment cannot be overlooked. It is the role of physical and behavioral processes in the cross-shelf transport and dispersal of marine invertebrate larvae that is the focus of this study.

Continental shelf waters are dynamic; over the course of a few hours (one tidal cycle) to a few days (the time it can take for upwelling to begin in the lower latitudes (Barber & Smith, 1981)), the physical characteristics of a water mass may completely change. Reversals in current direction, vertical mixing, and tidal fronts are just a few examples of physical phenomena which routinely disturbs coastal waters. So what do these changes mean for a larva that is dispersed by advective and diffusive processes within this environment? The answer depends upon what role the organism plays in its own transport. If dispersal and transport of meroplanktonic larvae are not simply random processes and larvae are able to actively select a water mass in which to reside, perhaps larvae can avoid

being swept offshore. But to avoid potentially harmful physical occurrences a larva must have some mechanism for detecting changes in its environment.

Abiotic variables such as light, temperature, and salinity have been suggested as possible cues affecting larval behavior. Bayne (1964) demonstrated that young veligers (prior to prodissoconch I shell formation) of the mussel *Mytilus edulis* showed negative phototaxis in response to horizontal directional light at normal temperatures. But as development continued (to the eyed-veliger stage), a positive phototactic behavior developed. Then, with the development of the foot and subsequent crawling, pediveligers become photonegative, presumably in preparation for metamorphosis and settlement on the bottom. Decreases in water temperature have been shown to cause crab larvae (*Rhithropanopeus harrisi* and *Neopanope sayi*) to swim upwards, while an increase in temperature produced the opposite response (Forward, 1990). The temperature at which the behavior of the crab larvae was altered was dependent upon zoeal stage and crab species, with the earliest stages of both species exhibiting the greatest sensitivity to temperature changes. Forward (1990) suggested this behavior may operate as a way for the larvae to avoid temperature extremes or as a means of remaining at depth in a particularly desirable water mass. Veliger larvae of the oyster *Crassostrea virginica* showed an increase in swimming speed in response to a gradual increase in salinity, a behavior which Hidu and Haskin (1978) termed the "salinity response". Under the same conditions larger, eyed-veligers swam almost three times faster than the smallest, straight-hinged larvae, a phenomenon which may explain why in an estuary larger veligers were found higher up in the water column during flood tide than were smaller larvae.

These studies indicate that larvae are able to modify their behavior in response to environmental cues. By avoiding particular salinities or temperatures or actively seeking particular light conditions, larvae may be able to alter their position within the water

column. By changing its position within the water column, a larva's transport is going to be affected.

But what role does physical oceanography play in the transport of benthic invertebrate larvae? The shelf waters off of North Carolina are regularly affected by such physical phenomena as upwelling events, internal waves, and freshwater plumes from the Chesapeake bay. All of these physical occurrences have the potential to dramatically affect the dispersal of the larvae whose embryos were spawned in these waters. It is of critical importance to determine the effect that these oceanographic events have on the distribution of meroplanktonic larvae, not just in the waters off of North Carolina, but in coastal areas everywhere.

Perry *et al.* (1993) found that a frontal system and associated strong current jet on the edge of the Georges Bank prevented mixing between zooplankton populations on and off the bank. Within deeper layers along the bank edge, however, where the along-bank current was much weaker, there was more evidence for cross-bank transport between populations. Along the central California coast onshore movement of surface water associated with the relaxation of upwelling was shown to cause a recruitment pulse of barnacle larvae (Farrell *et al.*, 1991). The researchers inferred that this increase in recruitment was due to the shoreward transport of barnacle larvae by the onshore-moving surface waters. Recruitment of larvae ended once upwelling-favorable winds began to blow and the shoreward movement of surface waters ceased. Internal waves are also known to contribute to the shoreward transport of a variety of larvae (Shanks & Wright, 1987; Shanks, 1988). Larvae become trapped in the convergence zones or "slicks" which form over internal waves. As these waves move onshore, larvae can be transported toward shore.

The research presented in this chapter of the thesis addresses all three hypotheses put forth in the general introduction. By following the cross-shelf movement of larvae over a

four-day period, the role of physical and possible behavioral processes in transport and dispersal should be made clearer.

Methodology

Field Studies

On 21, 23, 25, and 27 August, 1994, sampling was conducted from aboard the research vessel *Cape Hatteras* along a cross-shelf transect that began approximately 1 km offshore from the U.S. Army Corps of Engineers' research pier at Duck, North Carolina (36.2°N, 75.8°W). The cross-shelf transects continued from 1 km offshore out to approximately 20 km offshore (Fig. 1) (these cross-shelf transects will hereafter be referred to as "line surveys"). The number of stations sampled along a line survey depended upon weather conditions (for station locations, see Table 1). Station 1 (1 km offshore) was often omitted during periods of rough seas because of the shallow depth.

Plankton samples were collected with an on-board electric centrifugal pump. The opening of a 5 cm diameter hose was attached to a CTD rosette and the hose was clamped to the intake valve of a 3 hp electric motor. Another 5 cm diameter hose was attached to the outlet valve and directed into on-board 100 μ m mesh plankton nets with attached cod ends. By attaching the hose to the CTD in this manner, we were able to record measurements of depth while sampling populations of larvae. At each depth, approximately 680 L of water were sampled. The decision to sample this volume of water was made because: 1) this volume was approximately the same volume of water that was being sampled by automated zooplankton pumps attached to subsurface moorings directly off of Duck, NC (Butman, in prep.), and 2) this volume provided a reasonable sampling of the larval invertebrates present within the water column. The pumping rate was 227.1 L min⁻¹. After pumping was complete, samples were rinsed from the cod ends into plastic jars and preserved with

FIGURE 1. Map of Study Site. "O"s are Station Locations for Cross-Shelf Transport Study, "X" is Station Location for Vertical Migration Study.

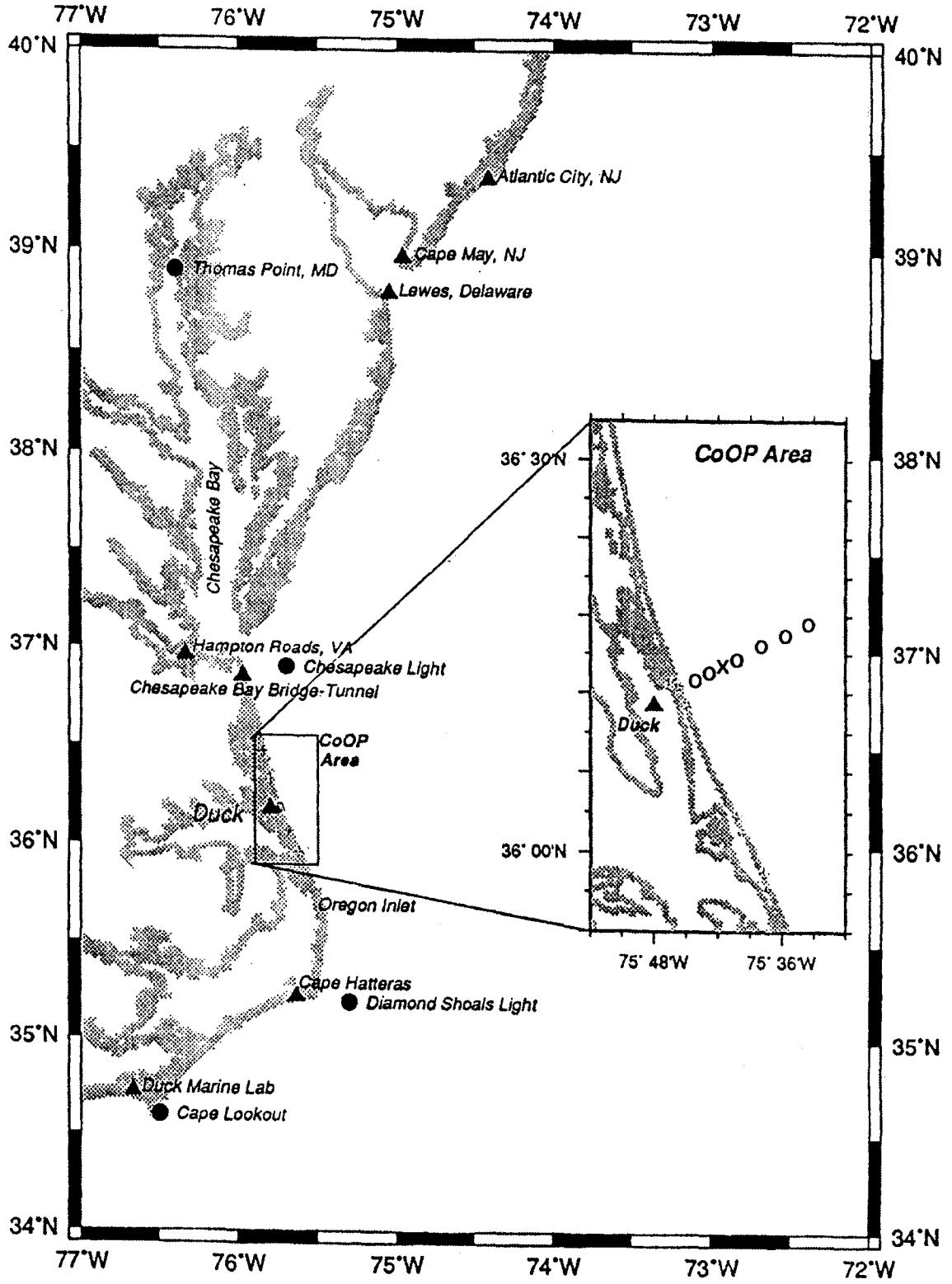


TABLE 1. Station Numbers, Locations, and Sampling Depths at Each Station for Each of Four Line Surveys Conducted During August, 1994

	21 August						23 August				25 August					27 August					
Stn.#	1	2	3	4	5	6	2	3	4	5	2	3	4	5	6	1	2	3	4	5	6
Distance from Shore (km)	1	2	5	10	14	19	2	4	10	14	2	5	10	14	19	1	2	5	10	14	19
Sampling Depth (m)	2	2	2	2	2	2	2	3	3	3	2	2	2	2	2	3	2	2	2	2	2
	7	8	5	5	6	7	9	11	7	8	8	9	10	9	7	7	5	8	6	7	7
		13	8	8	9	12	14	17	12	13	13	17	18	15	12		9	13	10	12	12
			13	14	16	18			15	18				19	18		12	17	14	18	18
									18	23				22	24				18	25	24

10% CaCO₃ buffered formalin for later sorting.

Plankton samples were collected from discrete depths at each station (Table 1). The sampling depths were selected based upon station depth and weather conditions. With reasonably calm seas, depths were as follows:

If the station depth was ≤ 10 m, 3 depths were sampled,

- 1 to 2 m off the bottom
- half-way between the bottom and surface, and
- 2 m below the surface.

If the station depth was >10 m, 5 sample depths were chosen,

- 1 to 2 m off the bottom
- half-way between the bottom and the thermocline
- within the thermocline
- half-way between the thermocline and the surface, and
- 2 m below the surface.

If seas were rough, surface sampling was done at 3 m and bottom sampling was done 3-4 m off the bottom.

In addition to zooplankton samples, physical oceanographic data were also collected with a CTD (depth, temperature ($^{\circ}$ C), salinity (‰), density). Once on station, the plankton pump hose was attached to the CTD and the CTD was lowered over the side of the ship until it was approximately 1 m off the bottom. Sampling depths were selected based upon the descending CTD profile, and zooplankton sampling was done as the CTD ascended.

For a complete data report of all biological and oceanographic sampling that occurred in association with the CoOP study during the months of August and October, 1994, see Waldorf *et al.* (1995, 1996) and Alessi *et al.* (1996).

Laboratory Analysis of Samples

Plankton samples were filtered in the laboratory through 53 μm mesh to concentrate the plankton and remove formalin. After filtration, samples were transferred to a 250 ml beaker. Water was added to the beaker and an exact volume of 200 ml (200 g) was attained with the aid of an electronic balance. A 12 ml aliquot was removed with a Stempel pipette from the homogeneous 200 ml sample and placed in a sorting tray. Concentrated plankton samples were sorted under a dissection microscope equipped with a polarizing filter. Polarization aids in the identification of the larval shells of various molluscs, including bivalves and gastropods, because the shells appear to "glow" under the polarized light. Biorefracton of the shells is due to the reflection of the polarized light from the microcrystalline aragonitic structure of the larval shells (Gallager *et al.*, 1989).

The number of 12 ml aliquots sorted per sample depended upon the concentration of the most abundant organism: aliquots were counted until at least 100 individuals of the most common organism were enumerated to yield a sample standard deviation of approximately 10% for the most abundant organism (between 10-20% for all other organisms (Venrick, 1978)). To assure that the aliquoting technique provided an accurate representation of the number and size of larvae in each sample, four samples were counted in their entirety as well as sorted by the aliquoting technique. No statistical differences were found in the number of larvae m^{-3} between the two sorting methods (Mann-Whitney *U*-Test, $\alpha = 0.05$).

Bivalve larvae were identified to species with the aid of various identification guides (Thorson, 1946; Sullivan, 1948; Rees, 1950; Loosanoff *et al.*, 1966; Chanley & Andrews, 1971) and the size of bivalve shells was measured (anterior to posterior) with an ocular micrometer. Gastropod larvae were identified to genus using identification guides provided by Thorson (1946) and Thiriot-Quievreux (1980, 1983). Polychaete larvae were identified to family with keys provided by Thorson (1946), Korn (1960), and Bhaud & Cazaux

(1982). Trochophore stage polychaetes were simply grouped together as "trochophores". The types of all bivalve, gastropod, and polychaete larvae identified in the line survey samples is summarized in Table 2.

To test the hypothesis that a larva's vertical position within the water column was unrelated to larval body size or competency to settle, each species of bivalve larvae was separated into two groups on each of the four sampling days. Group 1 included those larvae sampled within the upper half of the water column, and group 2 included larvae sampled from the lower half of the water column. Size frequency histograms were constructed for each of the four species of bivalves, and t-tests were performed to determine any difference in the mean size between the two groups of larvae within each species.

Cross-shelf profiles of water density and larval distributions were completed with Spyglass Transform software. The raw CTD data were provided by Walt Waldorf of Oregon State University. Because of the large number of types of organisms identified, only those larvae that were most abundant and whose identification was known to be completely accurate were chosen for analysis in this thesis.

Results

Over the course of the four day sampling period, the winds changed direction on more than one occasion, and as a result, many changes in the density structure of the water column occurred. On 21 August, winds blew from the southwest (wind data not shown) and low density surface waters were deflected offshore (Fig.2). These low density waters were part of the Chesapeake bay plume that was present up against the shore on 20 August during a period of weak downwelling. The offshore transport of these low density surface waters was coupled with the upward transport of bottom waters within 10 km of shore, as seen by the upward trending isopycnals. Higher density bottom waters were upwelled and

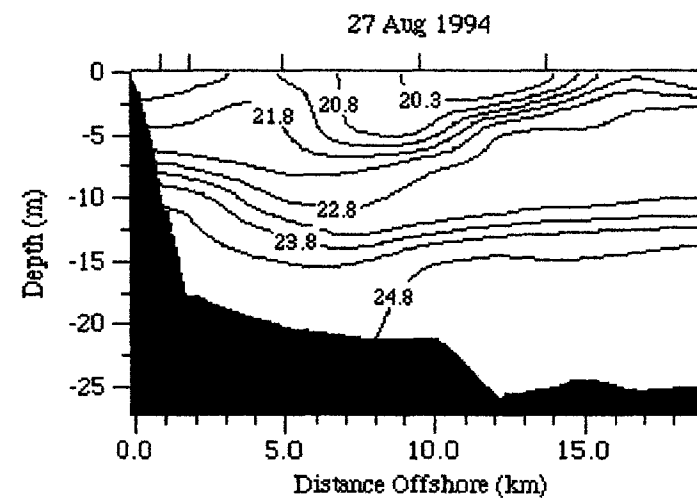
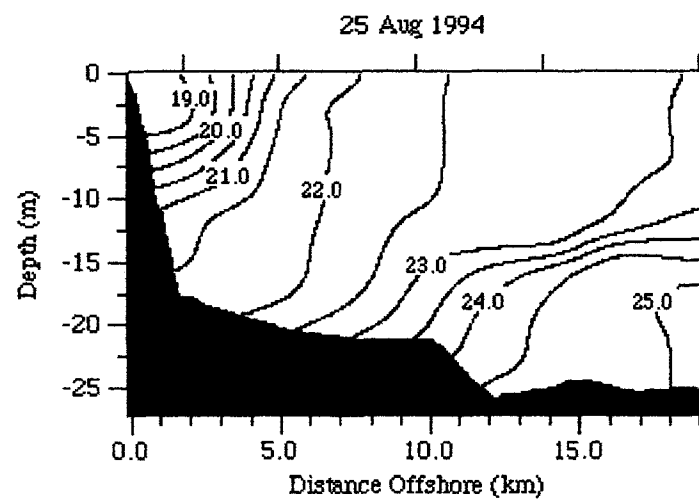
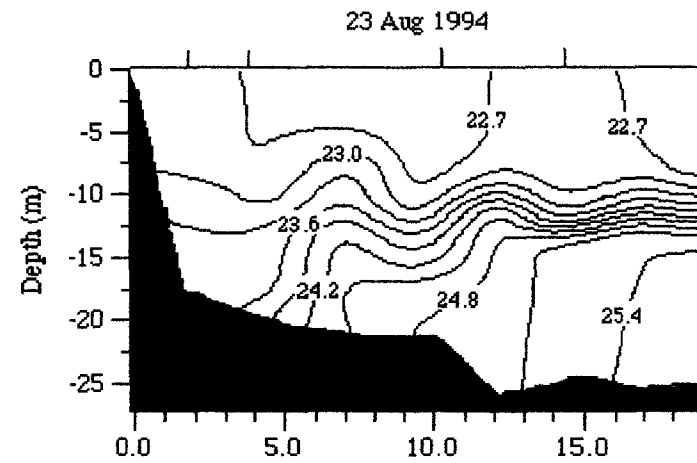
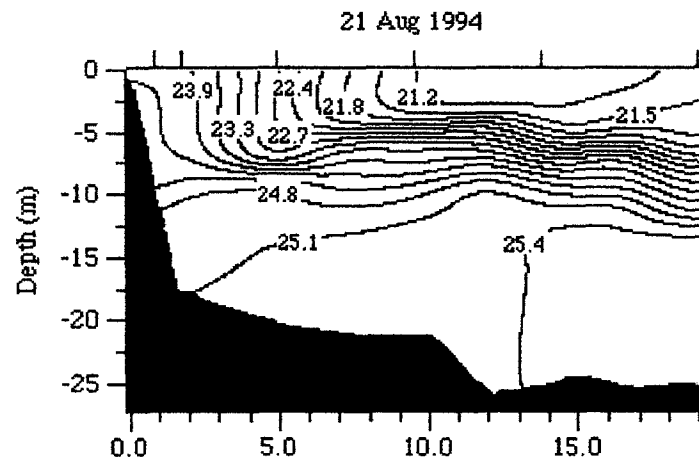
TABLE 2. Benthic Invertebrate Larvae Found in Plankton Samples From Cross-Shelf and Vertical Migration Studies.

BIVALVES	GASTROPODS	POLYCHAETES
<i>Spisula solidissima</i> †§	<i>Littorina spp.</i> †§	Spionidae †§
<i>Mya arenaria</i> †§	<i>Lacuna sp.</i>	Orbiniidae
<i>Laevicardium mortoni</i>	<i>Natica sp.</i>	Phyllodocidae †§
<i>Mercenaria mercenaria</i>	<i>Hydrobia sp.</i> §	Nereidae
<i>Tellina agilis</i> †§	<i>Cratena sp.</i>	Pectinereidae †§
<i>Cyrtopleura costata</i> †§	<i>Caecum sp.</i>	Magelona
<i>Petricola pholadiformis</i>	<i>Elysia sp.</i>	Trochophores †§
<i>Pitar morrhuana</i>	<i>Bittium sp.</i> †§	
<i>Mytilus edulis</i>	<i>Odostomia sp.</i> †§	
<i>Anadara transversa</i>	<i>Retusa sp.</i>	
<i>Aequipectens irradians</i>	<i>Certhiopsis sp.</i>	
<i>Glycymeris glycymeris</i>	<i>Nassarius sp.</i>	
<i>Teredo navalis</i>		
<i>Anomia simplex</i>		
<i>Kelia suborbicularis</i>		
<i>Gemma gemma</i>		
<i>Mulinia lateralis</i> §		
<i>Ensis directus</i>		
<i>Modiolus demissus</i>		
<i>Cardium pinnulatum</i>		
<i>Barnea truncata</i>		
<i>Zirfaea crispata</i>		
<i>Hiatella arctica</i>		
<i>Arcacea sp.</i>		
<i>Lima sp.</i>		
<i>Mysella spp.</i>		
4 Unknowns		

† Animals included in the cross-shelf transport study

§ Animals included in the vertical migration study

FIGURE 2. Cross-Shelf Profiles of Water Density (in Sigma-T Units). Vertical Ticks Along Top Axes Represent Locations of Sampling Stations.



replaced lower density surface waters . A strong pycnocline, centered at 8 m depth, was present approximately 5 km offshore.

On 22 August, the winds shifted and began to blow from the northeast. The result on 23 August was a reversal of conditions that were present on 21 August (Fig.2). A strong pycnocline was still present beginning approximately 10 km offshore at a depth of 12 m. Lower density surface waters were moved back onshore and, as seen from the downward trending isopycnals, bottom waters were transported offshore.

This downwelling pattern continued through 25 August (Fig.2), with surface waters continuing to move shoreward and a subsequent offshore movement of bottom waters. Within 14 km of shore, the pycnocline had disappeared. A weak pycnocline was present at 15 m between 15 and 19 km offshore. The most distinct oceanographic feature was a low density plume of water present within 4 km of shore. This plume was caused by low salinity estuarine water from the Chesapeake bay flowing southward along the coast . Densities within this plume were much lower than had previously been observed ($<21 \text{ sigma-t}$). A frontal zone was apparent at the eastern edge of this plume. This front separated the low density Chesapeake bay waters on the shoreward side from downwelling waters on the seaward side. This front stopped the low density plume waters from being downwelled.

Between 25 and 27 August, the winds had shifted and were once again blowing from the southwest. These winds are favorable to upwelling and produced offshore transport of the low density plume that was present on 25 August, and a shoreward movement of bottom waters. Upwelling occurred within 5 km of the shore (Fig.2). A relatively weak pycnocline was present between 10 and 12 m.

It is important to keep in mind when looking at the cross-shelf plots of larval densities that only transport in the cross-shore direction can be detected from these figures. Undoubtedly larvae were also transported in the alongshore direction, and that some of the

changes in larval numbers between days is due to this north-south dispersal. However, movement in this plane was unobservable based upon our cross-shelf sampling technique.

Tellina agilis

Over the course of the four day study period, larvae of *Tellina agilis*, the dwarf tellin clam (Fig.3), were found primarily within 10 km of shore. Larval concentrations varied considerably among days; fewer than 1000 larvae m^{-3} were sampled within 5 km of shore on the 21st, while greater than 8000 larvae m^{-3} were encountered in this same location on 27 August. Beginning on 21 August, the highest concentration of larvae were within 3 km of shore and between 5 and 10 m depth, concurrently with upwelling of higher density bottom waters. On 23 August, larval numbers had increased to a maximum concentration of approximately 1500 larvae m^{-3} just below the pycnocline between 7 and 10 km offshore. A cloud of larvae occurred within 5 km of shore near the surface. The majority of *T. agilis* larvae present on the 25th were found close to shore (within 5 km) and predominantly between above 15 m, within and just below the low density Chesapeake bay plume. Very few larvae were found more than 6 km offshore, regardless of the depth. On 27 August, when upwelling had resumed, larvae had become highly concentrated (up to 8,000 larvae m^{-3}) within 2 km of shore and between 5 and 10 m depth. Concentrations elsewhere along the line survey were less than 1000 larvae m^{-3} .

Cyrtopleura costata

The angel wing clam, *Cyrtopleura costata*, had larval densities considerably lower than those for *T. agilis*, with a maximum density of just over 2100 larvae m^{-3} for *C. costata* (Fig.4). On 21 August, a cloud of larvae was located above the pycnocline in offshore-moving low density plume waters. Less than 500 larvae m^{-3} were found

FIGURE 3. Cross-Shelf Profiles of Densities of *Tellina agilis* Larvae, with Overlays of Water Density (as in Figure 2). Vertical Ticks Along Top Axes Represent Locations of Sampling Stations.

Tellina agilis

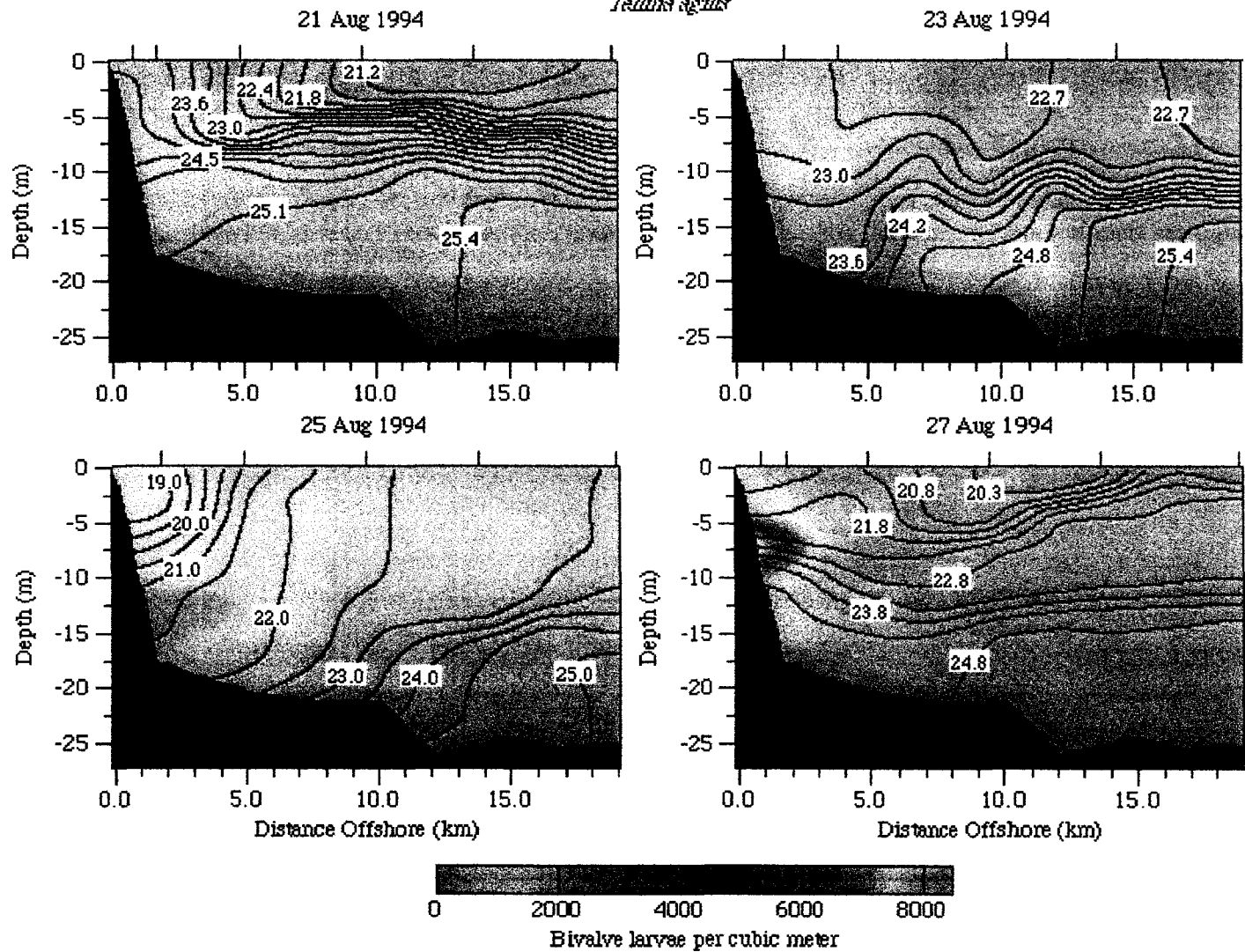
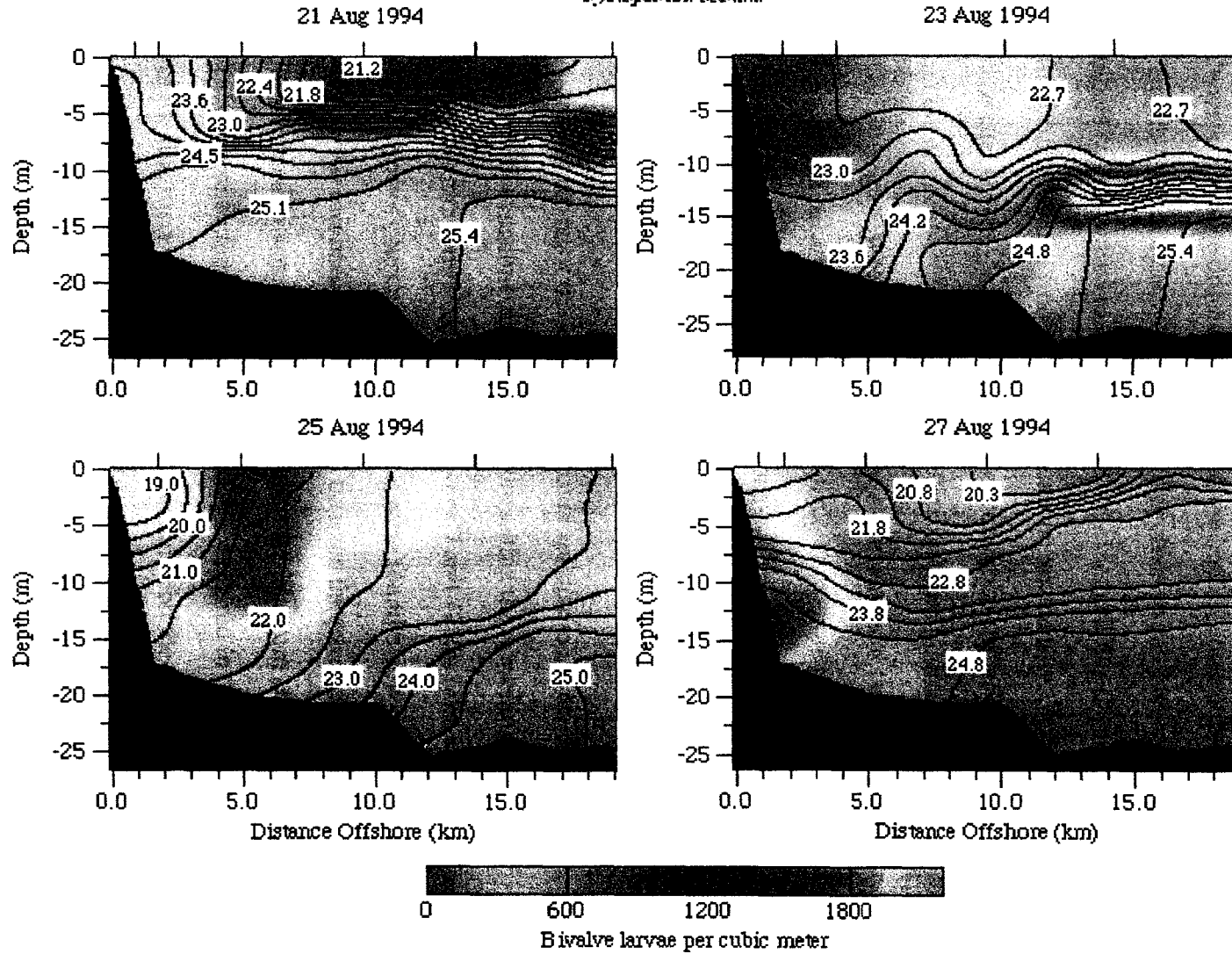


FIGURE 4. Cross-Shelf Profiles of Densities of *Cyrtopleura costata* Larvae, with Overlays of Water Density (as in Figure 2). Vertical Ticks Along Top Axes Represent Locations of Sampling Stations.

Cyrtopleura costata



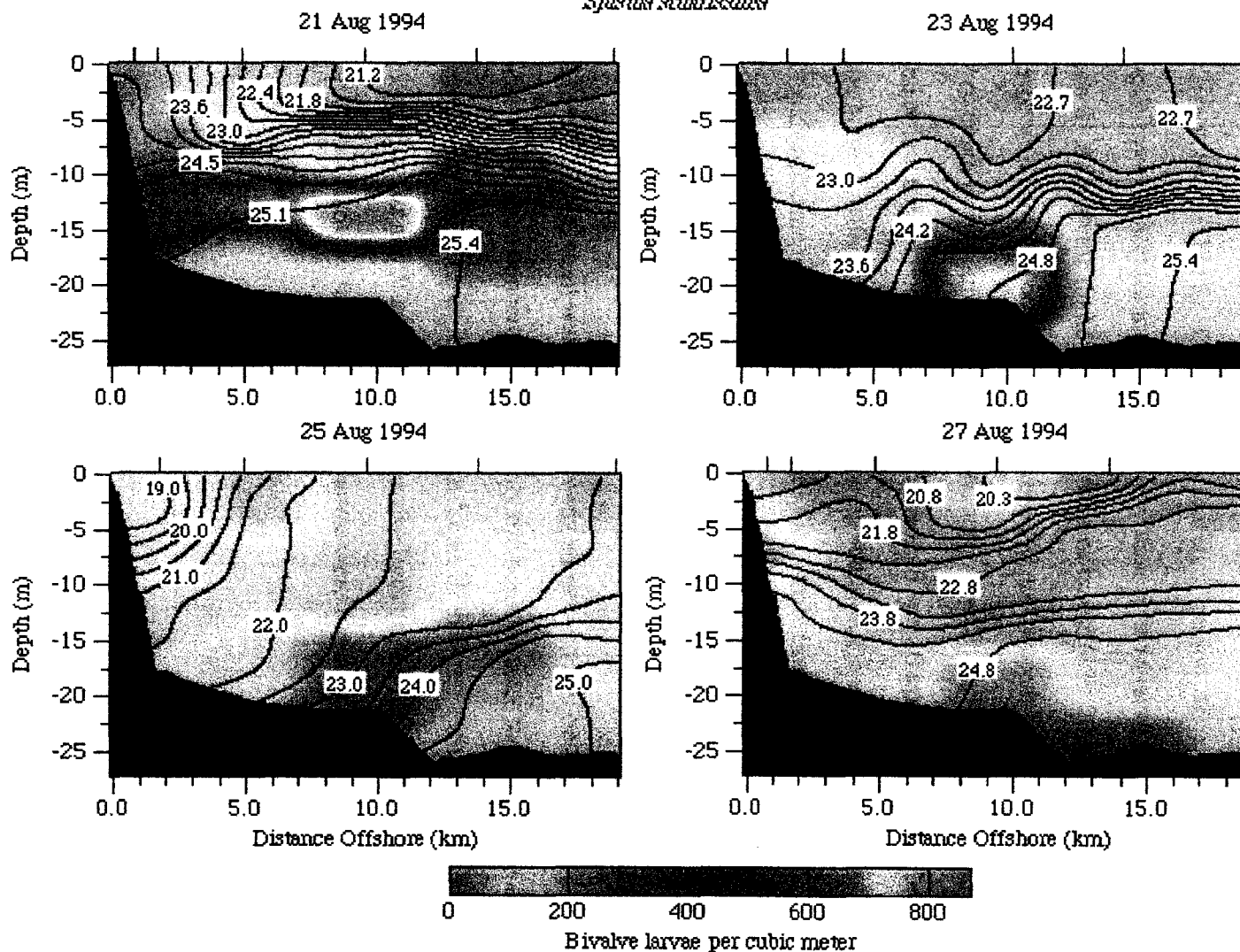
elsewhere along this line survey. On 23 August, high concentrations of *C. costata* larvae were found within 10 km of shore, at the surface and between the pycnocline and the bottom, in waters that were downwelled. By far the highest concentration of larvae ($>2100\text{ m}^{-3}$) were encountered in a narrow band 12-19 km offshore and just below the pycnocline. Larval numbers had decreased to less than 1200 m^{-3} by the 25th. On this day, a cloud of larvae were found within the frontal zone between the low density Chesapeake bay plume waters, and coastal waters. Somewhat lower concentrations of larvae ($<300\text{ m}^{-3}$) were found within the plume itself. Few larvae were encountered farther than 7 km offshore. On 27 August, when the low density plume waters of the 25th had begun to move offshore, larvae became concentrated even closer to shore than they were on the 25th, being found primarily within 3 km of shore and between 7 and 12 m depth.

Spisula solidissima

On 21 August larvae of the surf clam, *Spisula solidissima*, were distributed across the shelf just below the pycnocline and close to shore within the upwelling zone (Fig.5). Highest larval concentrations were located between 7 and 12 km from shore, between 10 and 15 m depth. Lower concentrations of larvae were found below 20 m and above 8 m. On 23 August, larvae had become concentrated between the pycnocline and the bottom in offshore-flowing bottom waters, approximately 6 to 11 km from shore. Very few larvae were found elsewhere on this day, with no larvae encountered in the surface waters along the length of the line survey. As downwelling continued on the 25th, highest concentrations of larvae remained concentrated in the same location as on the 23rd, but a small cloud of larvae ($\sim 200\text{ m}^{-3}$) were also found within the low density plume frontal zone. On 27 August, larvae were concentrated below the pycnocline near the bottom. A small group of larvae (between $225\text{-}300\text{ m}^{-3}$) were found in waters being upwelled close to shore, between 5 and 10 m depth.

FIGURE 5. Cross-Shelf Profiles of Densities of *Spisula solidissima* Larvae, with Overlays of Water Density (as in Figure 2). Vertical Ticks Along Top Axes Represent Locations of Sampling Stations.

Saxidomus nutalli



Mya arenaria

Cross-shelf distributions of the soft-shelled clam, *Mya arenaria*, were similar to those for *S. solidissima* larvae (Fig.6). Over the four day study period, *M. arenaria* larvae were found in much lower concentrations than were the other bivalve larvae ($<200 \text{ m}^{-3}$). During upwelling on 21 August, the highest concentrations of larvae ($150\text{-}200 \text{ m}^{-3}$) were located throughout the water column within 5 km of shore and just beneath the pycnocline at roughly 12 m depth from 5 km out to 19 km offshore. On 23 August, larvae were concentrated below the pycnocline, primarily between 5 and 10 km offshore, and between 17 m and the bottom, with virtually no larvae being found in the upper half of the water column. This distribution is strikingly similar to the distribution of the larvae of *S. solidissima* on this same day. As downwelling proceeded on the 25th, *M. arenaria* larvae became concentrated within the pycnocline and between 12 and 16 km offshore. A few larvae ($\sim 40 \text{ m}^{-3}$) were found within the low density plume and associated frontal zone. Finally, on the 27th, as bottom waters were moving shoreward and being upwelled close to shore, bivalve larvae were concentrated primarily offshore and near the bottom. A small cluster of larvae ($\sim 125 \text{ m}^{-3}$) was found between 5 and 10 m depth within 2 km of shore. Larvae of both *T. agilis* and *S. solidissima* were also found in a small cloud in this location on this same day. Relatively few *M. arenaria* larvae were found within or above the pycnocline on the 27th.

Littorina spp.

Littorina spp. larvae were found in very nearly the same locations on both 21 and 23 August (Fig.7), however, the concentrations changed between days (maximum of $500 \text{ larvae m}^{-3}$ on 21 August compared to $>1000 \text{ m}^{-3}$ on 23 August). Two clouds of larvae

FIGURE 6. Cross-Shelf Profiles of Densities of *Mya arenaria* Larvae, with Overlays of Water Density (as in Figure 2). Vertical Ticks Along Top Axes Represent Locations of Sampling Stations.

Mya arenaria

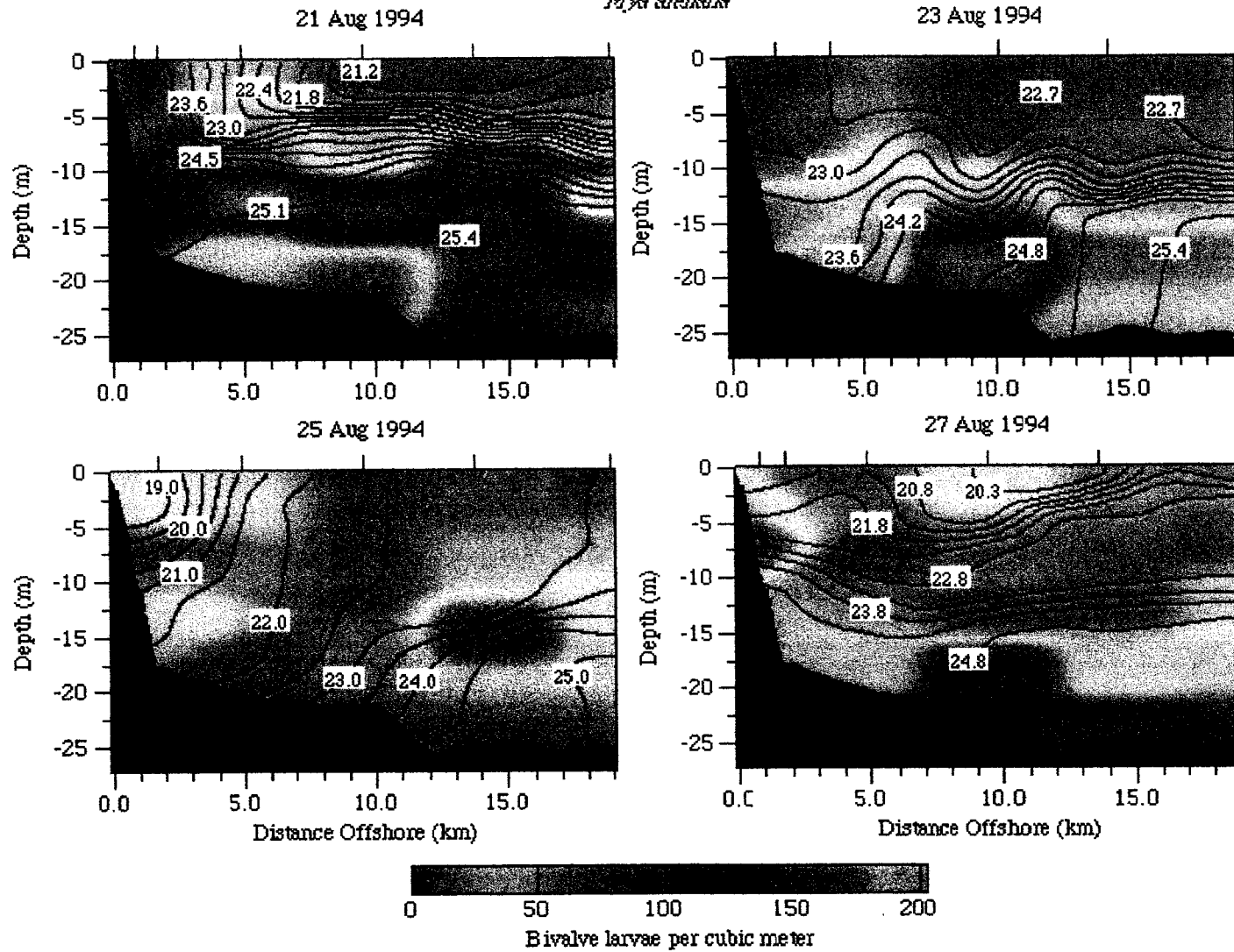
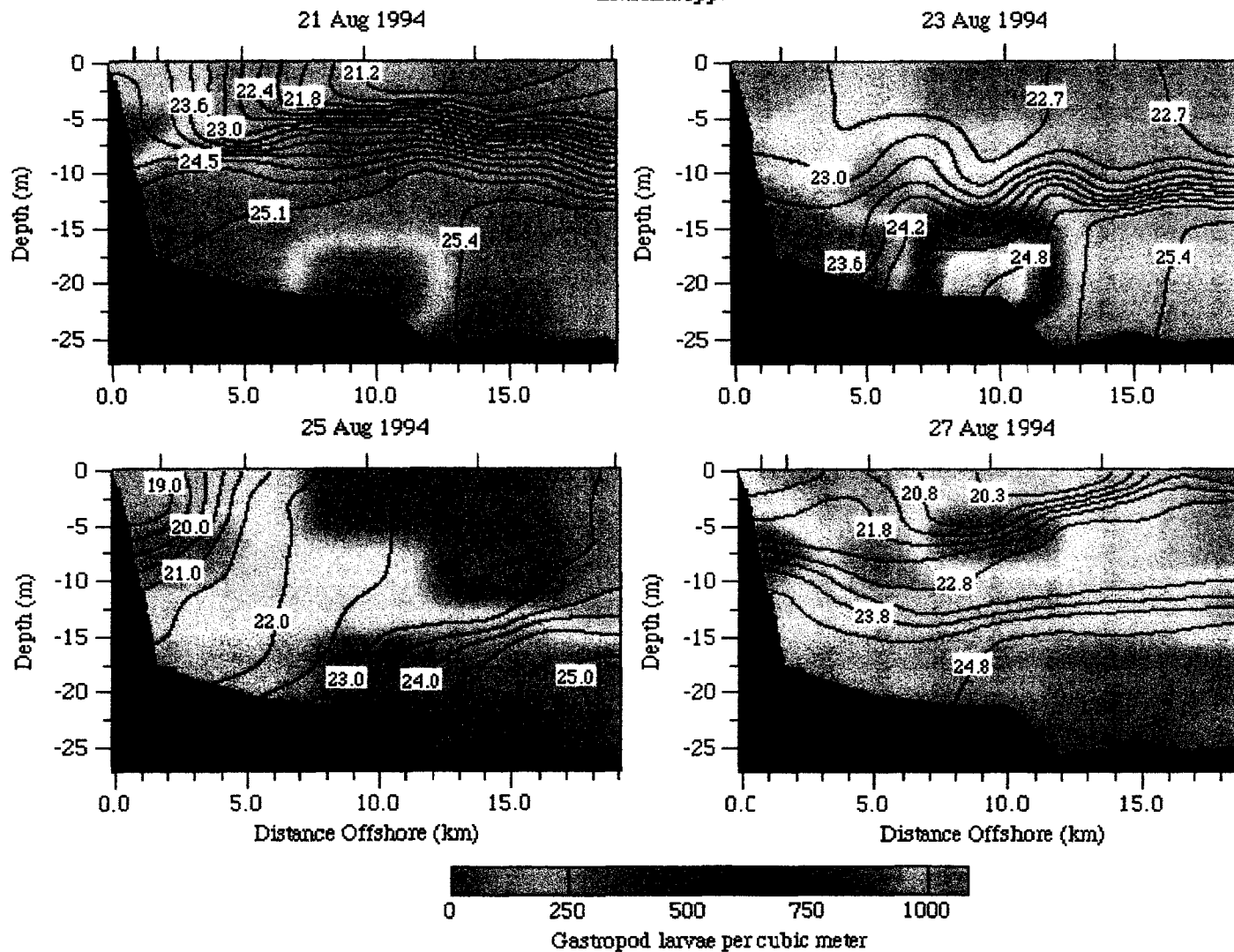


FIGURE 7. Cross-Shelf Profiles of Densities of *Littorina spp.* Larvae, with Overlays of Water Density (as in Figure 2). Vertical Ticks Along Top Axes Represent Locations of Sampling Stations.

Littorina spp.



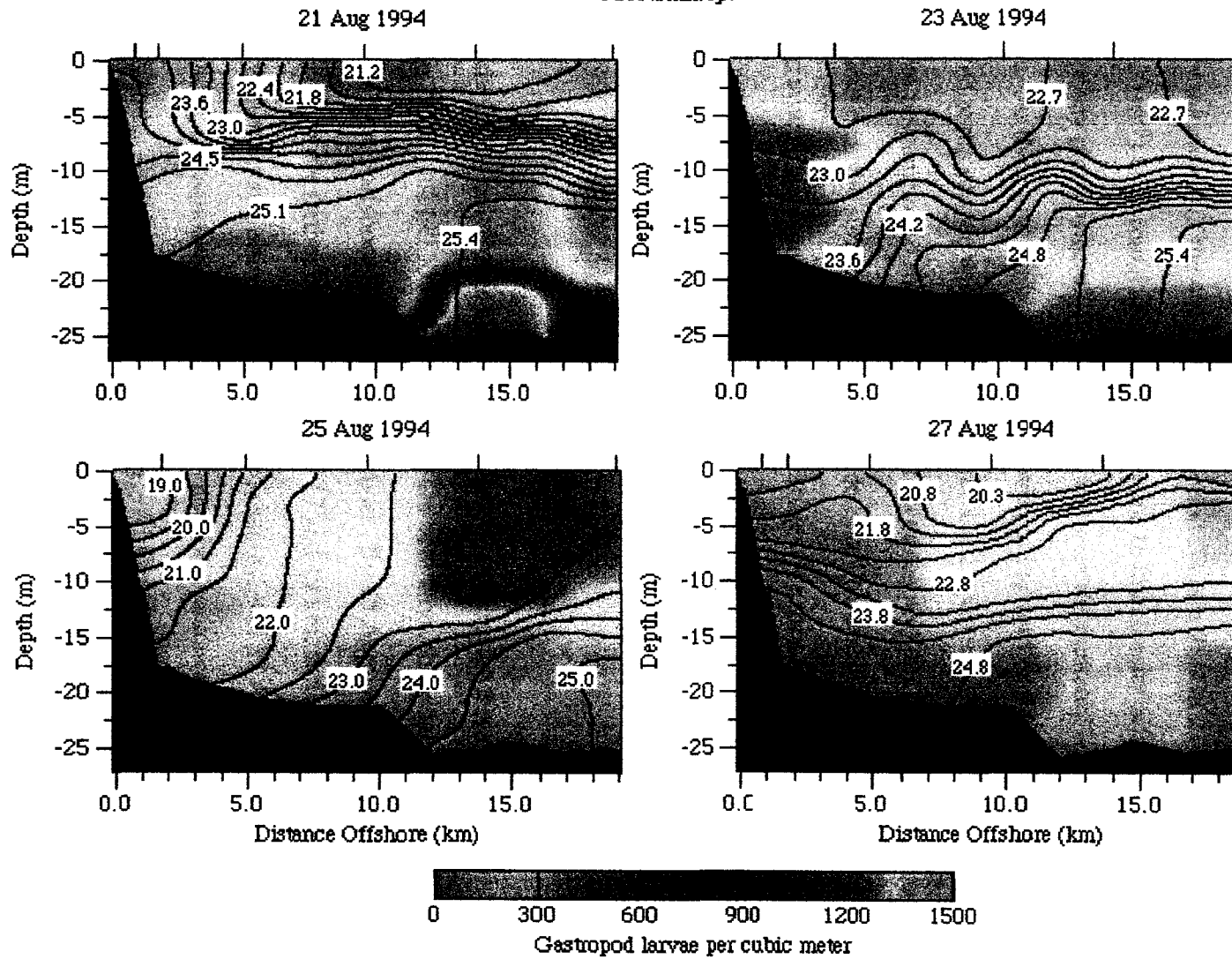
were present on these days, one of which was up against the shore in the area of upwelling. The second and much larger cloud was found below the pycnocline and between 7 and 10 km from shore. This distribution of *Littorina spp.* on the 23rd was nearly identical to that of *S. solidissima* and *M. arenaria* on the same day. As downwelling continued through the 25th, larvae were concentrated in the upper half of the water column, primarily between 8 and 16 km offshore, although there was a smaller, less dense cloud of larvae present in the plume waters. On the 25th, few larvae ($<100 \text{ m}^{-3}$) were located where they had been on the 23rd, namely between the pycnocline and the bottom between 7 and 10 km offshore. By the 27th, larvae were present in three small clouds, one up against the coast, one in offshore-moving low density surface waters, and one within the pycnocline between 18 and 19 km offshore. Very few larvae were encountered anywhere else.

Odostomia sp.

During upwelling on 21 August, gastropod larvae of *Odostomia sp.* were in highest concentration ($1500 \text{ larvae m}^{-3}$) offshore, just above the bottom (Fig.8). Relatively few larvae were found elsewhere along this line survey. By 23 August, once downwelling had begun, a cloud of larvae were found in the same location as on the 21st, namely below the 25.1 density isopycnal, but a portion of larvae from the 21st had moved shoreward, and were now found along the bottom within 4 km of shore. On 25 August, *Odostomia sp.* larvae were found in the surface layers above the pycnocline, and between 12 and 19 km from shore. Less than $150 \text{ larvae m}^{-3}$ were found elsewhere on this date, and no larvae were sampled from within the Chesapeake bay plume. On 27 August, as lower density surface waters were being transported offshore due to upwelling, *Odostomia sp.* larvae were present vertically throughout the water column between 7 and 19 km from shore. Larval concentrations reached a maximum of $300 \text{ larvae m}^{-3}$ on this day.

FIGURE 8. Cross-Shelf Profiles of Densities of *Odostomia sp.* Larvae, with Overlays of Water Density (as in Figure 2). Vertical Ticks Along Top Axes Represent Locations of Sampling Stations.

Odontaspis sp.



Bittium sp.

The majority of larvae of the gastropod *Bittium sp.* remained within lower density waters over the course of the 4 day sampling period (Figure 9). On 21 August, a cloud of larvae ($\sim 500 \text{ m}^{-3}$) were found above the pycnocline in low density offshore-moving Chesapeake bay plume waters. Virtually no larvae were encountered within or below the pycnocline. As these surface waters began moving shoreward on the 23rd, larvae were concentrated at the surface within 5 km of shore. On 25 August, as surface waters continued to be transported shoreward, the highest concentrations of larvae were found close to shore near the surface, within the low density Chesapeake bay plume. As winds shifted and upwelling resumed on 27 August, larvae were then found primarily offshore in a dense cloud ($>100 \text{ m}^{-3}$) with the low density surface waters. The highest concentration of larvae was located between 7 and 12 km offshore and between 5 and 7 m depth.

Pectinereidae

Relatively few polychaete larvae of the family Pectinereidae were encountered on either 21 or 23 August ($<1300 \text{ m}^{-3}$) (Fig. 10). On both days, those larvae which were present were found offshore within the pycnocline. By 25 August, larvae were concentrated slightly farther offshore, between 17 and 19 km, and nearer the surface. No larvae were encountered elsewhere along the line survey. On 27 August, larvae were found offshore, and concentrated within the pycnocline at a concentration of almost 5000 larvae m^{-3} , and at slightly lower concentrations ($\sim 3300 \text{ m}^{-3}$) between the pycnocline and bottom.

FIGURE 9. Cross-Shelf Profiles of Densities of *Bittium sp.* Larvae, with Overlays of Water Density (as in Figure 2). Vertical Ticks Along Top Axes Represent Locations of Sampling Stations.

Britinnia sp.

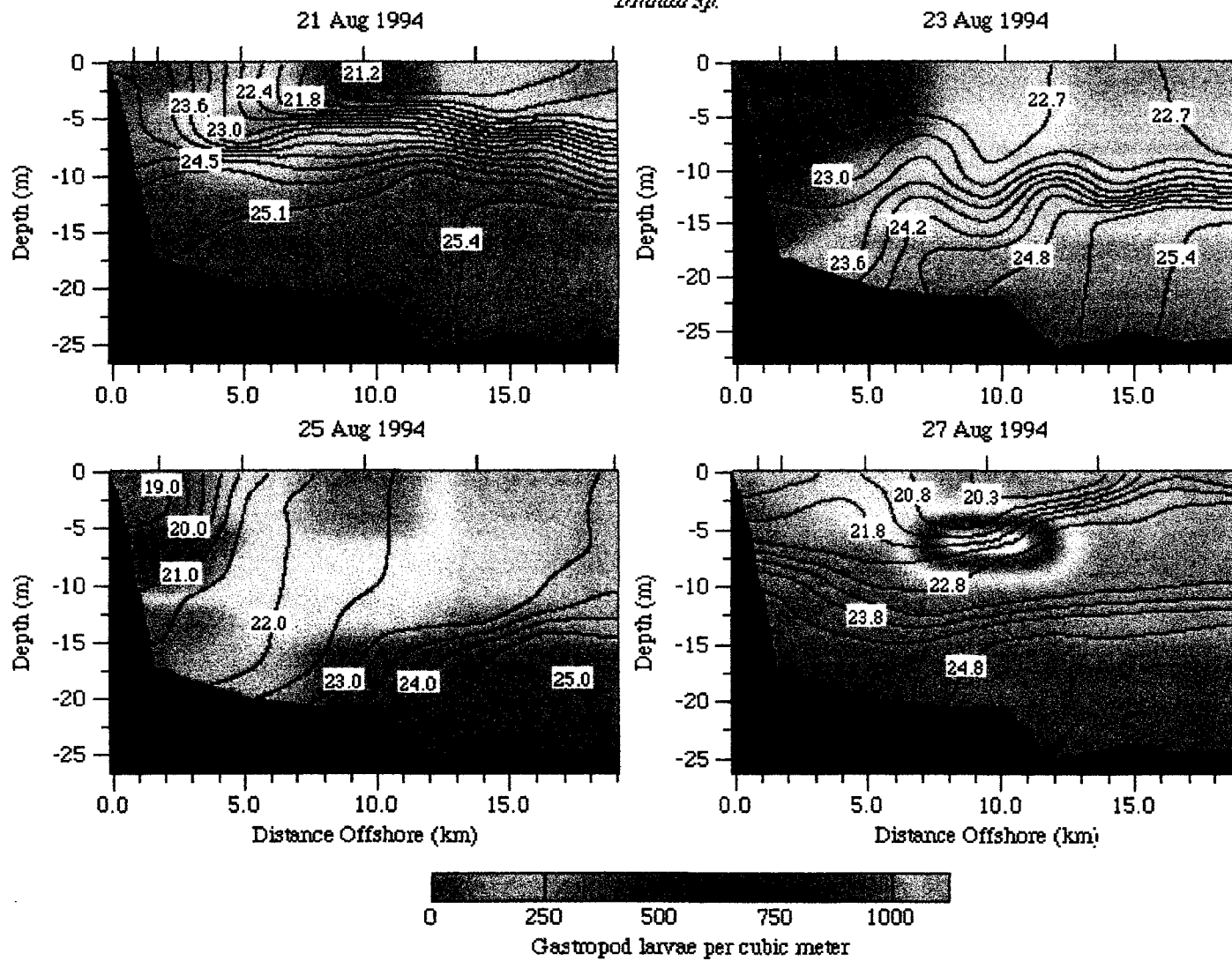
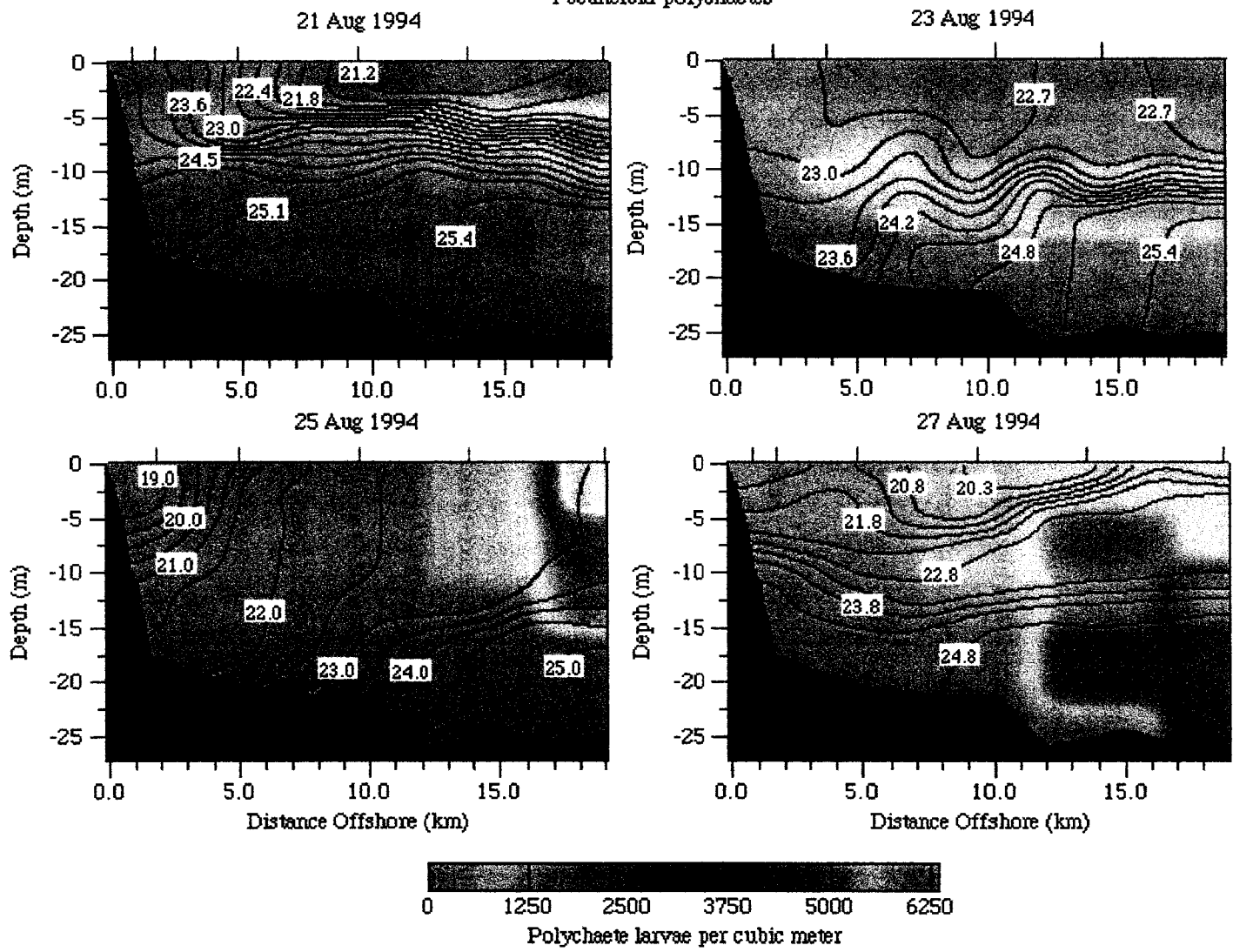


FIGURE 10. Cross-Shelf Profiles of Densities of Pectinereid Polychaete Larvae, with Overlays of Water Density (as in Figure 2). Vertical Ticks Along Top Axes Represent Locations of Sampling Stations.

Pectinereid polychaetes



Phyllodocidae

The highest concentration of phyllodocid polychaete larvae encountered ($>5500\text{ m}^{-3}$) over the four day study period was found on 21 August between 13 and 16 km from shore just below the pycnocline (Figure 11). After this date, larval numbers dropped considerably, to less than 1300 m^{-3} , regardless of depth or distance offshore. Despite the shifts in current direction over the four days, phyllodocid larvae remained either within or below the pycnocline, primarily below the 24.2 isopycnal, rarely being found above 10 m depth.

Spionidae

Spionid polychaete larvae also tended to remain within the lower half of the water column between 21 and 27 August (Fig.12). On 21 August, larvae were found below the pycnocline along the length of the line survey, with larval concentrations being relatively low, $<1200\text{ m}^{-3}$. Larval concentrations decreased even more on the 23rd. On this day, larvae were found close to the bottom in offshore-moving bottom waters. On 25 August, the trend was the same: no more than 250 larvae m^{-3} were encountered at any depth along the line survey. Once bottom waters began flowing shoreward again on the 27th, a high density ($>2250\text{ larvae m}^{-3}$) cloud of larvae were found along the bottom between 9 and 16 km from shore. A small, relatively low concentration cloud of larvae was also sampled up against the shore between 5 and 10 m. Clouds of *Tellina agilis*, *Cyrtopleura costata*, *Spisula solidissima*, *Mya arenaria*, and *Littorina spp.* larvae were also found in precisely the same location on the same day.

FIGURE 11. Cross-Shelf Profiles of Densities of Phyllodocid Polychaete Larvae, with Overlays of Water Density (as in Figure 2). Vertical Ticks Along Top Axes Represent Locations of Sampling Stations.

Phyllodocid polychaetes

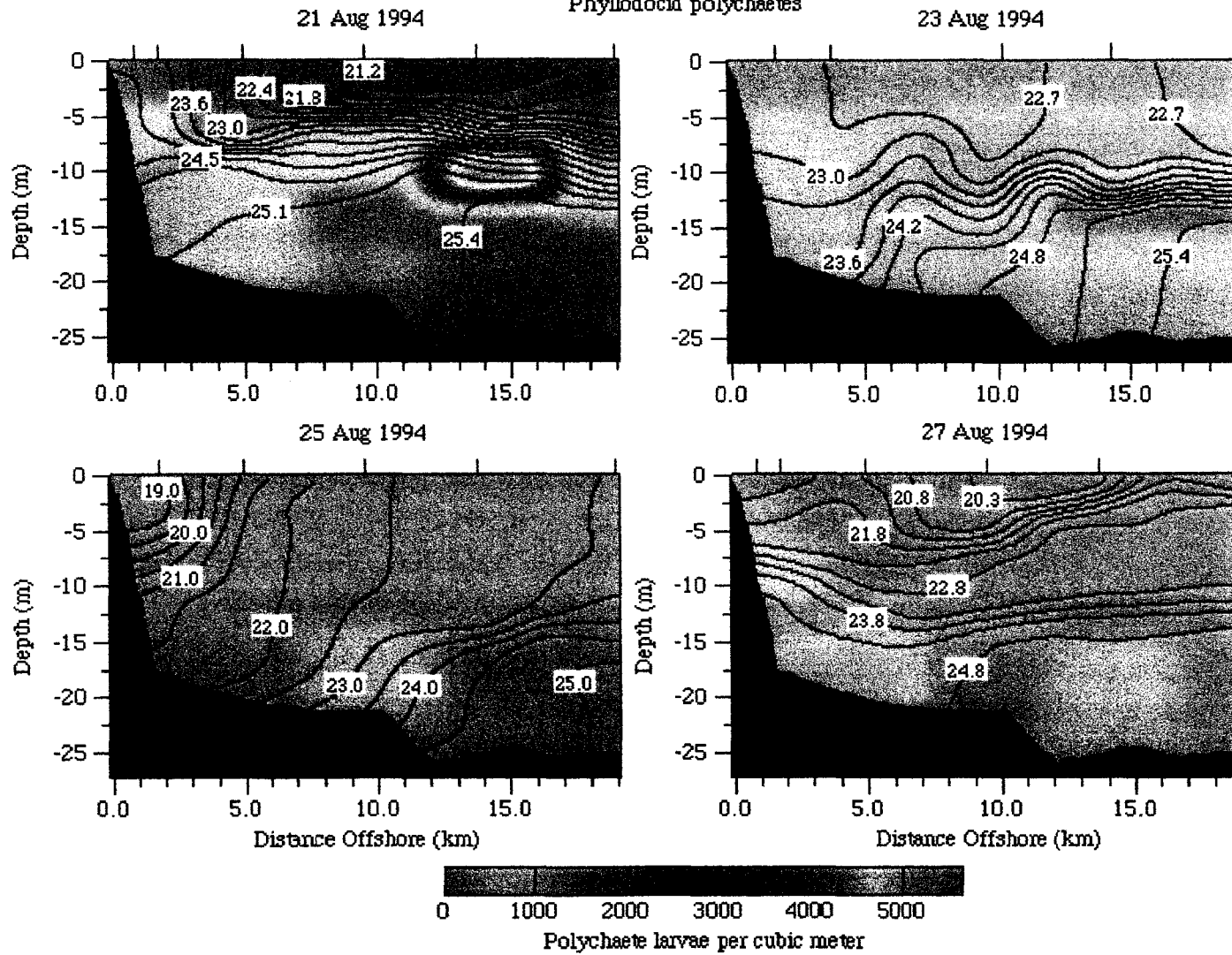
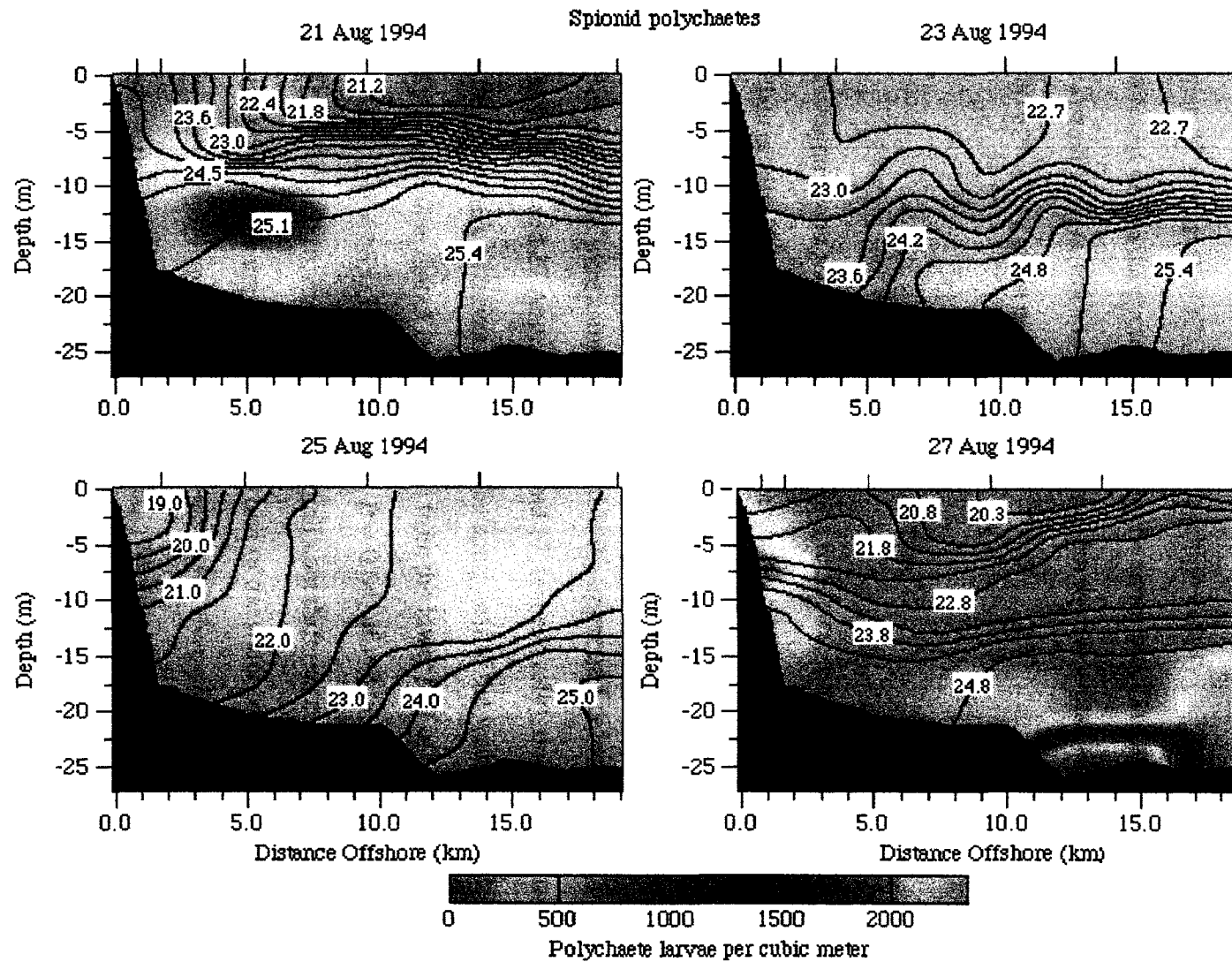


FIGURE 12. Cross-Shelf Profiles of Densities of Spionid Polychaete Larvae, with Overlays of Water Density (as in Figure 2). Vertical Ticks Along Top Axes Represent Locations of Sampling Stations.



Polychaete Trochophores

Polychaete trochophores were not encountered in any sizable concentration on any day other than 27 August (Fig.13), at which time a high density ($4000 \text{ larvae m}^{-3}$) cloud of larvae were found within the pycnocline between the shore and 4 km offshore. On the three other sampling days, trochophore concentrations were less than $\sim 800 \text{ m}^{-3}$, averaging closer to 300 m^{-3} at any given depth.

Size Frequencies

The histograms and statistical data point out a few interesting trends in the length-frequency data of larval bivalves. Length frequency histograms for the four bivalve species on each of the four days are shown in Figures 14-29. *Tellina agilis* had a mode in its size distribution in the 160-170 μm size range on each of the four days (Fig.14-17), regardless of whether or not larvae were sampled from within the upper half or lower half of the water column. On both 21 and 27 August (Figs.14 and 17, respectively), during periods of upwelling, the mean size of larvae sampled in the upper half of the water column was significantly smaller than that of larvae sampled from the lower half of the water column ($t = 1.96, P < 0.001, df = 685, 21 \text{ Aug}$; $t = 1.96, P = 0.04, df = 848, 27 \text{ Aug}$). On 23 and 25 August (Figs.15 and 16, respectively), no significant difference was found in the mean size of larvae between the upper half and lower half of the water column.

Histograms of the length frequency distribution for *Cyrtopleura costata* (Figs.18-21) show a mode in the length distribution in the 160-170 μm size class, similar to *T. agilis*. This mode shows up on all four study days regardless of the sampling depth. On all four days, the mean size of larvae near the bottom was significantly larger than those near the surface depths ($t = 1.97, P < 0.001, df = 244, 21 \text{ Aug}$; $t = 1.96, P < 0.001, df = 1052, 23 \text{ Aug}$; $t = 1.96, P = 0.01, df = 647, 25 \text{ Aug}$; $t = 1.97, P = 0.04, df = 407, 27 \text{ Aug}$). The

FIGURE 13. Cross-Shelf Profiles of Densities of Polychaete Trochophores, with Overlays of Water Density (as in Figure 2). Vertical Ticks Along Top Axes Represent Locations of Sampling Stations.

Polychaete trochophores

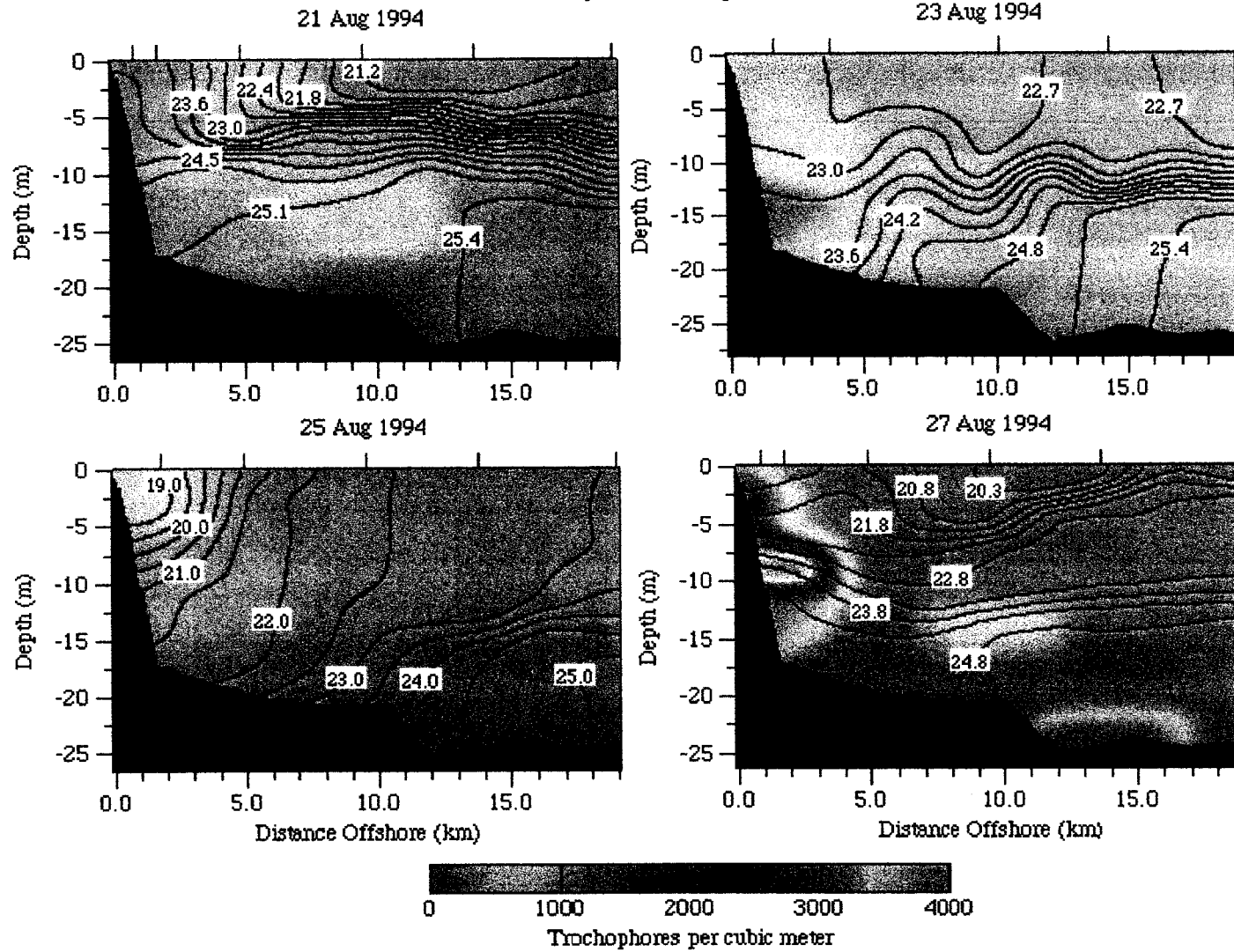


FIGURE 14. Cross-Shelf Length Frequency Histograms for the Bivalve *Tellina agilis* on 21 August. Asterisks Represent Average Size at Settlement. Sizes Shown Indicate the Mid-Point of the Range for Each Size Bin.

Tellina agilis

21 August

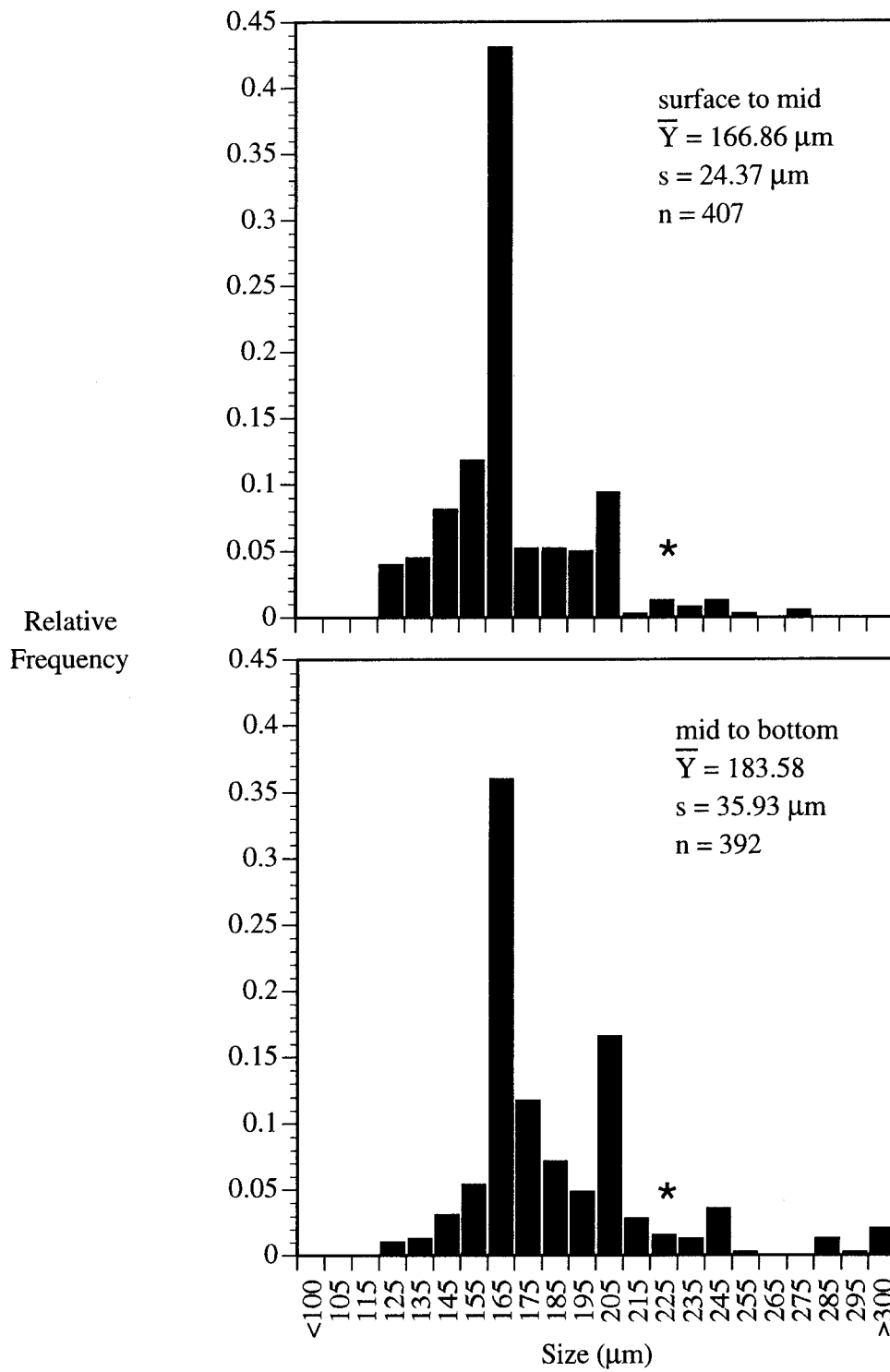


FIGURE 15. Cross-Shelf Length Frequency Histograms for the Bivalve *Tellina agilis* on 23 August. Asterisks Represent Average Size at Settlement. Sizes Shown Indicate the Mid-Point of the Range for Each Size Bin.

Tellina agilis
23 August

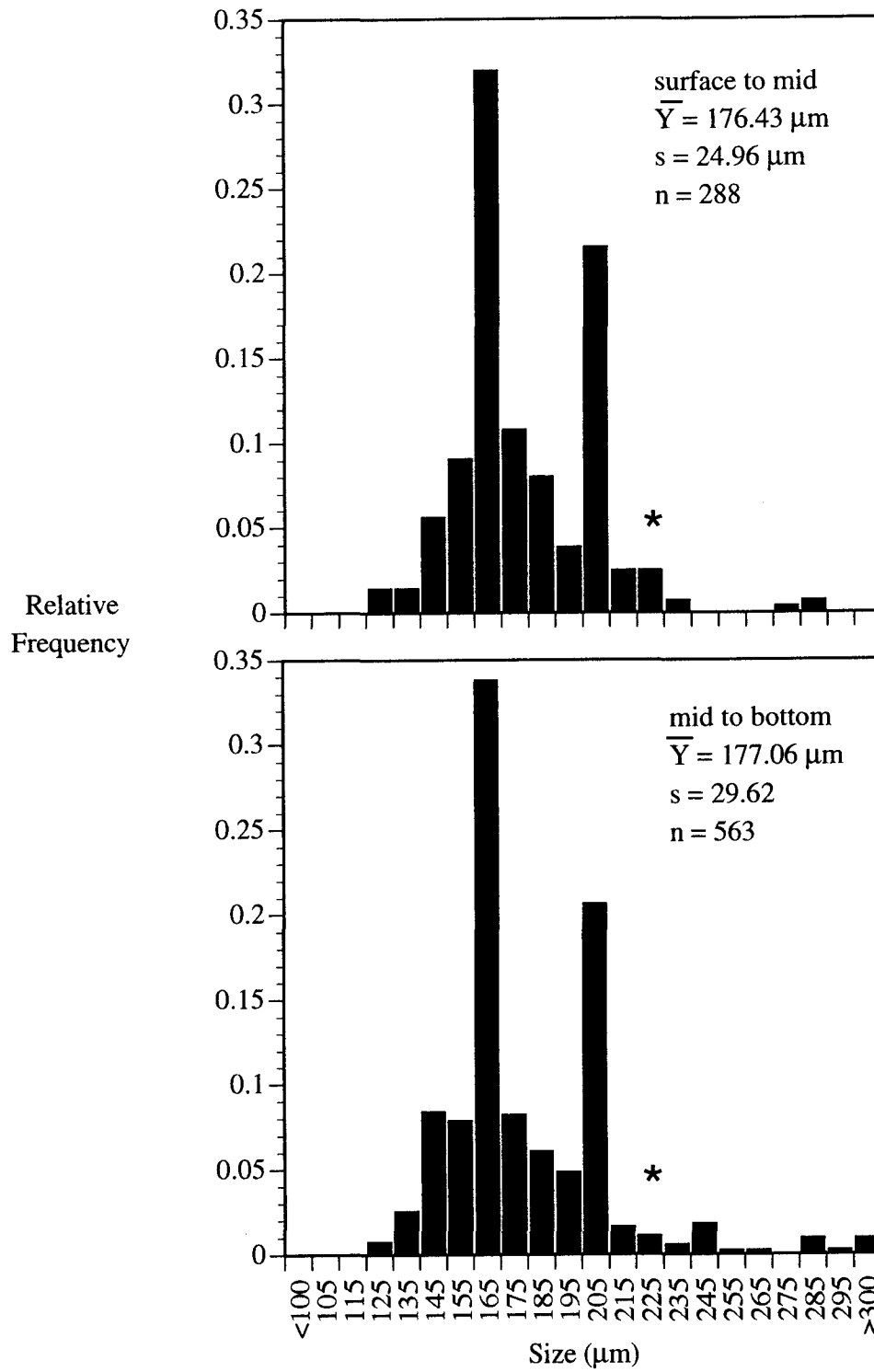


FIGURE 16. Cross-Shelf Length Frequency Histograms for the Bivalve *Tellina agilis* on 25 August. Asterisks Represent Average Size at Settlement. Sizes Shown Indicate the Mid-Point of the Range for Each Size Bin.

Tellina agilis
25 August

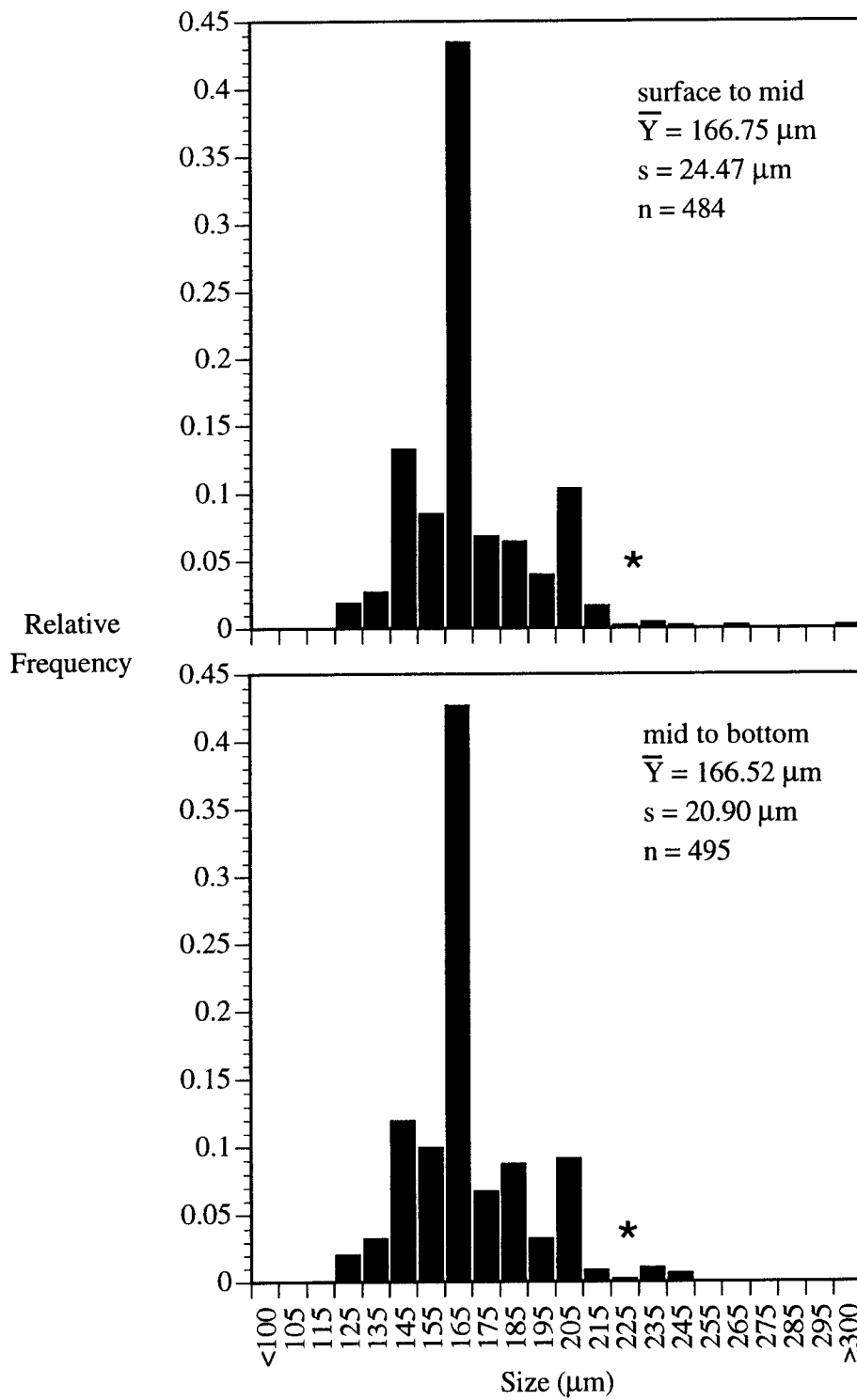


FIGURE 17. Cross-Shelf Length Frequency Histograms for the Bivalve *Tellina agilis* on 27 August. Asterisks Represent Average Size at Settlement. Sizes Shown Indicate the Mid-Point of the Range for Each Size Bin.

Tellina agilis
27 August

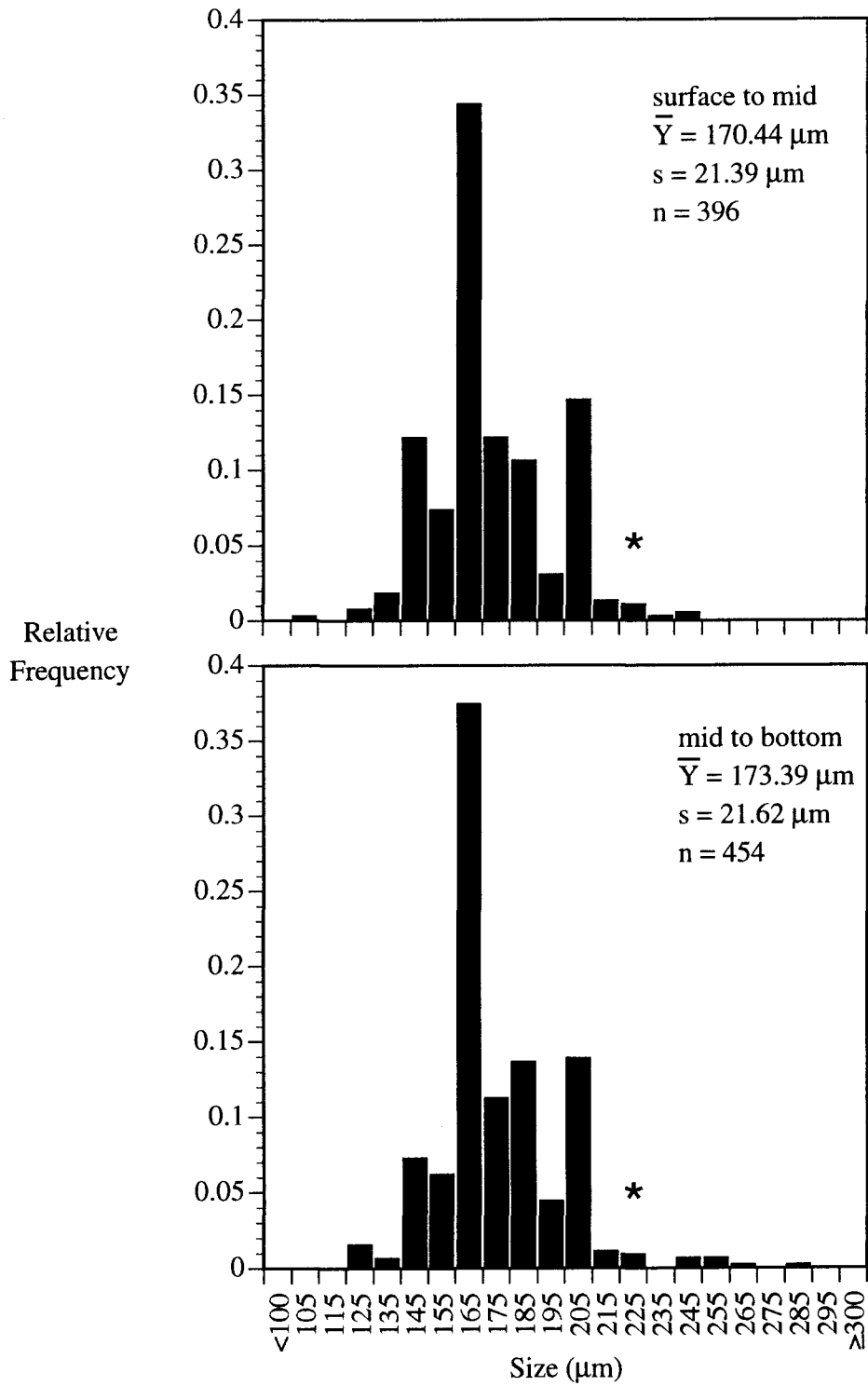


FIGURE 18. Cross-Shelf Length Frequency Histograms for the Bivalve *Cyrtopleura costata* on 21 August. Asterisks Represent Average Size at Settlement. Sizes Shown Indicate the Mid-Point of the Range for Each Size Bin.

Cyrtopleura costata
21 August

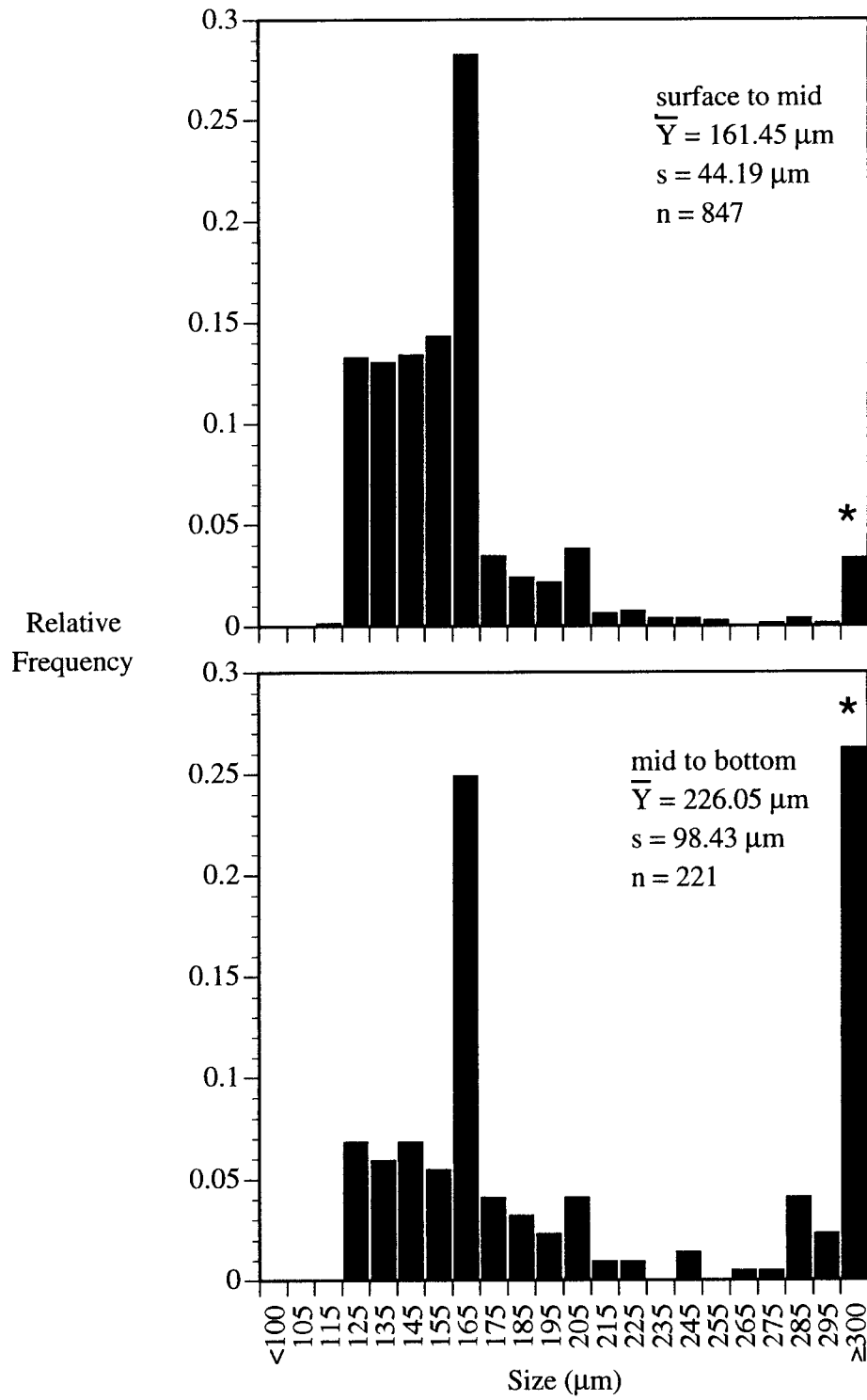


FIGURE 19. Cross-Shelf Length Frequency Histograms for the Bivalve *Cyrtopleura costata* on 23 August. Asterisks Represent Average Size at Settlement. Sizes Shown Indicate the Mid-Point of the Range for Each Size Bin.

Cyrtopleura costata

23 August

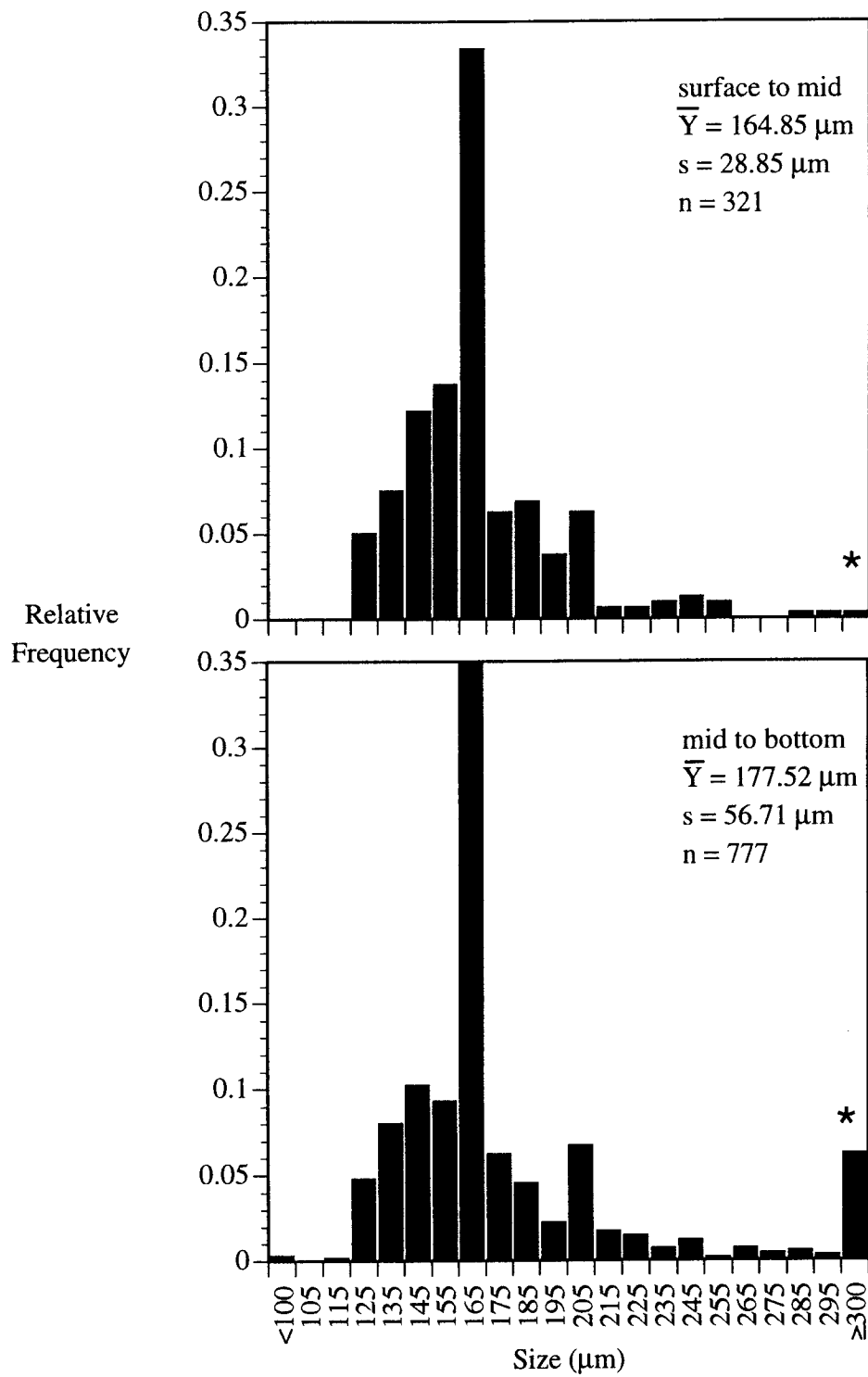


FIGURE 20. Cross-Shelf Length Frequency Histograms for the Bivalve *Cyrtopleura costata* on 25 August. Asterisks Represent Average Size at Settlement. Sizes Shown Indicate the Mid-Point of the Range for Each Size Bin.

Cyrtopleura costata
25 August

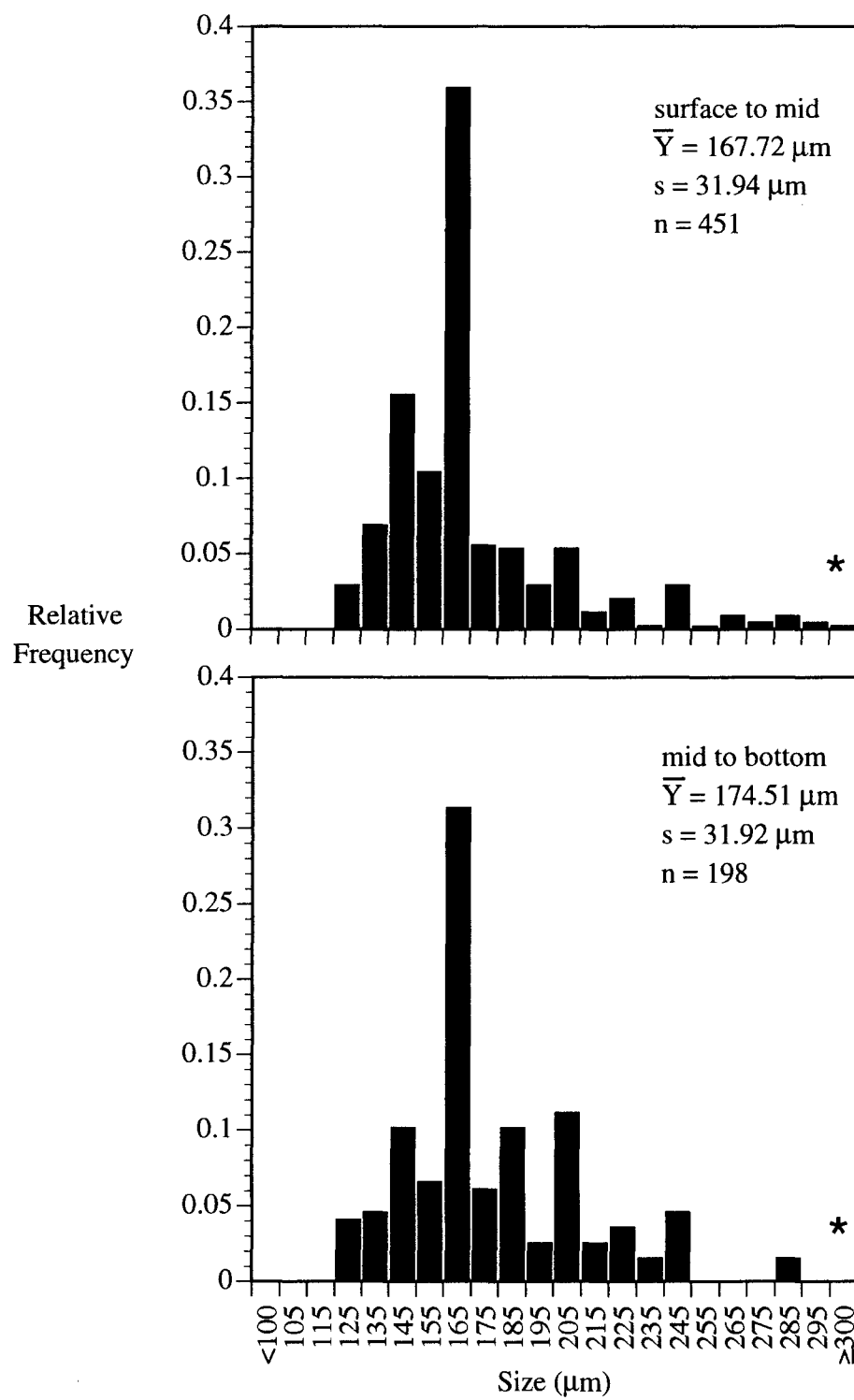
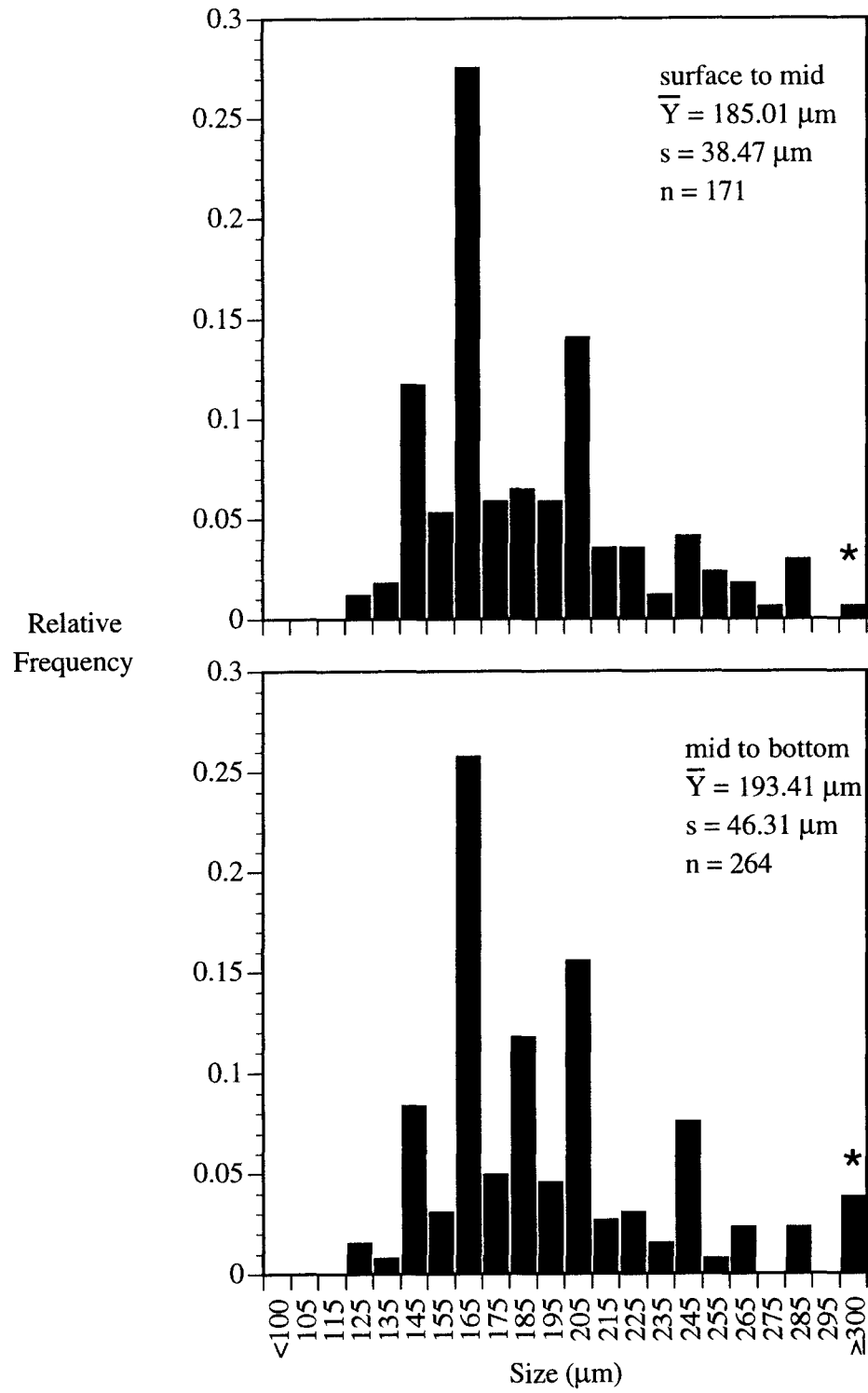


FIGURE 21. Cross-Shelf Length Frequency Histograms for the Bivalve *Cyrtopleura costata* on 27 August. Asterisks Represent Average Size at Settlement. Sizes Shown Indicate the Mid-Point of the Range for Each Size Bin.

Cyrtopleura costata
27 August



average difference between the two means was 23.12 μm . On 21 August (Fig.18), in the lower half of the water column, the highest percentage of larvae (>26%) were larger than 300 μm , while less than 4% of larvae in the upper half of the water column were at this same size.

Spisula solidissima larvae also had a peak in its size frequency distribution in the 160-170 μm size range on all four days regardless of depth (Figs.22-25), although this peak was much less pronounced than for *Tellina agilis* or *Cyrtopleura costata*. On 21 August (Fig.22) the mean size of larvae sampled from the lower half of the water column was significantly larger, almost 20 μm larger, than the mean size of larvae found within the upper half of the water column ($t = 1.96$, $P < 0.001$, $df = 909$). On the three other sampling days (Figs.23-25), no significant differences were found between the mean sizes of larvae from within the upper half of the water column and those from the lower half of the water column.

No significant differences were found between the mean sizes of *Mya arenaria* larvae between the two sampling depths on any of the four sampling dates. The sample sizes were quite low for *M. arenaria* (Figs.26-29). As a result, the histograms probably do not give an accurate account of the length distribution for larvae of this bivalve.

Discussion

The cross-shelf plots of larval distributions indicate one important feature that was common to all the larval types during the four day study period. Between days there were often large changes in the number of larvae that were present along the line surveys. From one sampling day to the next there was often greater than an order of magnitude difference between the number of larvae m^{-3} . Undoubtedly some of this difference was due to larvae being transported into and out of the sampling sites with the alongshore currents. Because sampling was carried out in the cross-shelf direction, movement in the alongshore plane

FIGURE 22. Cross-Shelf Length Frequency Histograms for the Bivalve *Spisula solidissima* on 21 August. Asterisks Represent Average Size at Settlement. Sizes Shown Indicate the Mid-Point of the Range for Each Size Bin.

Spisula solidissima

21 August

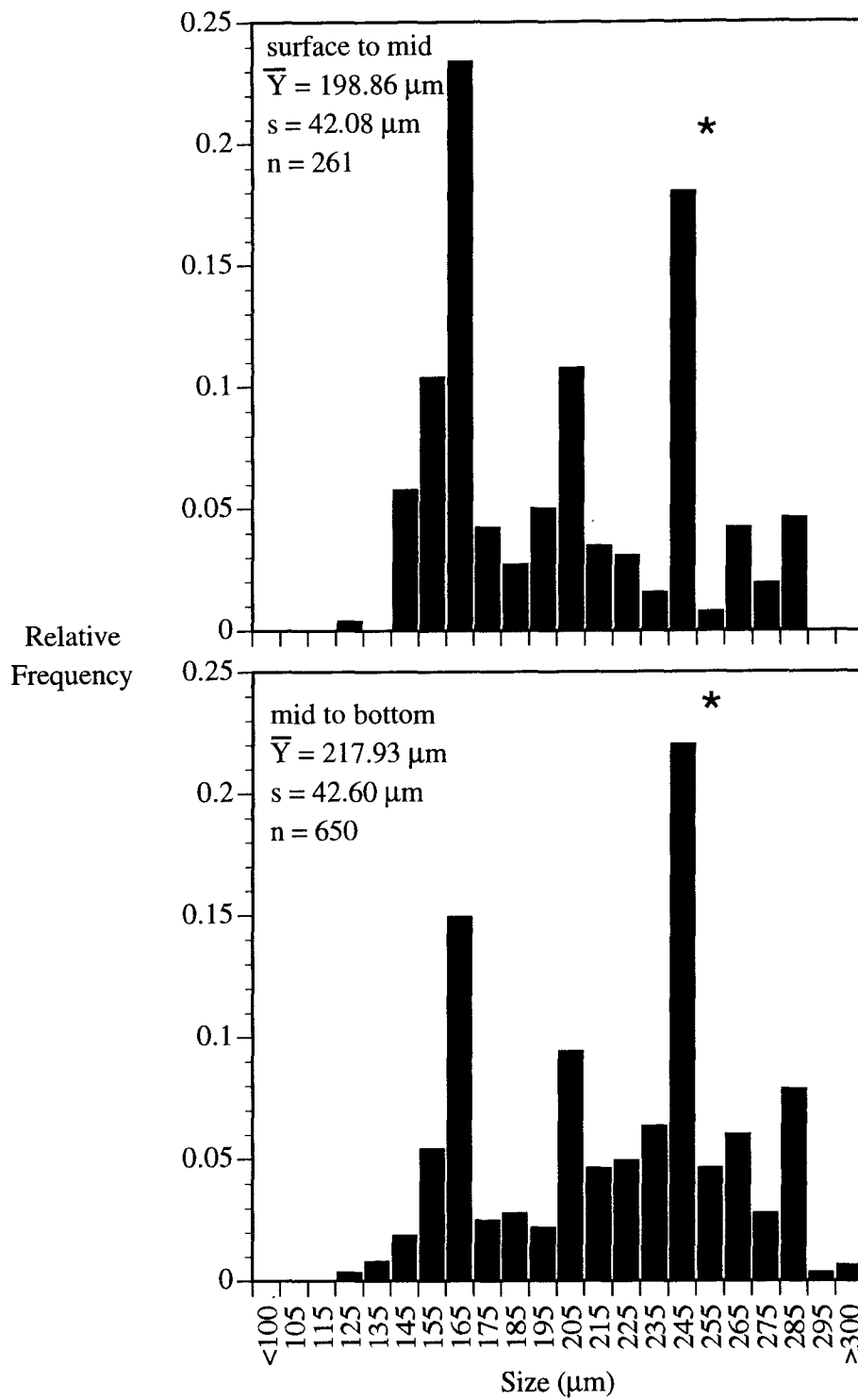


FIGURE 23. Cross-Shelf Length Frequency Histograms for the Bivalve *Spisula solidissima* on 23 August. Asterisks Represent Average Size at Settlement. Sizes Shown Indicate the Mid-Point of the Range for Each Size Bin.

Spisula solidissima
23 August

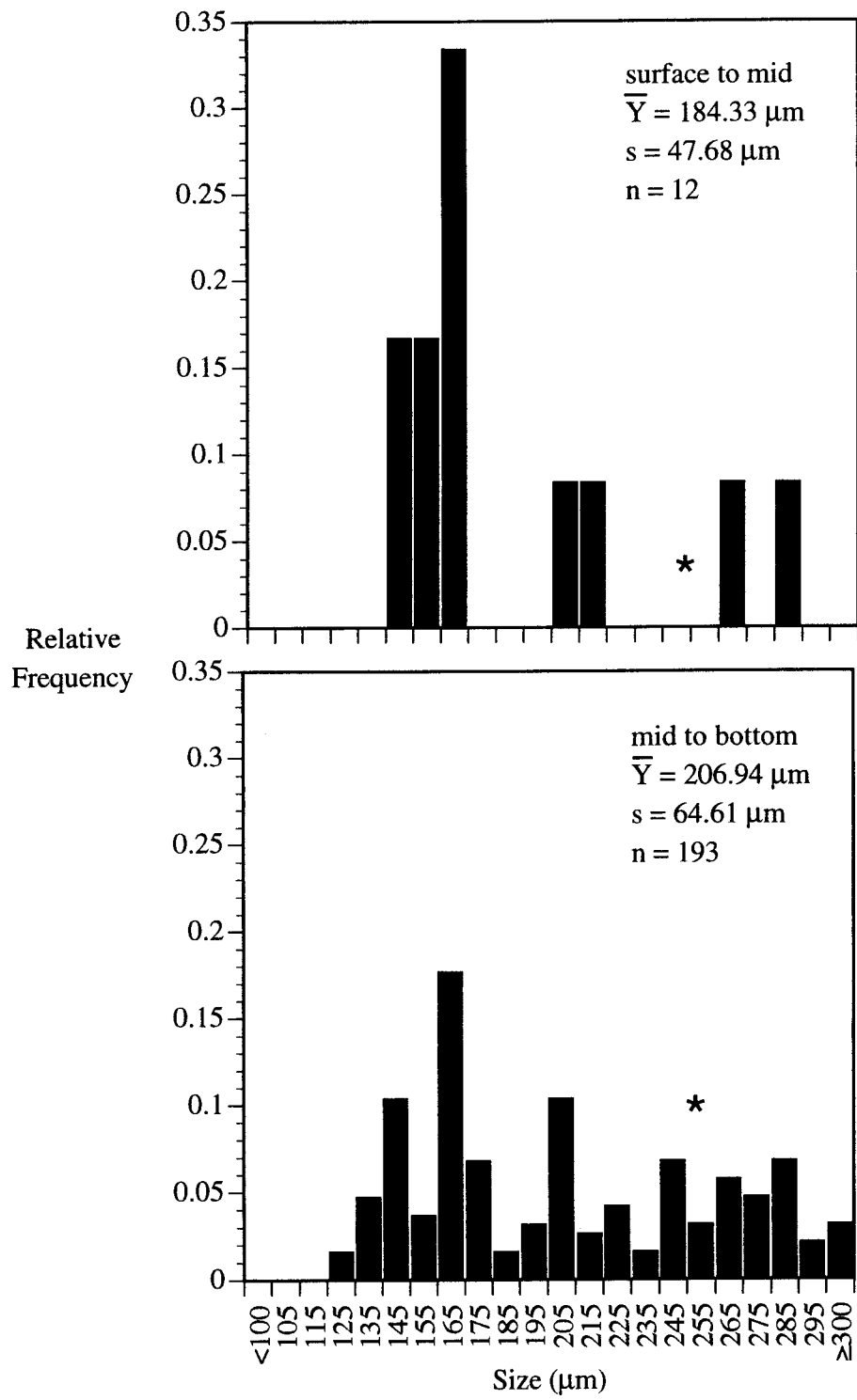


FIGURE 24. Cross-Shelf Length Frequency Histograms for the Bivalve *Spisula solidissima* on 25 August. Asterisks Represent Average Size at Settlement. Sizes Shown Indicate the Mid-Point of the Range for Each Size Bin.

Spisula solidissima
25 August

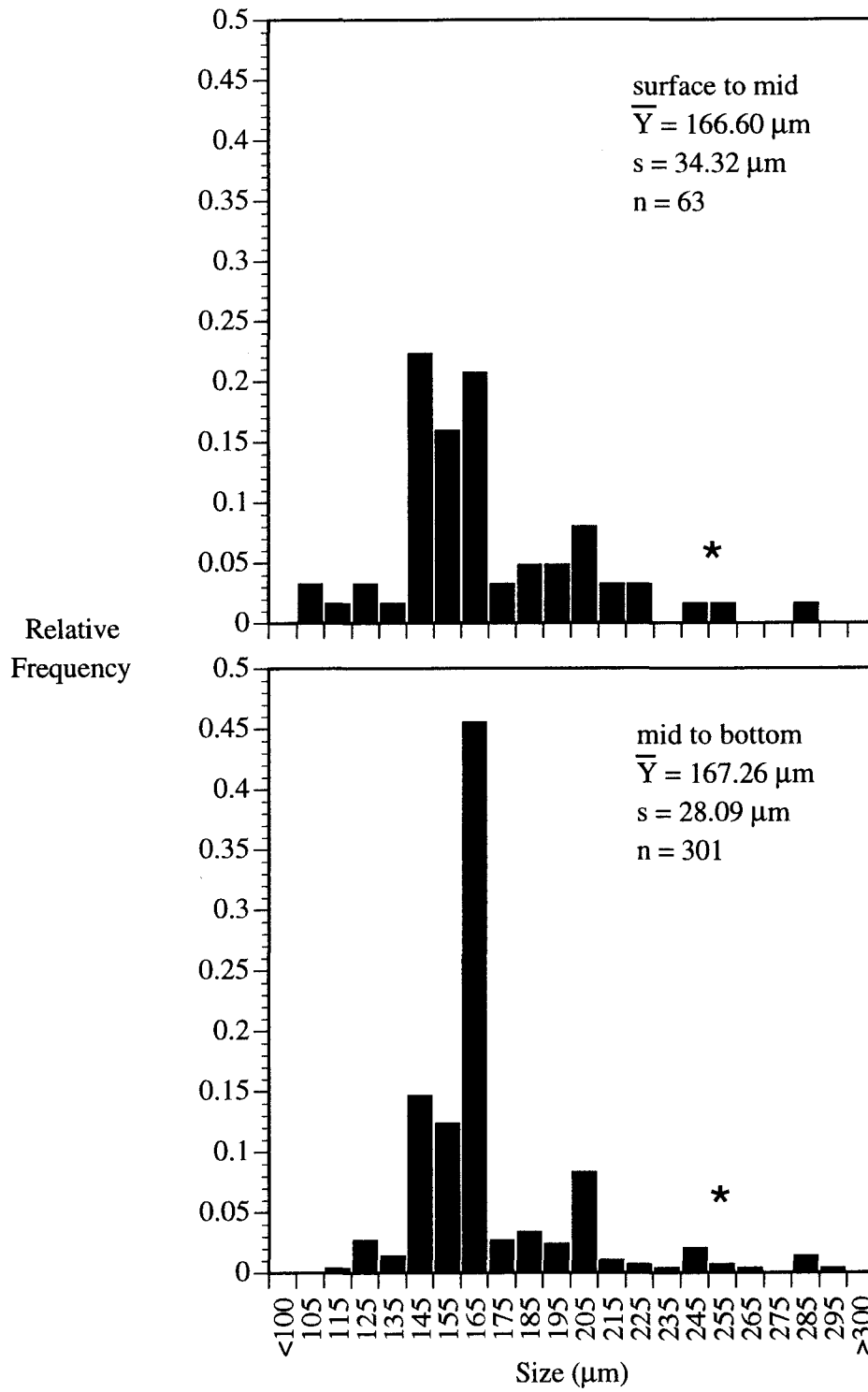


FIGURE 25. Cross-Shelf Length Frequency Histograms for the Bivalve *Spisula solidissima* on 27 August. Asterisks Represent Average Size at Settlement. Sizes Shown Indicate the Mid-Point of the Range for Each Size Bin.

Spisula solidissima
27 August

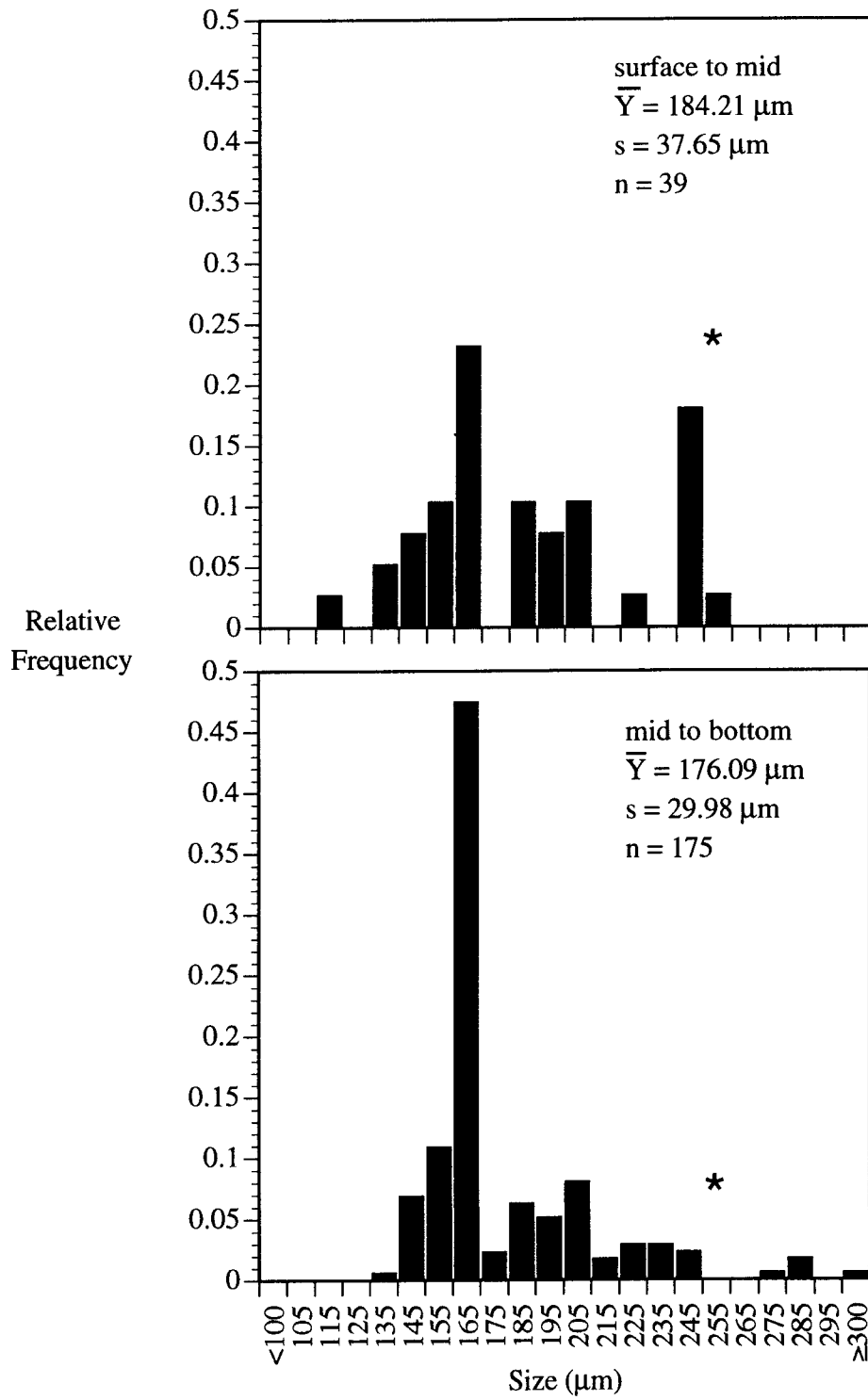


FIGURE 26. Cross-Shelf Length Frequency Histograms for the Bivalve *Mya arenaria* on 21 August. Asterisks Represent Average Size at Settlement. Sizes Shown Indicate the Mid-Point of the Range for Each Size Bin.

Mya arenaria
21 August

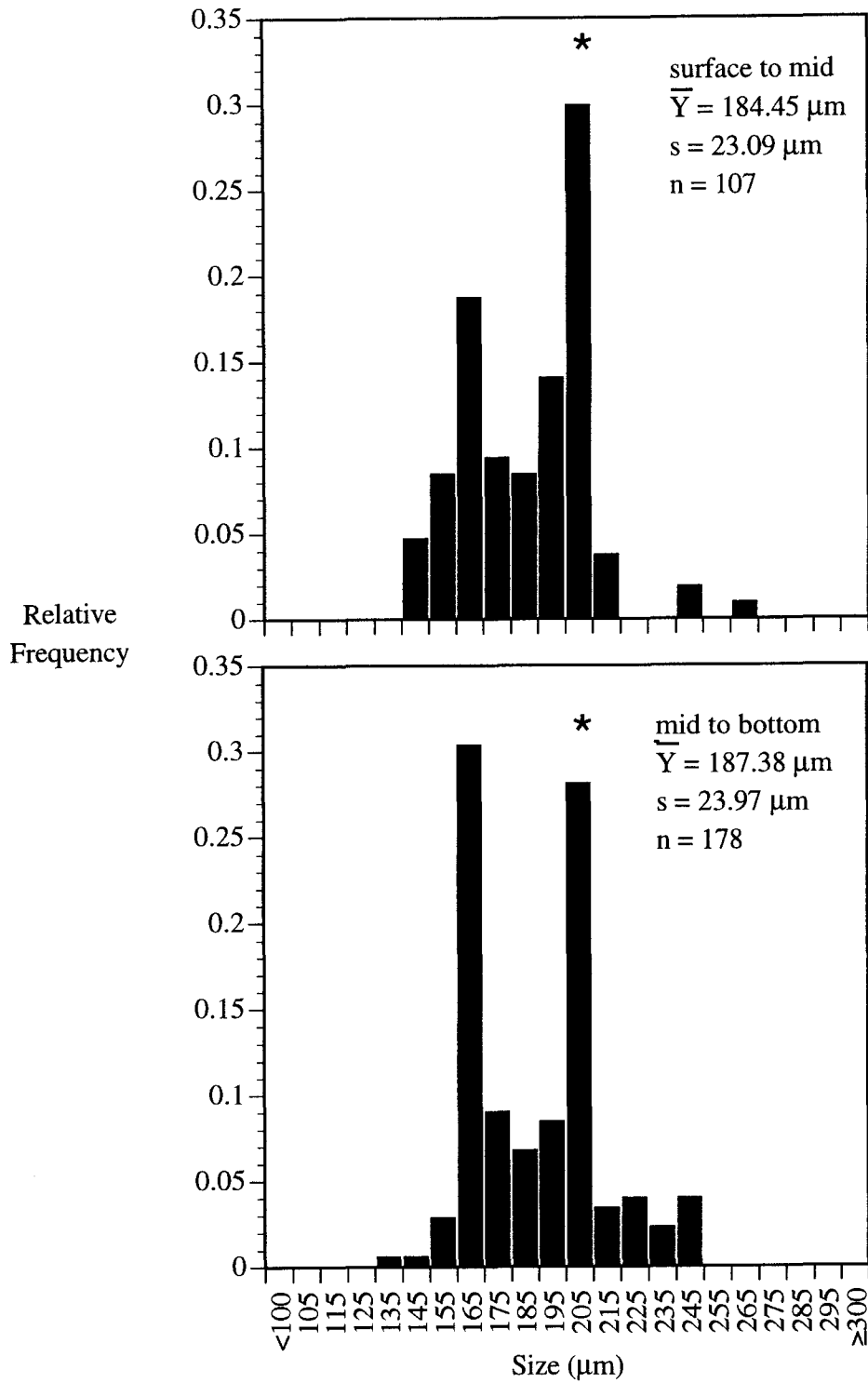


FIGURE 27. Cross-Shelf Length Frequency Histograms for the Bivalve *Mya arenaria* on 23 August. Asterisks Represent Average Size at Settlement. Sizes Shown Indicate the Mid-Point of the Range for Each Size Bin.

Mya arenaria
23 August

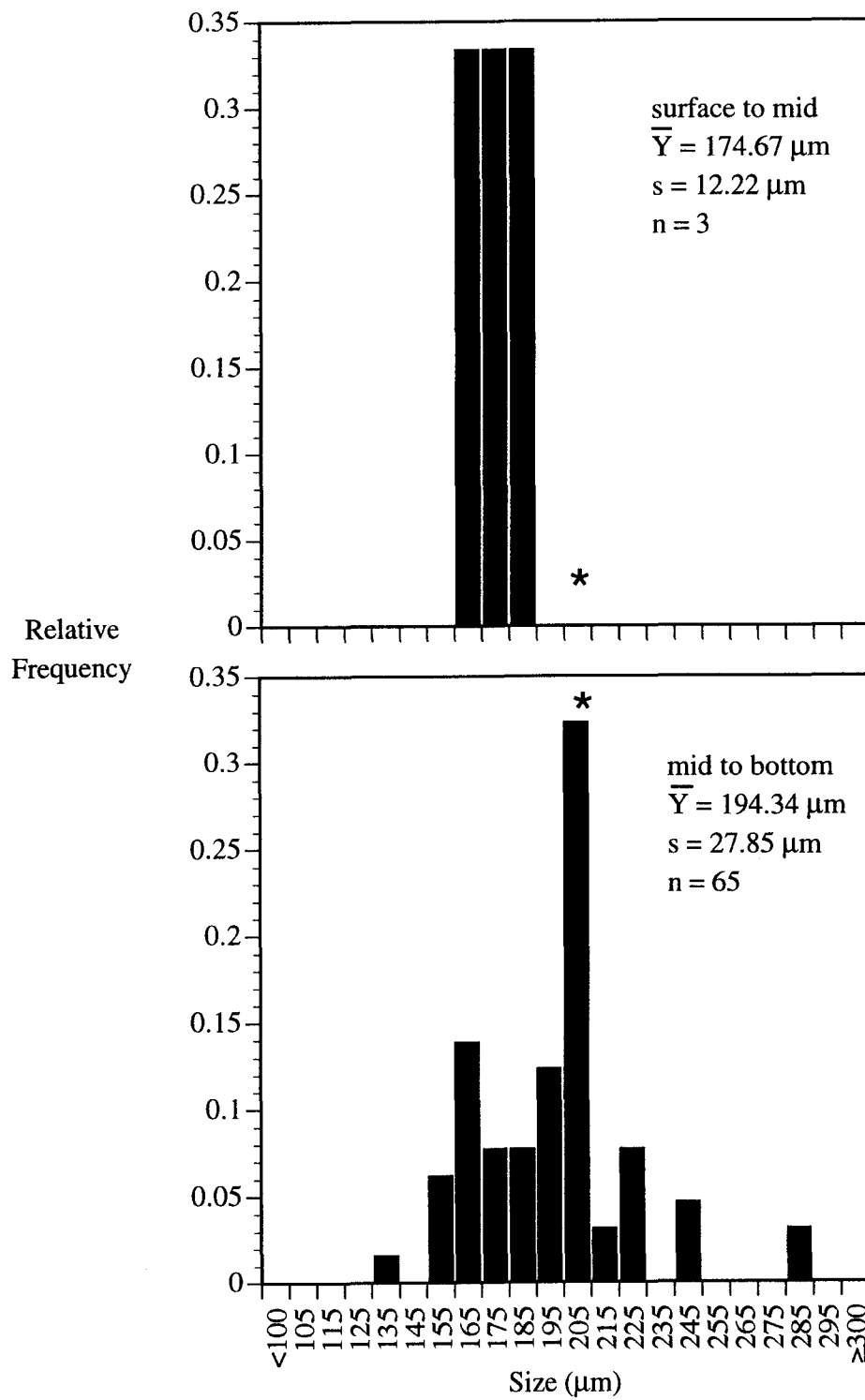


FIGURE 28. Cross-Shelf Length Frequency Histograms for the Bivalve *Mya arenaria* on 25 August. Asterisks Represent Average Size at Settlement. Sizes Shown Indicate the Mid-Point of the Range for Each Size Bin.

Mya arenaria
25 August

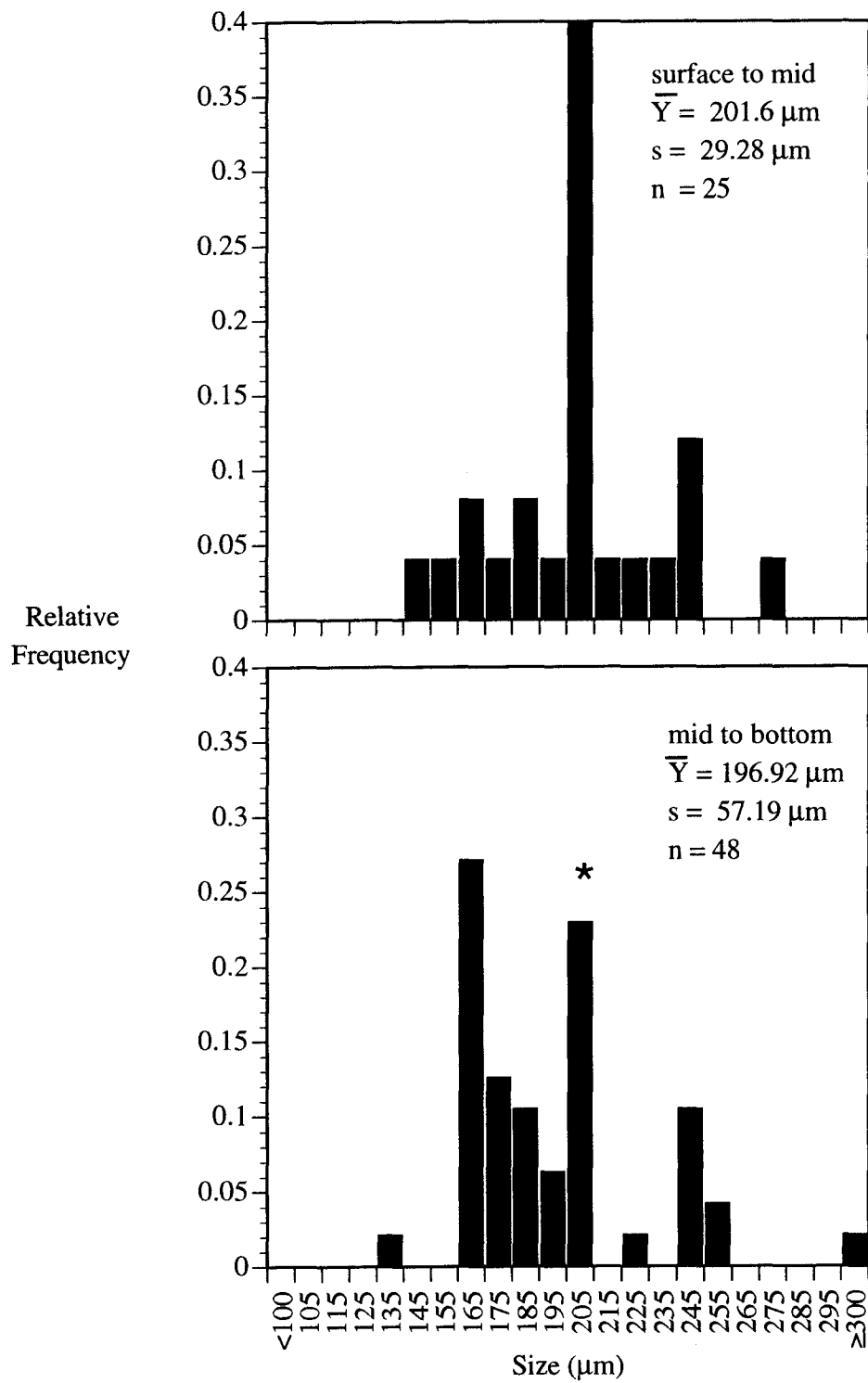
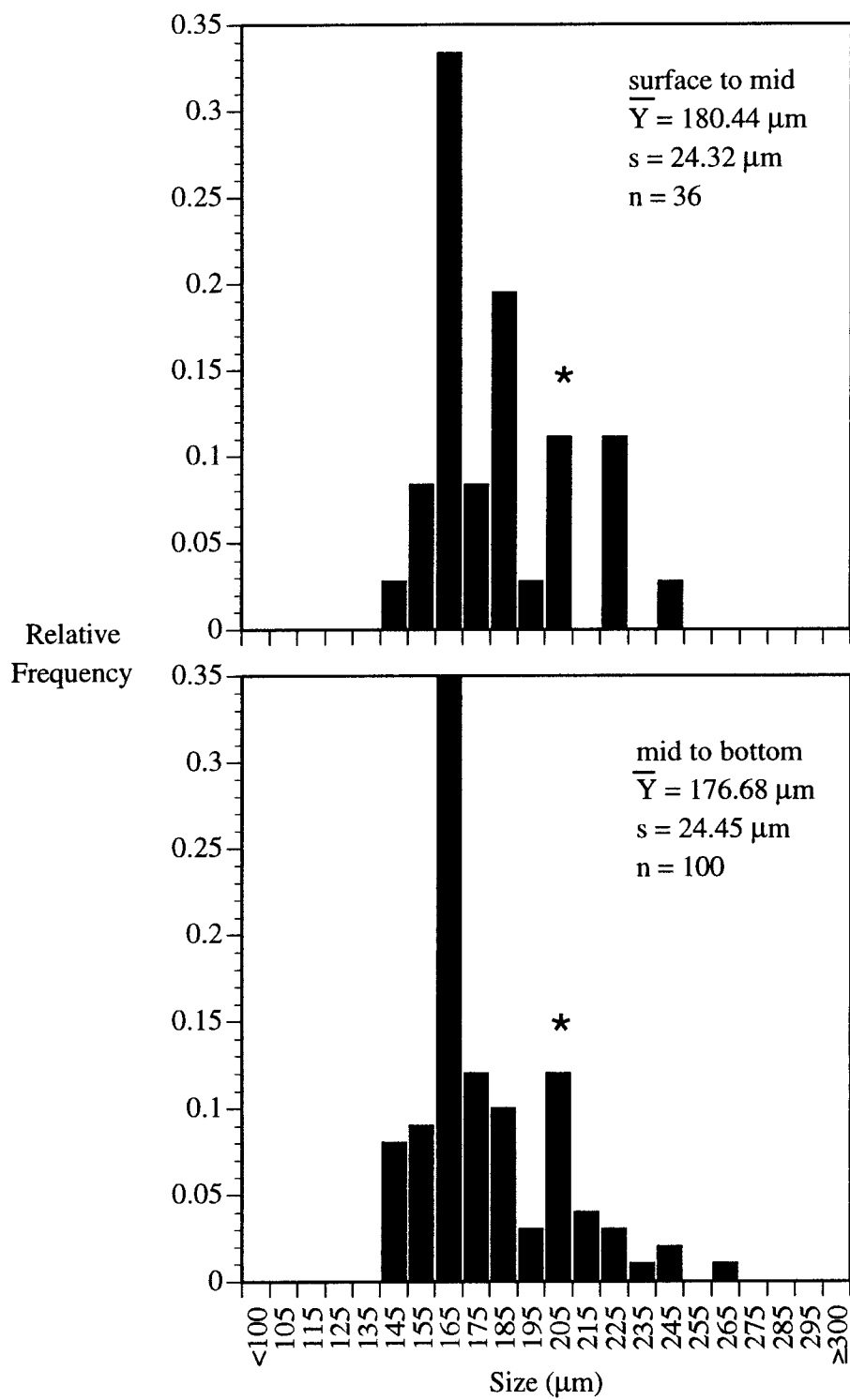


FIGURE 29. Cross-Shelf Length Frequency Histograms for the Bivalve *Mya arenaria* on 27 August. Asterisks Represent Average Size at Settlement. Sizes Shown Indicate the Mid-Point of the Range for Each Size Bin.

Mya arenaria
27 August



was undetectable. However, strong cross-shelf currents are detectable in the density contour plots. For instance, the 21.2 density isopycnal present just below the surface on 21 August is transported offshore between the 21st and 23rd, and then reappears within 5 km of the coast on the 25th (see Figure 2). By 27 August, this low density water had become spread across the surface of the ocean out to 15 km from shore (Fig.2). The cross-shelf current moving this low density water on and offshore transports larvae within this density structure in the cross-shelf direction. Thus some of the differences in larval concentrations between and among days was attributable in some part to the cross-shelf movement of larvae.

Although each larval type had a unique cross-shelf distribution over the four day sampling period, many similarities in larval distributions were seen among the sampling days. On 27 August, 6 of the 11 larval types sampled (*Tellina agilis*, *Cyrtopleura costata*, *Mya arenaria*, *Littorina spp.*, spionid polychaetes, and polychaete trochophores), were found in relatively high concentrations between 5 and 10 m depth and up against the coast (Figs.3, 4, 6, 7, 12, and 13). This was during a period of upwelling, when the low density Chesapeake bay plume waters found against the coast on 25 August were being transported offshore in seaward-moving surface waters. The inclination is to assume that these clouds of larvae were brought to this location by shoreward-moving bottom waters. But when looking at the distributions of larvae on the previous sampling day (25 August) the majority of larvae, regardless of larval type, were not found in the lower half of the water column where their shoreward transport on the 27th would have been possible. Rather larvae were found in the plume front or in the upper half of the water column. Therefore, were transport simply a passive process, these larvae would have been transported offshore on the 27th in these low density offshore-moving surface and plume waters rather than being concentrated in a patch up against the coast.

During the 25th and 27th of August, vertical current speeds offshore and within the downwelling (25 August) and upwelling zones (27 August) were relatively slow, on the order of mm sec^{-1} (Austin, personal communication). The cross-shelf currents, on the other hand, were moving between 8 and 16 cm sec^{-1} (Alessi *et al.*, 1996). Larval swimming speeds are typically on the order of <1 to 8 cm sec^{-1} (reviewed in Chia *et al.*, 1984). Larvae that swim horizontally against the currents will therefore result in a net transport in the direction of current flow. In order for larvae sampled from within the Chesapeake bay plume and surface waters on the 25th to end up against the coast on the 27th, during the period of upwelling, they would have had to swim or sink vertically against the vertical currents (in the case of larvae sampled from within the plume) or into shoreward moving bottom waters (in the case of larvae which were sampled offshore in surface waters). As long as vertical current speeds are not appreciably higher than larval swimming speeds, larvae are probably able to swim against these vertical currents to remain at a preferred depth. Because meroplanktonic larvae are relatively poor swimmers, migrating vertically throughout the water column into currents of differing directions and speeds would seem like a viable way for larvae to affect their own transport and dispersal.

The Chesapeake bay plume and associated front present on the 25th represents an interesting oceanographic event. A front is an area of large horizontal gradients of density, temperature, and/or salinity. The Chesapeake bay plume front was caused by low salinity waters of the Chesapeake bay flowing south along the North Carolina coast, causing a steep salinity gradient separating the low salinity Chesapeake bay water from the surrounding higher salinity shelf waters. Zooplankton are often concentrated in frontal zones, presumably due to convergent currents within the frontal zone causing accumulation of plankters (reviewed by Kingsford, 1990). Pingree *et al.* (1974) sampled crustacea within a frontal region in the English channel as well as 200-300 m outside the front. They found that on average, densities of these zooplankters were almost 75 times higher within

the front than outside of it. Thiébaud (1996) found concentrations of *Pectinaria koreni* larvae (polychaetes) to be an order of magnitude greater in the Seine river plume front than in the surrounding shelf waters. Surprisingly only 3 of the 11 larvae sampled during the line survey (*Tellina agilis*, *Cyrtopleura costata*, and *Spisula solidissima*) were found concentrated in the Chesapeake bay plume front on 25 August (Figs.3-5, respectively). Most larval types were absent from these plume waters and associated front, perhaps by swimming vertically into waters that were moving away from this low density region.

Several different types of larvae occurred within the Chesapeake bay plume waters on 25 August included *Mya arenaria*, *Littorina spp.*, *Bittium sp.*, and polychaete trochophores (Figs.6,7,9 and 13, respectively). These plume waters were moving southward along the coast at almost 40 cm sec^{-1} (Waldorf *et al.*, 1995), so it seems quite likely that larvae found within the plume were transported along the coast from the Chesapeake bay. Both *Mya arenaria* and *Bittium sp.* are estuarine organisms (Smith, 1964), which may explain why high numbers of these larval types were found within the Chesapeake bay plume waters. The adult habitat of the polychaete trochophores is unknown. *Littorina spp.* gastropods are littoral, so the reasons for the appearance of their larvae in these plume waters is unclear.

On 21, 23, and 25 August, a cloud of *Littorina spp.* larvae were present in the same general location as that of the plume waters on 25 August (against the coast within 5 km of shore). Perhaps these larvae were swimming vertically against the currents in order to remain in the same relative location during this four day sampling period. By remaining in this area, these larvae were close to the adult habitat and thus close to potential settlement sites. Once again, vertical movement appears to be a way for larvae to control their transport.

Some of the larval types sampled appeared to regulate their depth based upon the density of the surrounding waters. Both *Spisula solidissima* and *Mya arenaria* larvae were found in highest concentration below the 23.0 isopycnal (Figs.5 and 6, respectively). The

pectinereid larvae remained offshore between the 22.8 and 25.0 isopycnals, and as a result remained out of low density Chesapeake bay plume waters (Fig.10). *Bittium sp.* larvae, on the other hand, were primarily found in densities lower than 23.0, tending to remain in lower density surface waters (Fig.9). In a similar fashion, Tremblay and Sinclair (1990a) found that highest concentrations of sea scallop larvae in the Bay of Fundy were found within and around the pycnocline and that with increasing density stratification came increases in aggregation of larval sea scallops. Perhaps larvae are using density to orient themselves in particular water masses, water masses which may be more likely to transport them in the direction of the adult habitat.

The pectinereid polychaete larvae provide the best example of the role of larval behavior in transport (Fig.10). Although their numbers varied dramatically among the 4 sampling days, their distribution was relatively unchanged during this time. They were typically found offshore with highest concentrations of larvae centered in and around the pycnocline. On 21 and 23 August, pectinereid larvae were concentrated within the pycnocline. On 25 August, larvae became concentrated above the pycnocline in shoreward moving surface waters. This high concentration cloud was probably a combination of larvae that had been transported into the sampling area from farther offshore and of larvae that had migrated into surface waters from the pycnocline present on the 25th. On 27 August, larvae were primarily concentrated within and below the pycnocline. Had the pectinereid larvae been acting like passive particles, those larvae present on the 25th would have been transported offshore in offshore-moving surface waters on the 27th. What appears to have happened is that larvae migrated vertically to within and below the pycnocline and therefore were not swept farther offshore. By simply migrating up and down between the two different layers of water, the pectinereid larvae could theoretically remain the same distance offshore through time.

Despite many of the larval types appearing to exhibit some degree of control over their cross-shelf dispersal, others were passively transported by the currents. Both the phyllodocid and spionid polychaete larvae were moved offshore and out of the sampling site during periods of downwelling and were then brought back shoreward along the bottom during upwelling (Figs.11 and 12, respectively). Although these larvae are equipped with many swimming parapodia, their swimming speeds are unusually slow, on the order of 0.5 to 5.2 mm sec⁻¹ (Chia *et al.*, 1984; Butman *et al.*, 1988). These slow swimming speeds may provide some explanation as to why their dispersal appeared to be controlled mainly by physical processes.

The size frequency data of the bivalve larvae failed to produce any consistent trends in ontogenetic differences of larvae related to vertical position within the water column. Both *S. solidissima* and *M. arenaria* had sample sizes that were too small to allow for any valid conclusions to be drawn about larval size and their vertical positions within the water column (Figs.22-29). *Tellina agilis* had significantly larger sized larvae near the bottom on 21 August only (Figs.14-17). This was during the time when bottom waters were moving shoreward during upwelling. Over 12% of the larvae sampled within the lower half of the water column on this day were at or above the average settlement size for this species (Loosanoff *et al.*, 1966; Chanley & Andrews, 1971) and were theoretically competent to settle were they to find a suitable benthic habitat. It is possible that these larger larvae near the bottom accumulated in this dense water mass as a mechanism for transport shoreward toward the adult habitat in preparation for settlement.

Only *Cyrtopleura costata* larvae showed a consistent pattern of larger larvae near the bottom (Figs.18-21). Many of these larvae were well over (>100 µm over) the average settlement size (Loosanoff *et al.*, 1966; Chanley & Andrews, 1971).

Current speeds along the bottom varied between 5 and 40 cm sec⁻¹ over the four day sampling period (Alessi *et al.*, 1996). Bottom current velocities were highest during

downwelling periods. These velocities may have been high enough to induce settled larvae to become byssal thread drifters, which may explain why so many very large larvae were sampled near the bottom. The exact current velocity needed to induce byssus thread production is unknown. Since Sigurdsson *et al.* first coined the phrase "byssus drifting" in 1976, many researchers have observed this phenomenon in both post-settlement sized bivalves and gastropods (Lane *et al.*, 1985; Martel & Chia, 1991; Cummings *et al.*, 1993). Byssal thread drifting is a way for bivalve and gastropod larvae to sample new benthic habitats after settlement and the loss of the swimming velum has occurred, thereby aiding in their own dispersal.

One particular peak in the size distributions of all four bivalve species was evident. Many larvae were found to be between 160 and 170 μm long. This consistency between sampling depths and among days suggests that these larvae may have been spawned at similar times and have similar growth rates.

CHAPTER II

VERTICAL MIGRATION OF MEROPLANKTONIC LARVAE

Introduction

Vertical migration is a common behavior of marine and freshwater organisms (Levy, 1990; Neill, 1990; Ohman, 1990; Bollens *et al.*, 1992; Mills, 1983; Barile *et al.*, 1994). The words "vertical migration" typically conjure up images of organisms making diel migrations into surface waters at dusk to feed while avoiding visual predators and then descending back down to depth at dawn. But the types of vertical migrations made are as varied as the reasons put forth for them. Reverse migration, in which organisms reside in surface waters during the day and migrate/sink to deeper waters at night, have been displayed by such animals as *Daphnia* (Southern & Gardiner, 1926), the cladoceran *Podon* (Bosch & Taylor, 1973), and more recently by juvenile sockeye (Thorne, 1983). The reasons for such a reversal from the "norm" are still unclear, but the idea of avoidance of non-visual predators has been put forth (Bayly, 1986). There are also those plankters who vertically migrate not because of predators or time of day, but as a means of regulating their horizontal movement. By moving vertically between opposing currents, Nelson (1912) believed that poor swimming oyster larvae could either maintain their position or be transported horizontally to new locations. Since this early date, the idea of vertical migration as a means of horizontal transport and dispersal has received much attention (Longhurst, 1976; Rothlisberg, 1982; Shanks, 1986; Schlacher & Woolridge, 1995; Zeng & Naylor, 1996). Hardy (1953) even suggested horizontal transport to be the driving force for the evolution of vertical migration.

Controlling horizontal position within the water column is a unique problem for

meroplankton. Most meroplanktonic larvae, and especially the animals studied in this thesis, cannot swim well enough to control their position via horizontal swimming (Chia *et al.*, 1984; Sulkin, 1984; Butman *et al.*, 1988). A mechanism of horizontal transport through tidally-timed vertical migration, termed "selective tidal stream transport", is commonly used by meroplanktonic larvae residing in estuaries: larvae rise during the flood tide, and descend during ebb tide, with net transport being shoreward or up an estuary. McCleave and Kleckner (1982) showed that glass eels (*Anguilla rostrata*) are able to control their movement up an estuary by using just such a mechanism. Wood and Hargis (1971) found similar results with veliger larvae of the oyster *Crassostrea virginica*; veligers ascended during flood tides and returned to the bottom during the ebbing tide, with a resulting net transport up the estuary towards the adult habitat. Mud crab zoeae (*Rhithropanopeus harrisi*) were found to vertically migrate in synchrony with the tidal cycle as a means of retention in the upper Newport river estuary, North Carolina (Cronin & Forward, 1982). Olmi (1991) found that blue crab megalopae were vertically migrating during the nighttime flood tide with a resultant net transport up the York river estuary (Virginia) toward the adult marsh habitat. The precise mechanisms used by larvae to determine when to ascend and descend is still up for debate, however (Carriker, 1951; Wood & Hargis, 1971; Cronin & Forward, 1982).

Ontogenetic differences in the vertical distributions of larvae are also possible. The developmental stage and thus size of a larva will influence the behavior of that organism. For instance, a benthic polychaete larva that is competent to settle is less likely to survive if it migrates into the surface waters where it runs the risk of being transported away from potential settlement sites. In this case the animal may remain close to the bottom, nearer the adult habitat. Ontogenetic differences in the vertical distributions of larvae are often seen. A study of the vertical distributions of giant scallop larvae, *Placopecten magellanicus*, revealed that larger larvae were consistently found at greater depths in lab mesocosms than

were smaller larvae, which tended to remain near the surface (Gallager *et al.*, 1996). Bayne (1964) showed that as development proceeded and settlement approached, larvae of the mussel *Mytilus edulis* became increasingly photonegative and large larvae tended to be found near the bottom. Thorson (1946) believed younger larvae were concentrated near the surface because of the rich food source in these waters, while older larvae were found closer to the bottom because of the proximity to settlement sites.

Two of the hypotheses addressed in this thesis are: 1) planktonic larvae act as stochastically transported passive particles, and 2) the vertical position of these larvae is unrelated to their size or competency to settle. By following the course of movement of larvae over a period of 23 hours, it is perhaps possible to determine the role of physical movements of water masses in larval transport and possibly how much of the transport/dispersal process is controlled by active larval movements.

Methodology

Field Studies

While at anchor approximately 2.5 km from the Duck pier, NC (Figure 1), plankton samples were collected every hour (as described under Methodology, Chapter I) beginning at 0730 hrs on 22 August, 1994, and continuing until 0630 hrs on 23 August, 1994. Due to rough seas at 0330 hrs on 23 August, sampling was not conducted at that time, but was resumed at 0430 hrs. Because the station depth remained constant, sampling depths remained relatively unchanged between sampling times (with minor adjustments made depending upon the thermocline depth). Five sampling depths were chosen, at 2, 5, 8, 10, and 12 m. CTD casts were made every half hour during the course of the study.

Alongshore and cross-shore current speeds were recorded by vector measuring current meters (VMCMs) attached to both surface and sub-surface moorings located

approximately 3 km offshore in 13 m of water. The VMCMs were located 4.15, 6.45, 8.70, and 11.0 m below the surface. Current data were recorded every 4 minutes and then transformed into hourly averages (Alessi *et al.*, 1996).

Laboratory Analysis of Samples

Anchor station samples were sorted using the same methods as those for line surveys (Methodology, Chapter I). Due to time constraints only every other hour's samples were sorted, which provided ample resolution for determining temporal variations in larval distributions. The meroplanktonic larvae identified in these samples were similar to those found in the cross-shelf samples, and are listed in Table 2. Both biological and physical data were analyzed using Spyglass Transform software. Raw CTD data were provided by Walt Waldorf of Oregon State University; current meter data were provided by Jay Austin of Woods Hole Oceanographic Institution.

To test the hypothesis that a larva's vertical position within the water column was unrelated to its size or competency to settle, individuals of each species of bivalve larvae were divided into two groups: those sampled from the upper half of the water column over the course of the 23 hour period, and those sampled from the lower half of the water column during this same time period. Size frequency histograms were constructed for each of the five species of bivalves, and t-tests were performed to determine any difference in the mean size between the two groups of larvae within each species.

Results

During the course of the 23 hour vertical migration study wind direction and speed changed dramatically. When sampling began at 0730 hrs on 22 August, winds were blowing from the southwest at approximately 2 m sec^{-1} (wind data not shown) and

continued to do so until early afternoon. Around 1400 hrs wind direction began to shift and by 1630 hrs was blowing from the northeast. Winds continued to blow from the NNE at an average of 4 m sec^{-1} until sampling ended at 0630 hrs on 23 August.

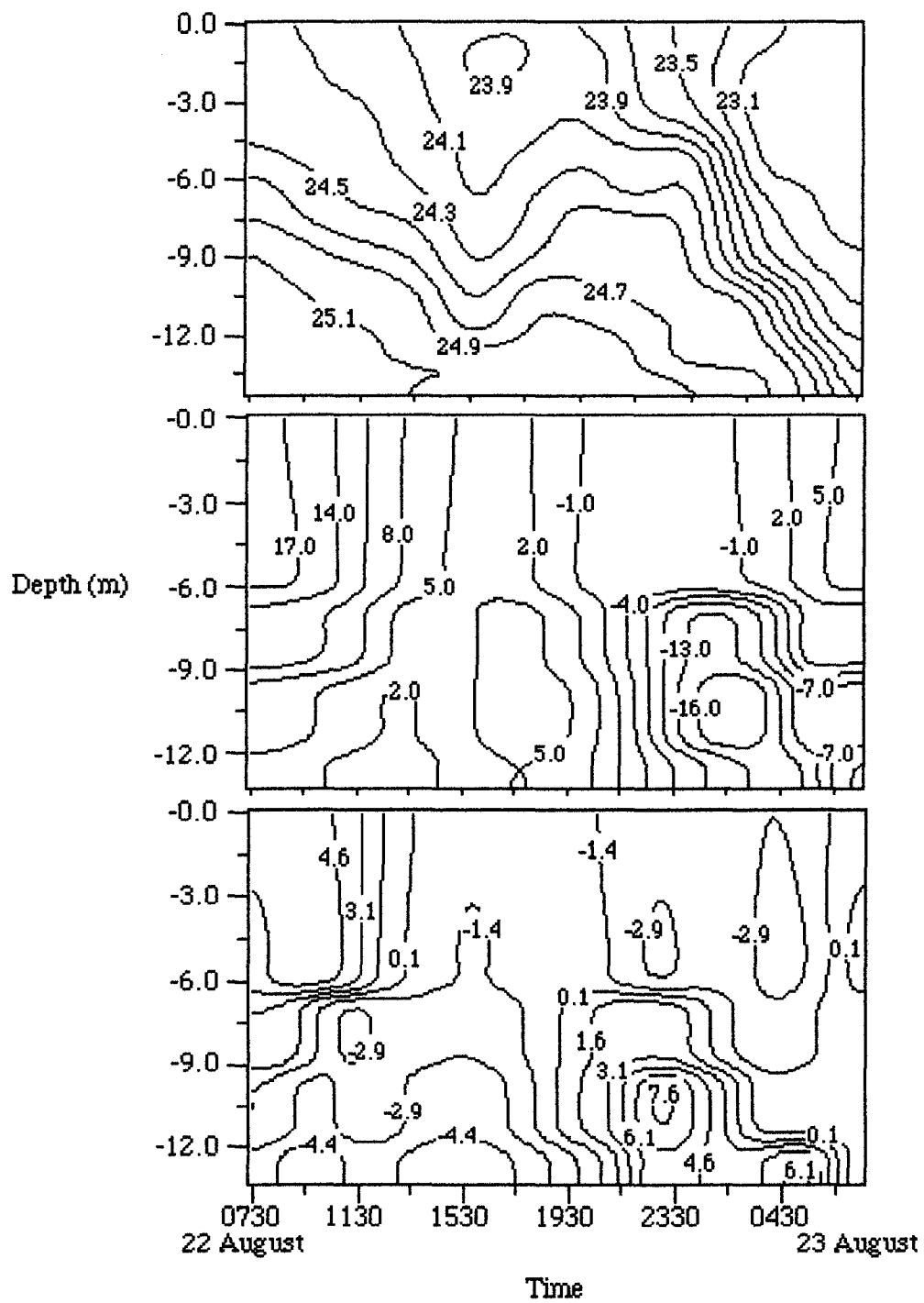
It is important to keep in mind when looking at the vertical migration contour plots that the spatial scale remains unchanged: plankton samples were collected at the same location over the course of the 23 hours. It is only the temporal scale that changed.

Alongshore and cross-shore current profiles (Fig.30) show that as winds were blowing from the southwest during the morning and early afternoon of the 22nd, shelf waters were moving northward and surface waters were transported offshore. To replace these offshore-moving surface waters, bottom waters were transported shoreward. As wind direction began to change and wind speed declined, alongshore surface current speeds dropped from 17 cm sec^{-1} at 0930 hrs to 2 cm sec^{-1} by about 1900 hrs. A corresponding decrease in cross-shelf surface current speeds during the same time period from 4.6 to 0.1 cm sec^{-1} .

After wind direction shifted and wind speeds increased at approximately 1630 hours, a complete reversal in current direction occurred. Alongshore currents had now shifted to the south, reaching a velocity of 16 cm sec^{-1} between depths of 9 and 12 m at midnight on the 22nd. Surface waters were moving shoreward while bottom waters were moving in the offshore direction. These offshore-moving bottom waters reached a maximum velocity of 7.6 cm sec^{-1} just prior to midnight on the 22nd. Alongshore current speeds were moving over twice as fast (16.0 cm sec^{-1}) as the alongshore currents during this time.

Between 0730 and 1530 hrs on 22 August a weak pycnocline was present between 6 and 9 m depth (Fig.30). High density bottom waters were being upwelled, replacing offshore-moving surface waters of lower density. As the winds changed direction from the southwest to the northeast, the pycnocline disappeared, and the water column became weakly stratified with a change of only 1 sigma-t unit between surface and bottom waters.

FIGURE 30. Contour Plots of Water Density (Top Figure, in Sigma-T Units), Alongshore Current Velocity (Middle Figure, in cm sec^{-1} , Poleward is Positive), and Cross-Shore Current Velocity (Bottom Figure, in cm sec^{-1} , Offshore is Positive). Due to Rough Seas, the 0330 hr Sampling Time was Skipped and Sampling was Resumed at 0430 hrs.



As wind speed gradually increased from the northeast during the afternoon and evening of the 22nd, a pycnocline was advected back into the sampling site at approximately 4 m. This pycnocline appeared to correspond to a frontal zone separating downwelling waters from low density surface waters that were being transported back onshore. Throughout the night and into the morning of 23 August, the pycnocline depth gradually increased as low density surface waters continued to move onshore and be downwelled.

Tellina agilis

The contour plots of Figure 30 have been overlain atop larval distributions in Figures 31-43. Larvae of the dwarf tellin clam, *Tellina agilis*, were found in relatively high concentrations ($>2500 \text{ m}^{-3}$) during the morning and afternoon of 22 August between 3 and 11 m depth (Fig.31). The depth range of this concentration corresponded roughly to the depth of the pycnocline. Those larvae found above 6 m were being transported north and offshore, while larvae below 6 m were caught in shoreward-moving bottom waters. Between 1530 and approximately 2230 hrs, larval concentrations decreased, becoming more uniformly distributed throughout the water column with a maximum concentration of about $1250 \text{ larvae m}^{-3}$. This was also the time when the winds shifted and the water column became more uniformly stratified. Between 2330 and 0130 hrs a reoccurrence of a high concentration ($>2500 \text{ larvae m}^{-3}$) larval cloud was seen within a meter of the bottom, in swiftly moving offshore-flowing bottom waters. After 2330 hrs, as low density waters were found throughout the water column, *T. agilis* numbers once again decreased to less than $750 \text{ larvae m}^{-3}$ throughout the water column.

Cyrtopleura costata

Contour plots of *Cyrtopleura costata*, the angel wing clam (Fig.32), suggest that

FIGURE 31. Density Distributions for Larvae of the Bivalve *Tellina agilis* With Overlays of Physical Measurements (as in Figure 30). Due to Rough Seas, the 0330 hr Sampling Time was Skipped and Sampling was Resumed at 0430 hrs.

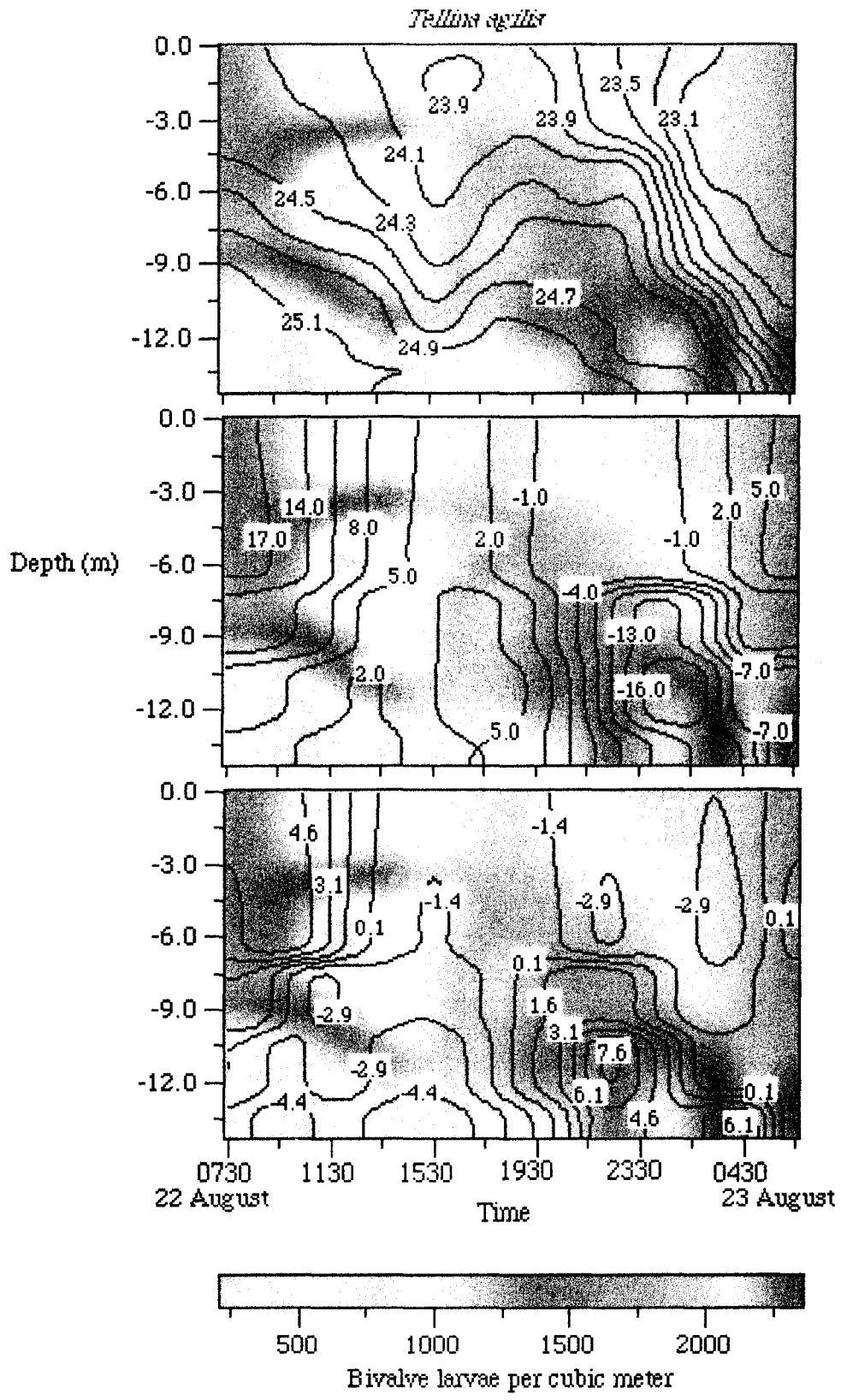
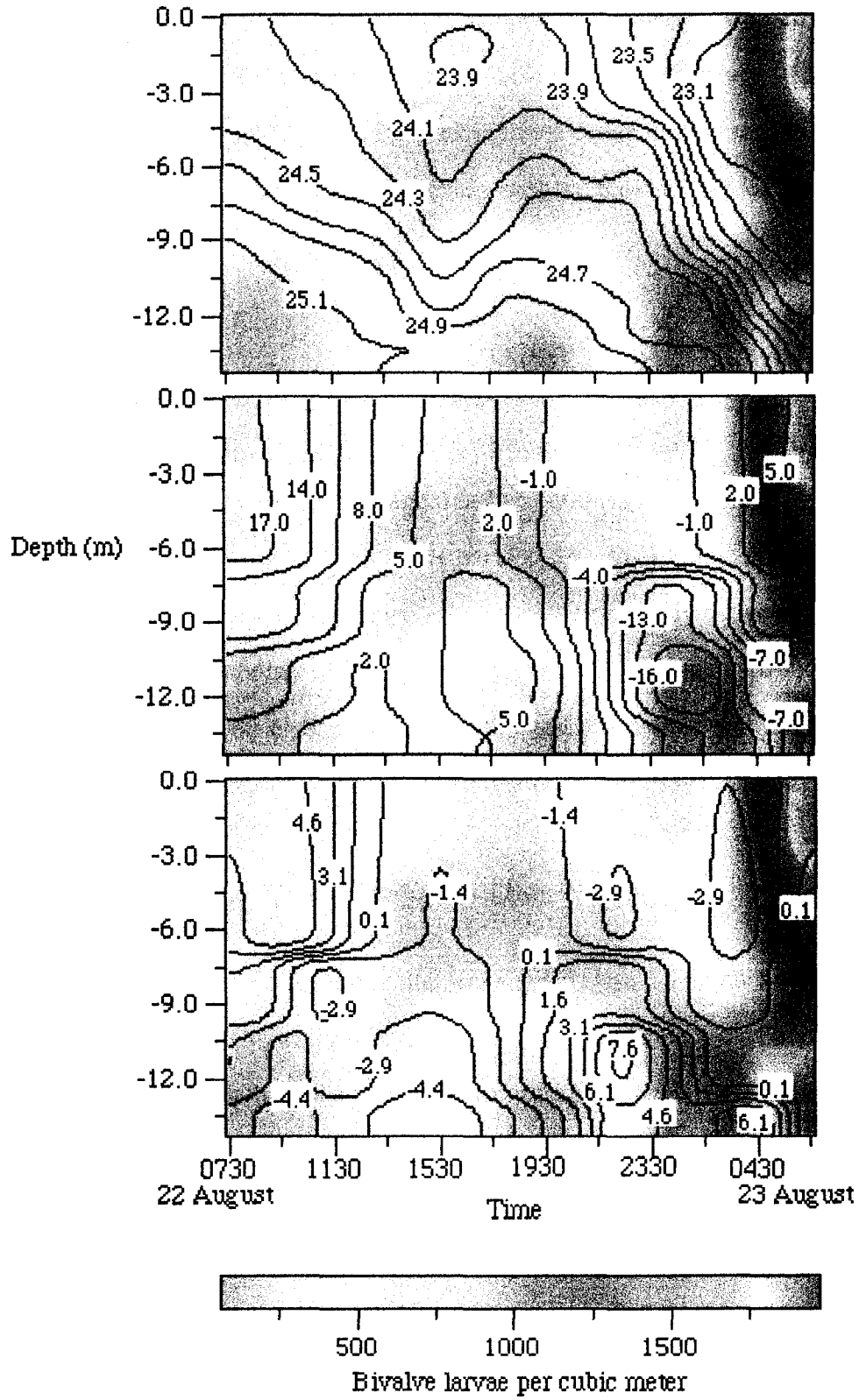


FIGURE 32. Density Distributions for Larvae of the Bivalve *Cyrtopleura costata* With Overlays of Physical Measurements (as in Figure 30). Due to Rough Seas, the 0330 hr Sampling Time was Skipped and Sampling was Resumed at 0430 hrs.

Cyrtopleura costata



larvae were following isopycnals over much of the 23 hour period. From just after 1130 hrs until 0430 hrs on the 23rd, the highest concentration of larvae (between 700-1050 larvae m^{-3}) was found between the 23.9 and 24.7 isopycnals. Between 0430 hrs and the termination of sampling at 0630 hrs, the peak in larval concentration moved up from the bottom and became concentrated in low density onshore-moving surface waters at greater than 1750 larvae m^{-3} .

Spisula solidissima

Between 0730 and 1730 hours on 22 August, larvae of the surf clam, *Spisula solidissima*, were found in relatively high numbers (500-800 m^{-3}) in northward-moving waters, gradually increasing in depth with time (Fig.33). During this time, the center of larval mass seemed to follow the pycnocline, remaining primarily between the 24.5 and 25.1 isopycnals. The majority of larvae were concentrated in shoreward-moving bottom waters. When the currents changed direction, the vast majority of *S. solidissima* larvae were no longer in the sampling area, with larval concentrations dropping to $<200 m^{-3}$.

Mya arenaria

Concentrations of *Mya arenaria*, the soft-shelled clam, were much lower than the other bivalves (Fig.34). Maximum concentration was 300 larvae m^{-3} , but on average, concentrations were usually closer to 125 larvae m^{-3} . Larvae tended to remain below the 24.3 isopycnal, either within or below the pycnocline. At this depth, larvae were initially caught in shoreward-moving bottom waters, but once currents changed direction, they were then being transported offshore along the bottom. Two relatively high concentration larval clouds were apparent. One was between 4 and 6 m depth at 0730 hrs. These larvae were caught in the northward-moving current traveling up to $17 cm sec^{-1}$ and offshore at

FIGURE 33. Density Distributions for Larvae of the Bivalve *Spisula solidissima* With Overlays of Physical Measurements (as in Figure 30). Due to Rough Seas, the 0330 hr Sampling Time was Skipped and Sampling was Resumed at 0430 hrs.

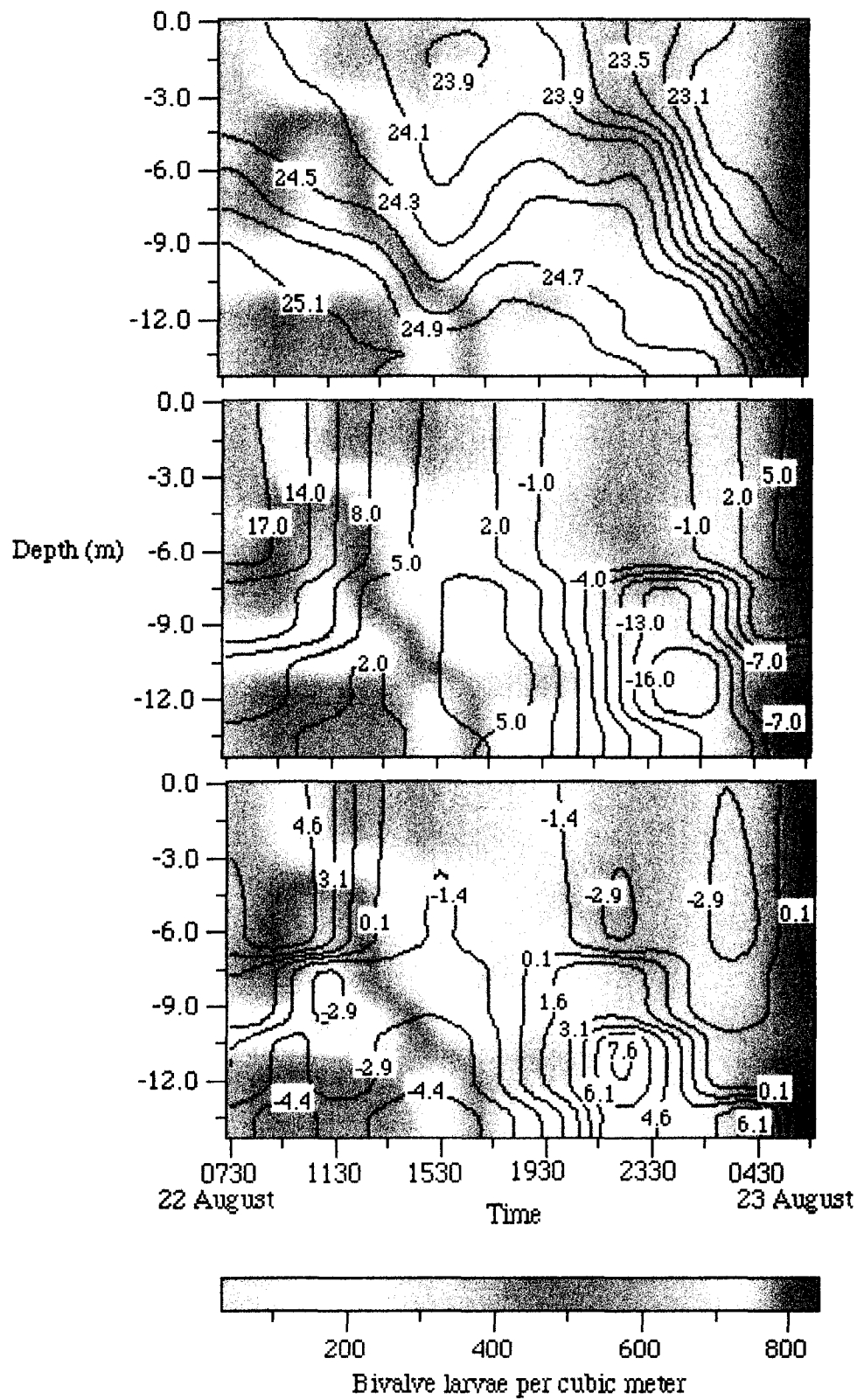
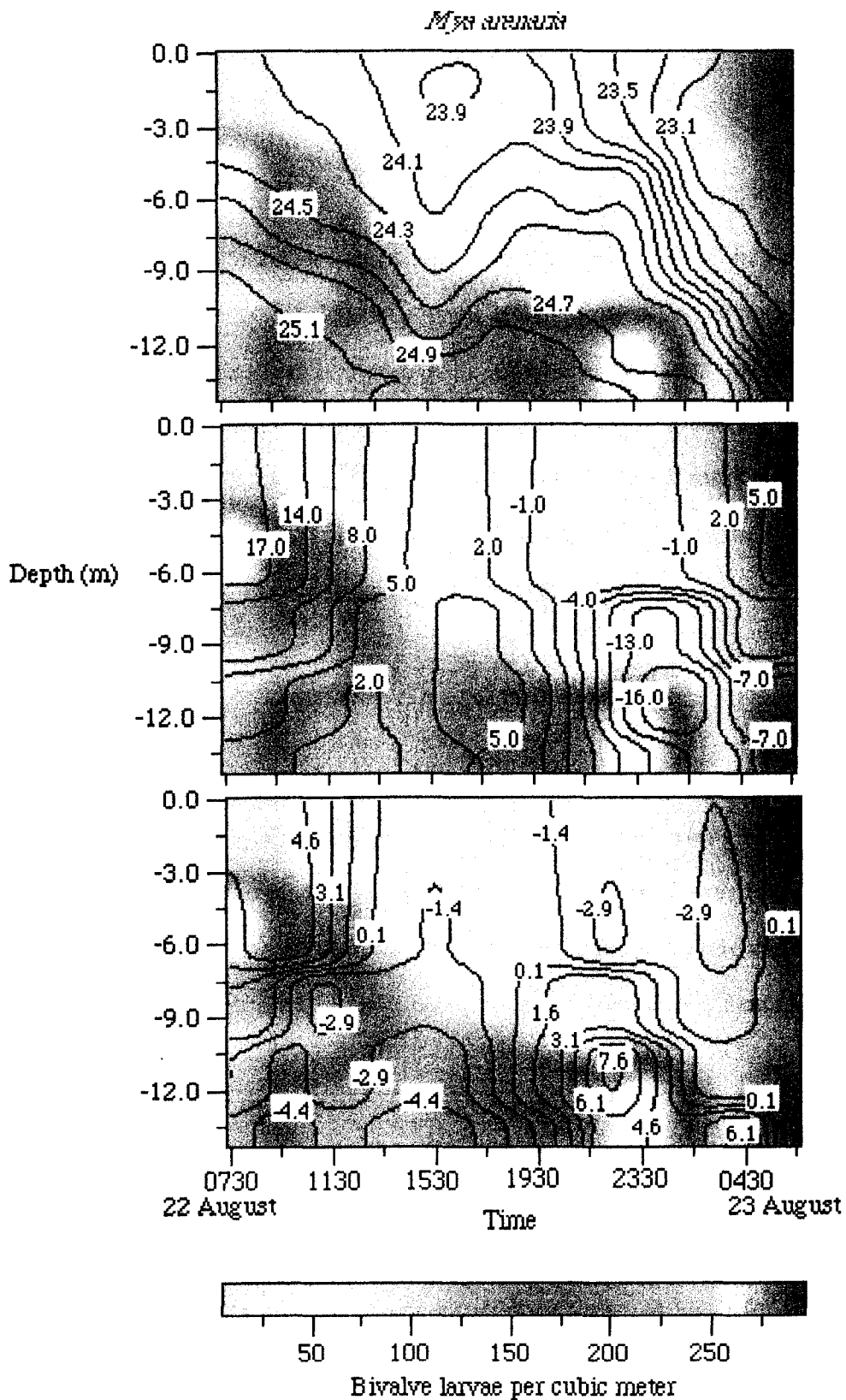
Spisula solidissima

FIGURE 34. Density Distributions for Larvae of the Bivalve *Mya arenaria* With Overlays of Physical Measurements (as in Figure 30). Due to Rough Seas, the 0330 hr Sampling Time was Skipped and Sampling was Resumed at 0430 hrs.



4.6 cm sec⁻¹. The other cloud was found in offshore-moving bottom waters, between 12 m and the bottom, just prior to midnight on the 22nd.

Mulinia lateralis

Mulinia lateralis, the dwarf surf clam, is another bivalve whose larvae appear to have followed density isopleths (Fig.35). In general, the majority of larvae tended to remain below the 24.1 isopycnal, thereby avoiding the lower density waters that dominated the water column from about 2330 hrs on. As the density contours gradually deepened throughout the day on 22 August, the depth of the center of larval mass gradually deepened as well. Very few larvae (<200 m⁻³) were found after 0430 hrs once the water column had become dominated by shoreward-moving lower density waters.

Littorina spp.

Larvae of the gastropod genus *Littorina*, at least two species of which were positively identified, were seen in relatively high concentrations (>900 m⁻³) only briefly during the 23 hour period (Fig.36). Between 0730 and 1330 hrs, a larval cloud was found within the pycnocline, caught between offshore-moving surface waters and shoreward-moving bottom waters. After this time, larval concentrations dropped to less than 500 larvae m⁻³ for the remainder of the study period.

Hydrobia sp.

The gastropod *Hydrobia sp.* exhibited a surprisingly similar larval distribution to that of *Littorina spp.* (Fig.37). Although concentrations were much lower for *Hydrobia sp.* than for *Littorina spp.* (max. concentration of 470 larvae m⁻³ compared to >1200 m⁻³ for *Littorina spp.*), *Hydrobia's* peak concentration was located in the same location as that of

FIGURE 35. Density Distributions for Larvae of the Bivalve *Mulinia lateralis* With Overlays of Physical Measurements (as in Figure 30). Due to Rough Seas, the 0330 hr Sampling Time was Skipped and Sampling was Resumed at 0430 hrs.

Mulinia lateralis

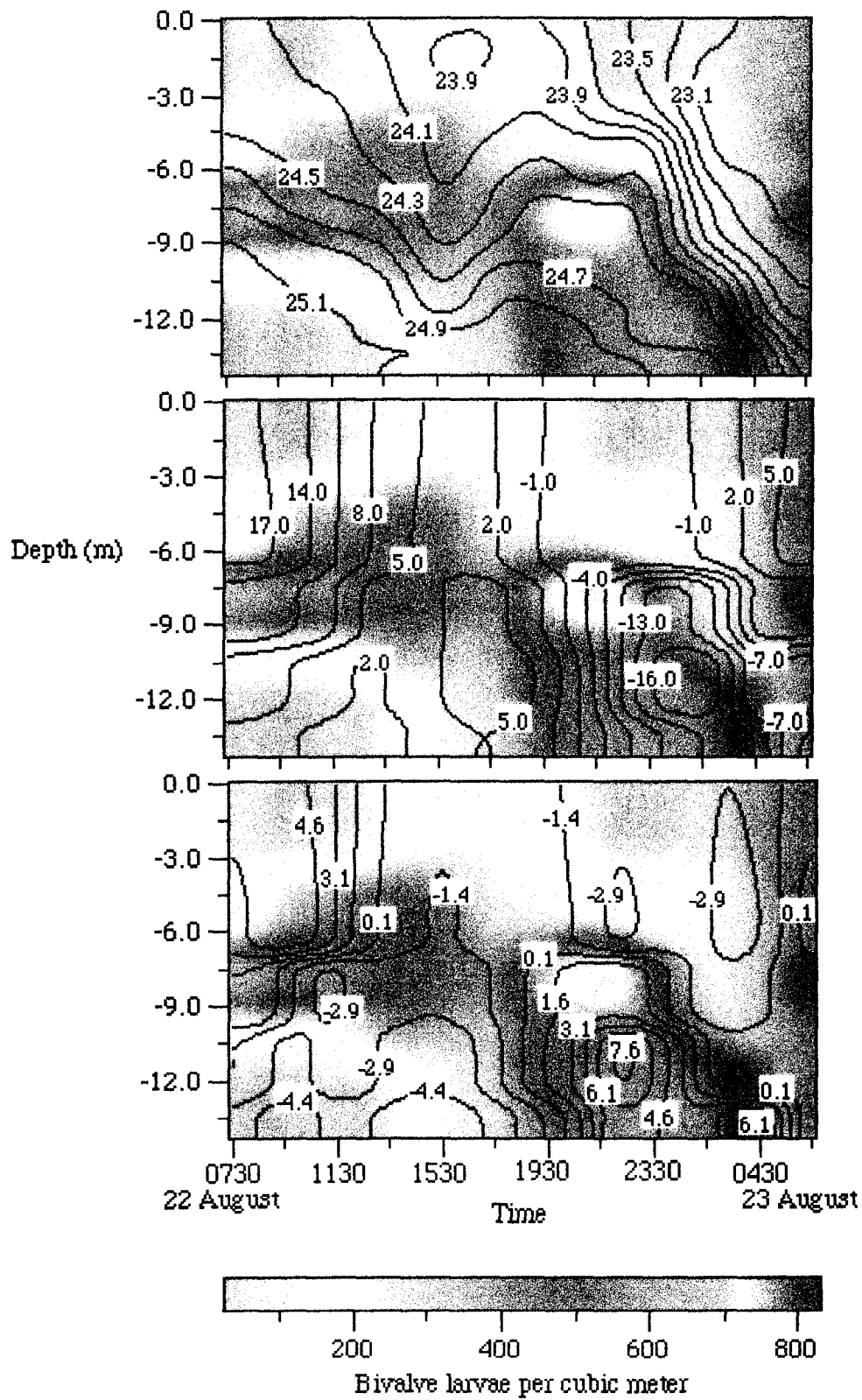


FIGURE 36. Density Distributions for Larvae of the Gastropod *Littorina spp.* With Overlays of Physical Measurements (as in Figure 30). Due to Rough Seas, the 0330 hr Sampling Time was Skipped and Sampling was Resumed at 0430 hrs.

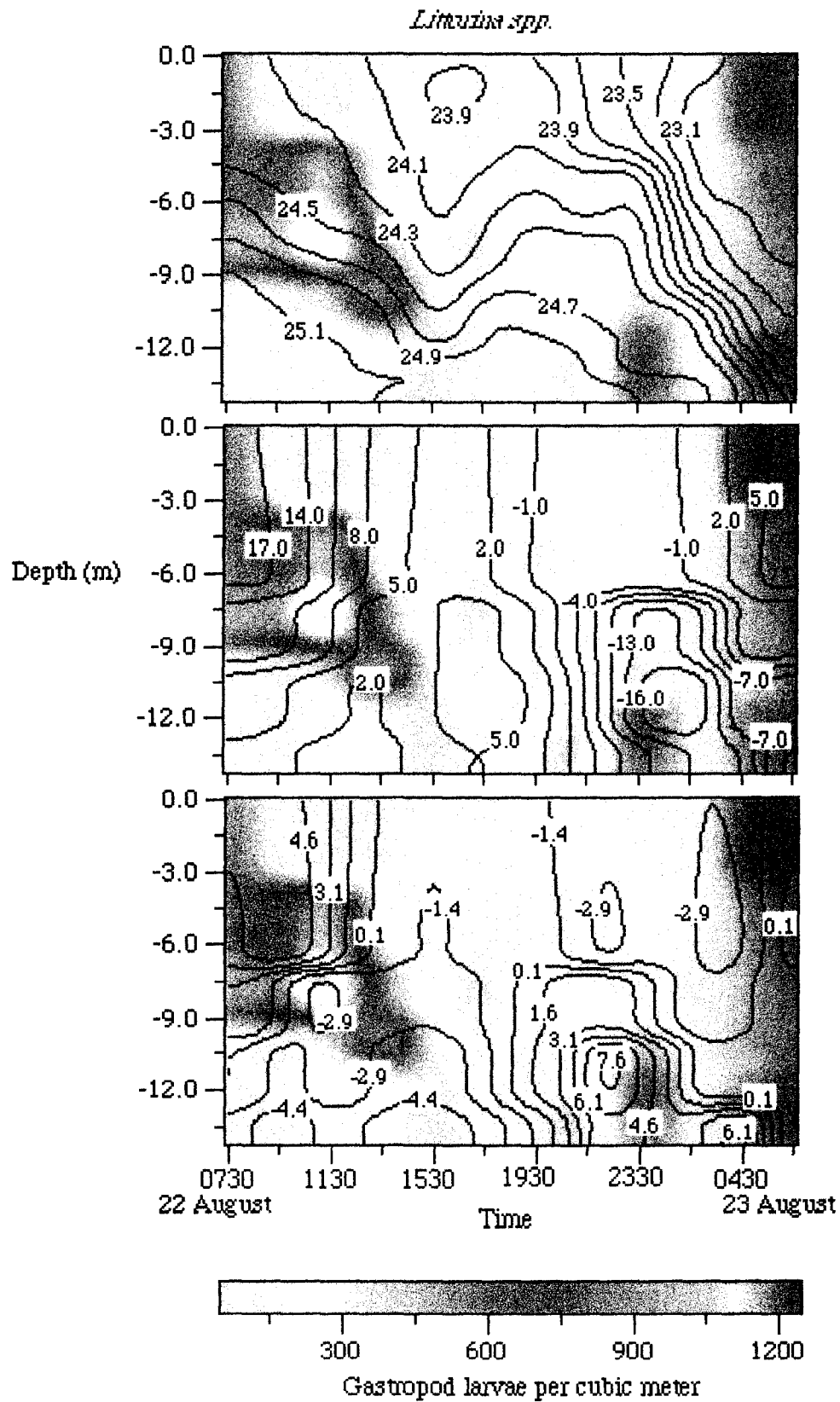
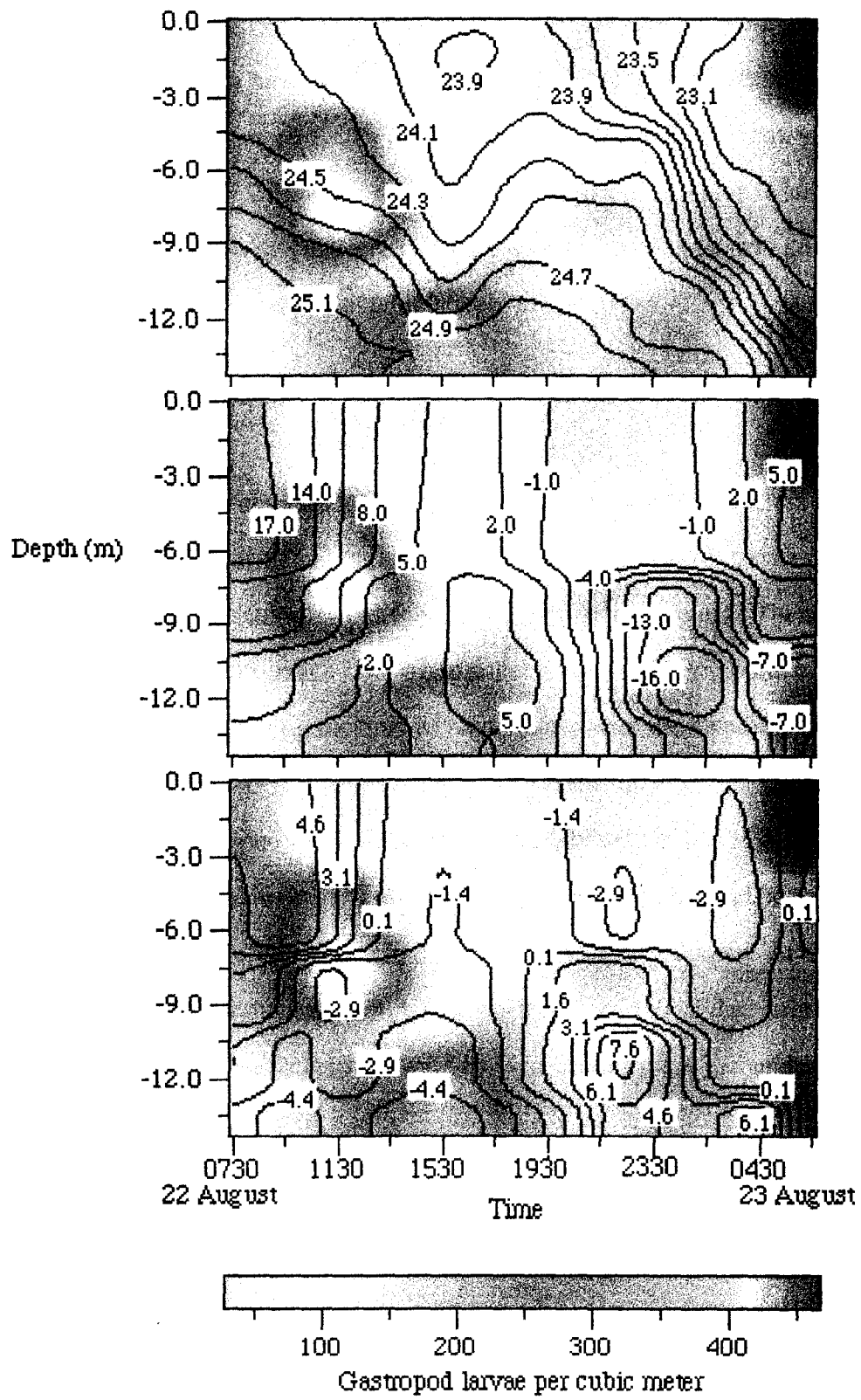


FIGURE 37. Density Distributions for Larvae of the Gastropod *Hydrobia sp.* With Overlays of Physical Measurements (as in Figure 30). Due to Rough Seas, the 0330 hr Sampling Time was Skipped and Sampling was Resumed at 0430 hrs.

Hydrobia sp.



Littorina spp., namely at 7.5 m, between the 24.5 and 24.7 isopycnals at 1130 hrs. Larvae at this depth were caught between surface waters moving offshore at the rate of 0.1-3.1 cm sec⁻¹, and bottom waters moving shoreward at a comparable speed. Between 1230 and 1430 hrs, larvae became more evenly distributed within the water column, with an average concentration of roughly 250 larvae m⁻³. Between 1430 and 1730 hrs, a larval cloud of approximately 350 larvae m⁻³ appeared near the bottom, but was quickly gone and from then on larval concentrations remained relatively low, <200 m⁻³.

Odostomia sp.

Larvae of the gastropod *Odostomia sp.* were found in lower concentrations than any of the other gastropods, with a maximum concentration of only 340 larvae m⁻³ (Fig.38). Despite this low concentration, two distinct larval clouds were found. The first was centered between 9 and 11 m at 1730 hrs, in water that was moving north along the coast at 5 cm sec⁻¹. This was during the time when bottom waters were undergoing a change in current direction, from moving onshore to gradually moving offshore. Larval concentrations then dropped for a period of roughly 6 hours until 0130 hrs when wind speeds had reached a maximum of 5 m sec⁻¹ and the water column had become less stratified with the depth of the pycnocline getting progressively deeper. At this time, larval concentrations reached a maximum of 340 m⁻³ in the upper half of the water column. Within this larval cloud surface waters were moving shoreward at just under 3 cm sec⁻¹.

Bittium sp.

The majority of larvae of the gastropod *Bittium sp.* remained above the 24.3 isopycnal, above the higher density bottom waters (Fig.39). In fact the highest concentrations of *Bittium sp.* larvae were concentrated around the 23.9 isopycnal. On two

FIGURE 38. Density Distributions for Larvae of the Gastropod *Odostomia sp.* With Overlays of Physical Measurements (as in Figure 30). Due to Rough Seas, the 0330 hr Sampling Time was Skipped and Sampling was Resumed at 0430 hrs.

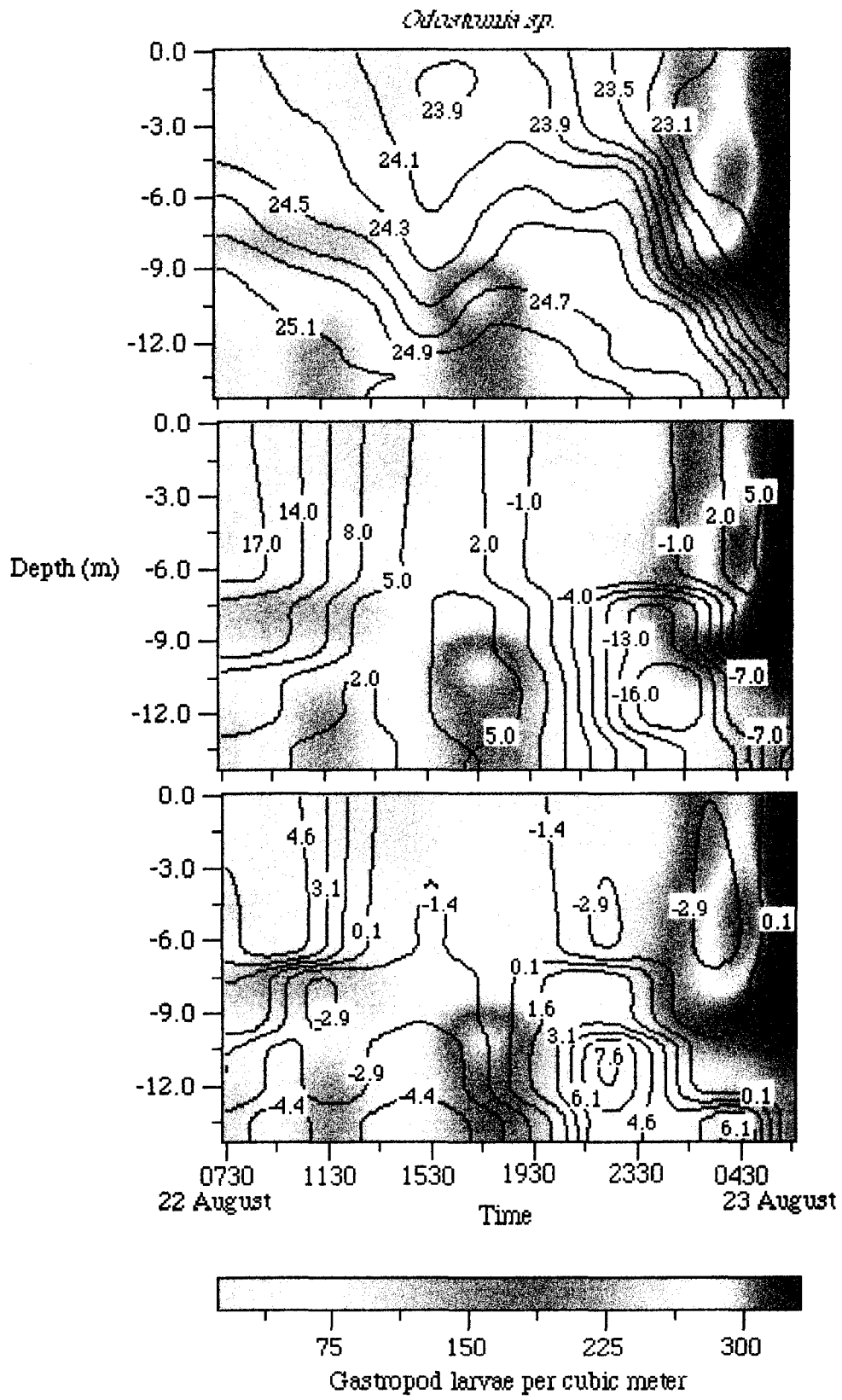
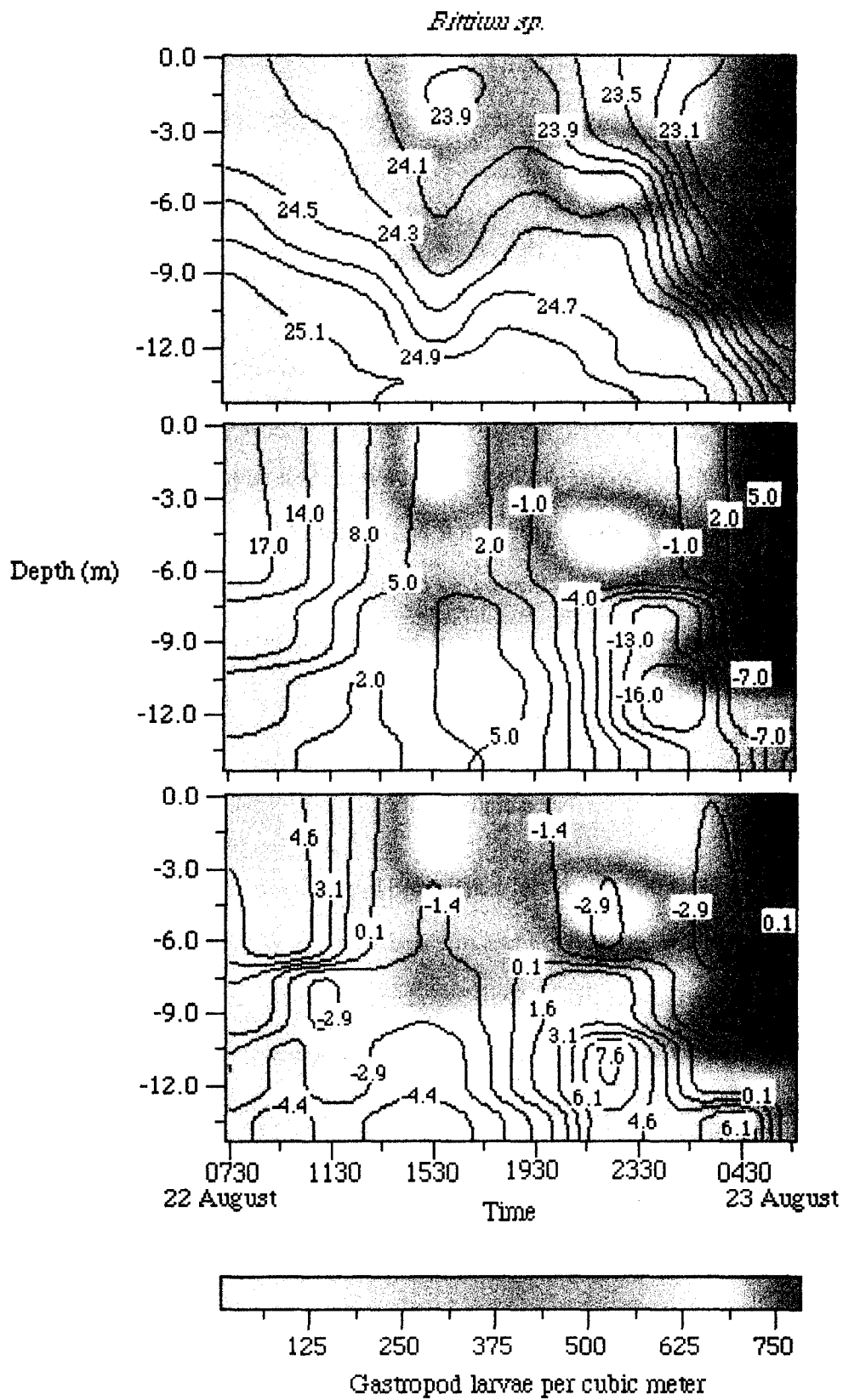


FIGURE 39. Density Distributions for Larvae of the Gastropod *Bittium sp.* With Overlays of Physical Measurements (as in Figure 30). Due to Rough Seas, the 0330 hr Sampling Time was Skipped and Sampling was Resumed at 0430 hrs.



separate occasions, once at 1530 hrs and then again at 2130-2330 hrs, high concentration ($750 \text{ larvae m}^{-3}$) larval clouds were sampled, both of which were centered in and around the 23.9 isopycnal. The remainder of the time, concentrations ranged from as much as $450 \text{ larvae m}^{-3}$ above the pycnocline to 0 larvae below the pycnocline and near the bottom.

Pectinereidae

Pectinereid polychaete larvae tended to remain either within or above the pycnocline at water densities above 24.9 (Fig.40). Except for two small larval patches of relatively high concentrations ($>200 \text{ larvae m}^{-3}$) in the morning of 22 August, larvae were relatively evenly distributed between the surface and 9 m, with densities averaging $100 \text{ larvae m}^{-3}$. Despite the change in current direction and speed midday on the 22nd, larvae remained in the upper $2/3$ of the water column. Larval concentrations below 9 m rarely got above 50 larvae m^{-3} .

Phyllodocidae

Highest densities of phyllodocid polychaete larvae ($>1500 \text{ m}^{-3}$) were consistently found lower in the water column, between 9 m and the bottom, where water densities were highest (Fig.41). Very few larvae were found above 6 m, and between 1130 and 2230 hrs no phyllodocid larvae were encountered in the upper 3 m of water where water densities were generally lower than 24.1. Larvae were able to remain near the bottom throughout the 23 hours despite the shift in current direction and speed at these depths.

Spionidae

Spionid polychaete larvae had a distribution that in many ways resembled that of the phyllodocids (Fig.42). No larvae were encountered between 1130 and 1930 hrs in low

FIGURE 40. Density Distributions for Pectinereid Polychaete Larvae With Overlays of Physical Measurements (as in Figure 30). Due to Rough Seas, the 0330 hr Sampling Time was Skipped and Sampling was Resumed at 0430 hrs.

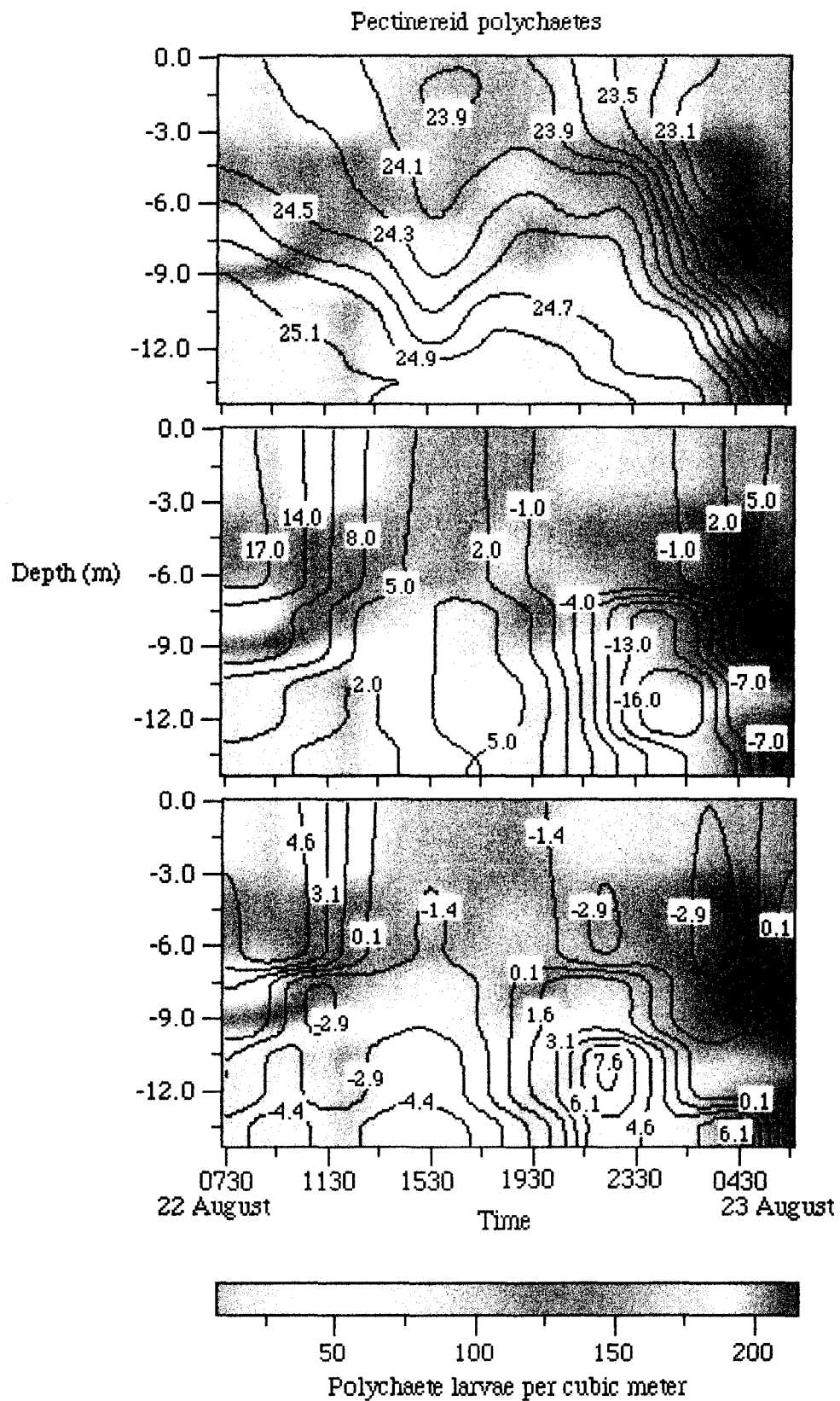


FIGURE 41. Density Distributions for Phyllodocid Polychaete Larvae With Overlays of Physical Measurements (as in Figure 30). Due to Rough Seas, the 0330 hr Sampling Time was Skipped and Sampling was Resumed at 0430 hrs.

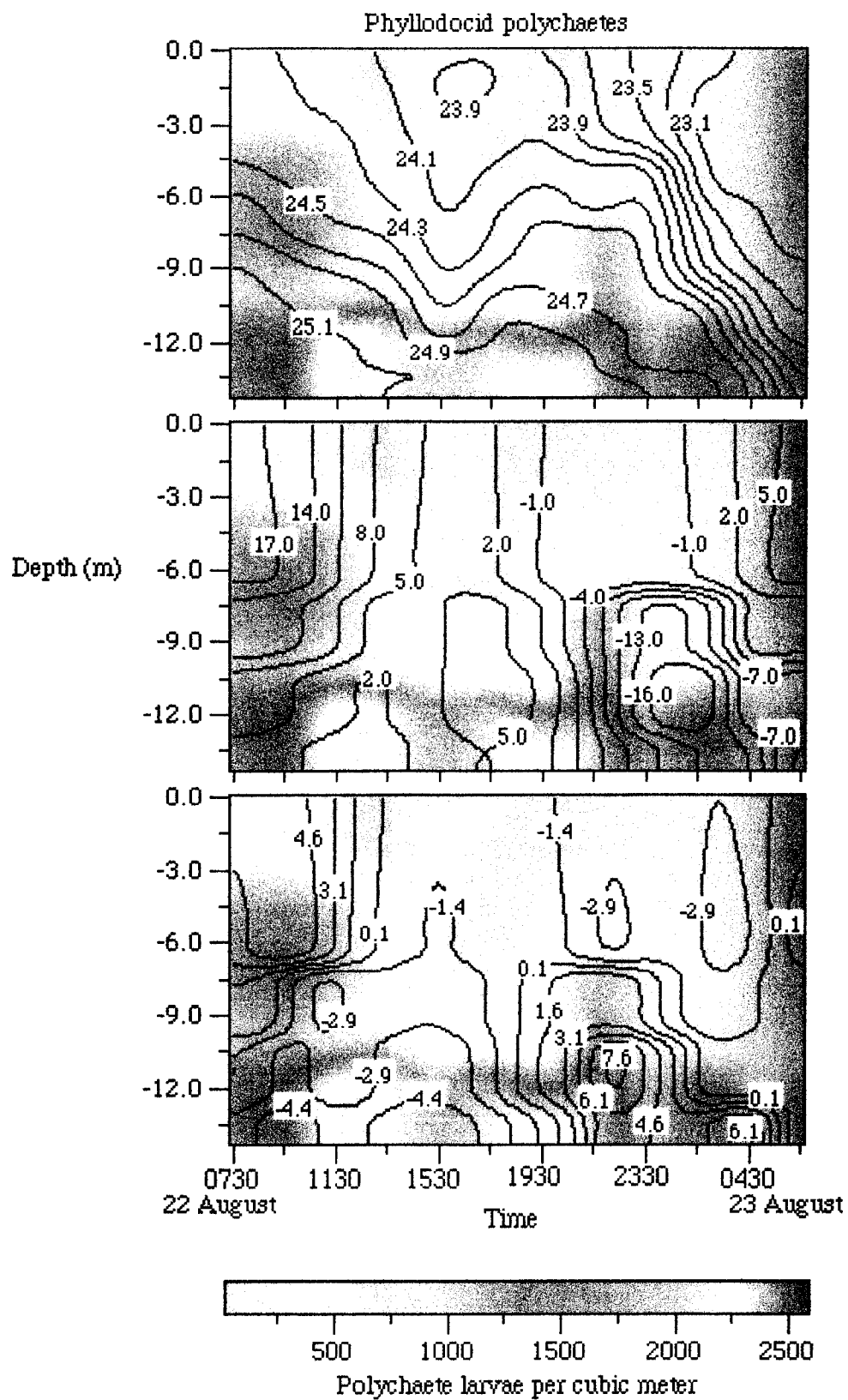
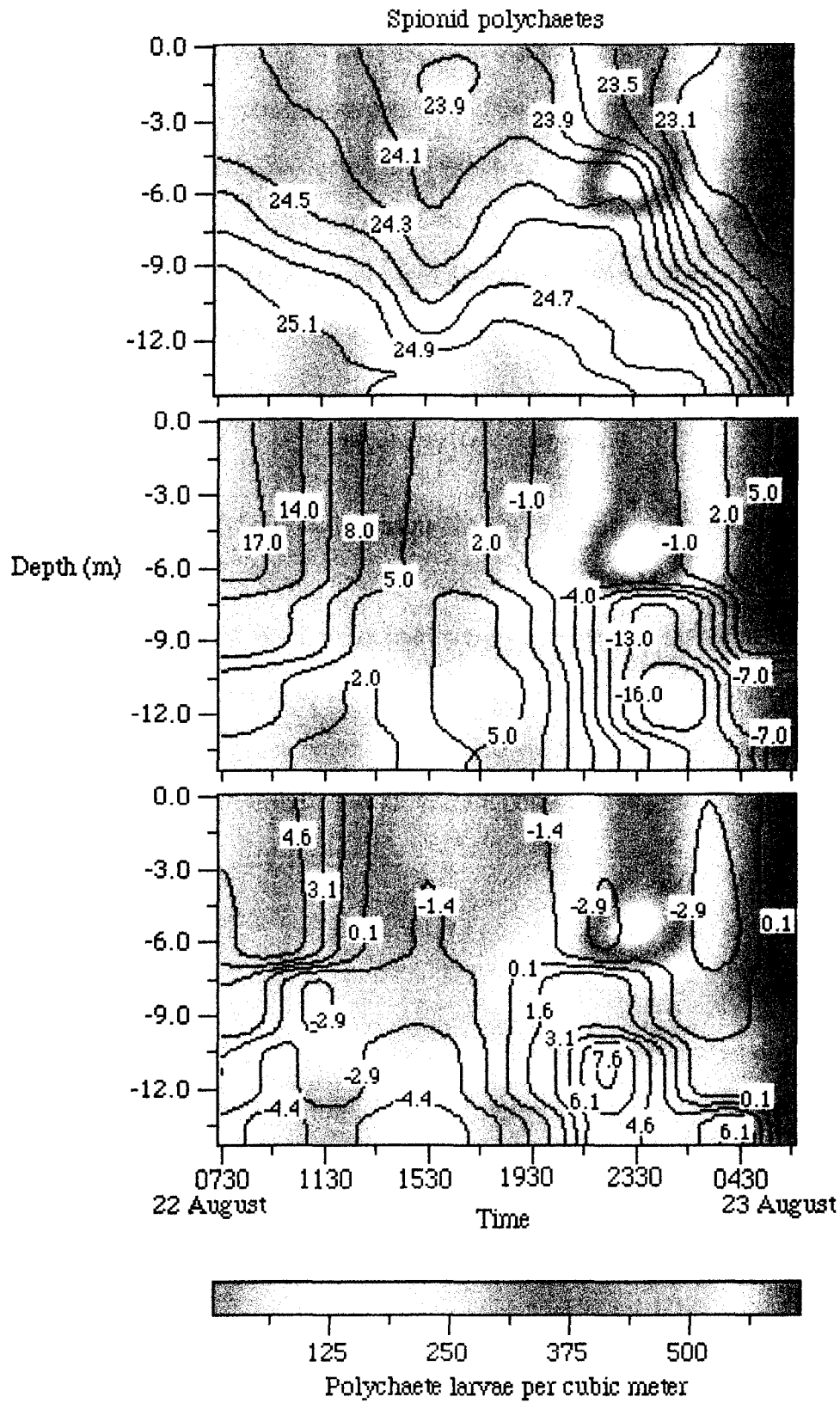


FIGURE 42. Density Distributions for Spionid Polychaete Larvae With Overlays of Physical Measurements (as in Figure 30). Due to Rough Seas, the 0330 hr Sampling Time was Skipped and Sampling was Resumed at 0430 hrs.



density (<24.3 sigma-t) water between the surface and 6 m. Until 1930 hrs, slightly higher concentrations (~ 250 larvae m^{-3}) were encountered between 12 m and the bottom. From that time on, larval concentrations dropped to <100 larvae m^{-3} throughout the water column except for a larval cloud (>500 larvae m^{-3}) which appeared just before midnight between 4 and 6m depth, within the frontal zone. As wind speeds increased and the water became more homogeneous, this cloud disappeared and concentrations dropped to less than 70 larvae m^{-3} by the end of the study at 0630 hrs.

Polychaete Trochophores

Throughout the 23 hour study period, the vast majority of polychaete trochophores ($750-1400$ larvae m^{-3}) remained near the bottom, below the 24.5 isopycnal (Fig.43). Concentrations above this density isopleth rarely got above 250 larvae m^{-3} and at many sample depths these larvae were absent. The highest concentration of larvae (>1250 m^{-3}) occurred within a meter of the bottom during the time when currents had begun to change direction, i.e. during the period when shoreward currents were moving at 4.4 $cm\ sec^{-1}$ and then shifted offshore at only 1.6 $cm\ sec^{-1}$.

Size Frequencies

The size frequency data for the bivalve larvae enabled ontogenetic differences in vertical distributions to be determined. Measuring lengths and creating size frequency histograms indicated whether or not the same size cohort was present between surface and bottom waters. Size frequency histograms for *Tellina agilis* (Fig.44) clearly show a bimodal distribution for those larvae in the upper half of the water column as well as those within the lower half of the water column. Distinct size peaks are evident in the 160-170 μm and the 200-210 μm size classes. Although the two distributions look nearly identical,

FIGURE 43. Density Distributions for Polychaete Trochophores With Overlays of Physical Measurements (as in Figure 30). Due to Rough Seas, the 0330 hr Sampling Time was Skipped and Sampling was Resumed at 0430 hrs.

Polychaete trochophores

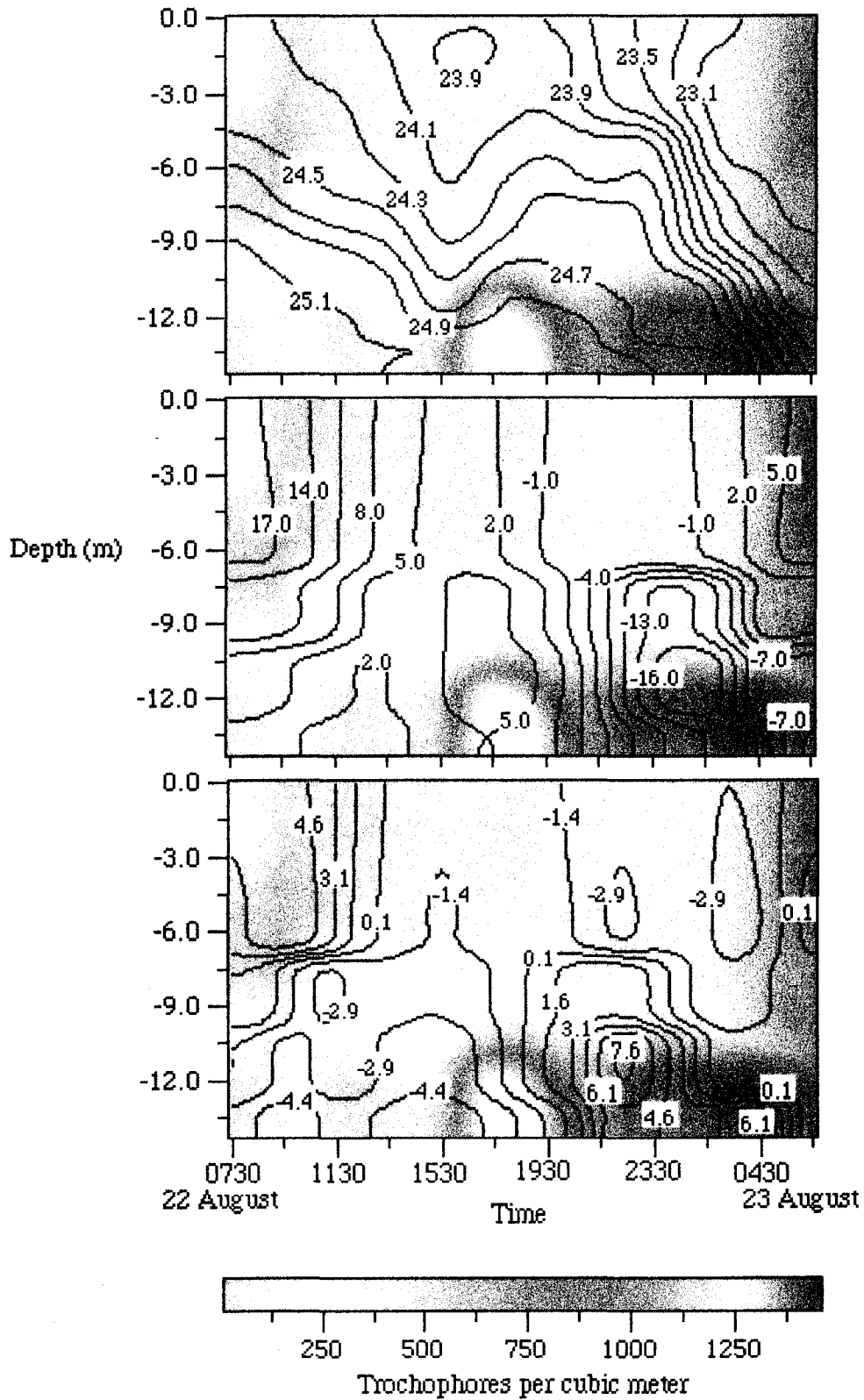
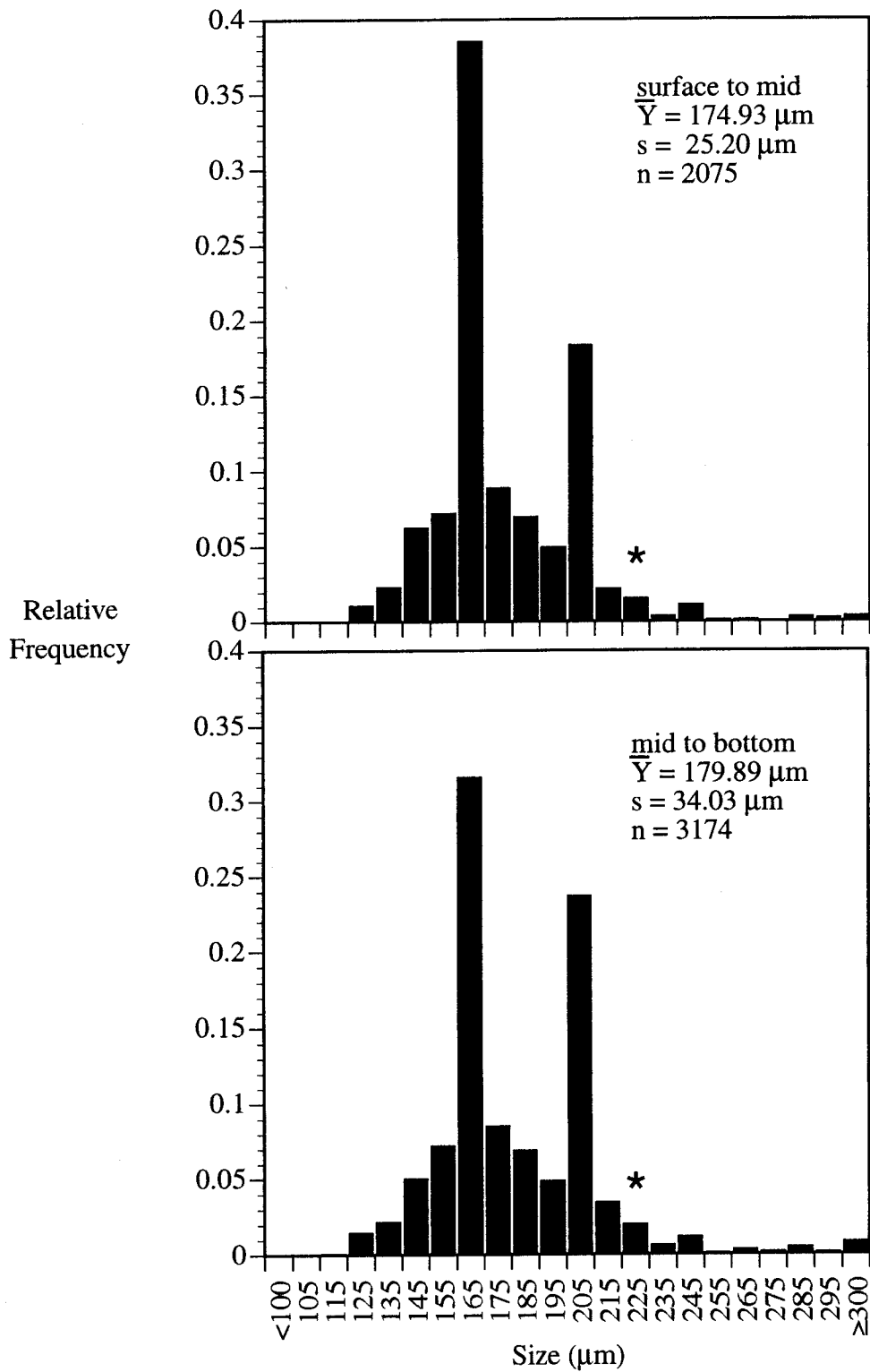


FIGURE 44. Size Frequency Histograms for Larvae of the Bivalve *Tellina agilis*. Asterisks Represent Average Size at Settlement. Sizes Shown Indicate the Mid-Point of the Range for Each Size Bin.

Tellina agilis



a t-test indicated that the two means were significantly different ($t = 1.96$, $P < 0.001$, $df = 5167$). Slightly larger individuals were found in the lower half of the water column.

Cyrtopleura costata had length frequency distributions very similar to those for *T. agilis* (Fig.45). The same two size classes, 160-170 μm and 200-210 μm , contained the highest percentage of larvae. The two sample means were also found to be significantly different ($t = 1.96$, $P < 0.001$, $df = 3028$). The mean size of larvae in the lower half of the water column was almost 10 μm larger than those in the upper layers.

Four peaks in the length frequency distributions of *Spisula solidissima* were evident from the histograms (Fig.46): in the 160-170 μm , 200-210 μm , 240-250 μm , and 280-290 μm size ranges. Over 25% of larvae in the lower half of the water column were found to be between 160-170 μm long, while just over 18% of larvae in the surface layers were in this same size class. The sample means of the two groups were not significantly different ($t = 1.96$, $P = 0.10$, $df = 706$).

Nearly $\frac{1}{3}$ of all the larvae of *Mya arenaria* were found to be in the 160-170 μm size bin, regardless of depth (Fig.47). There was, however, a much higher percentage of larvae between 190 and 200 μm residing in the upper half of the water column than there were nearer the bottom (>14% vs. 4%, respectively). Despite this difference in the two distributions, the two means were not significantly different ($t = 1.96$, $P = 0.79$, $df = 533$).

Larvae of *Mulinia lateralis* were found in a smaller size range than were other bivalve larvae. Most individuals were between 125 and 205 μm (Fig.48). Well over half of all larvae sampled, regardless of depth, were between 160 and 170 μm long. Not surprisingly, the two sample means were not significantly different ($t = 1.96$, $P = 0.70$, $df = 810$).

FIGURE 45. Size Frequency Histograms for Larvae of the Bivalve *Cyrtopleura costata*. Asterisks Represent Average Size at Settlement. Sizes Shown Indicate the Mid-Point of the Range for Each Size Bin.

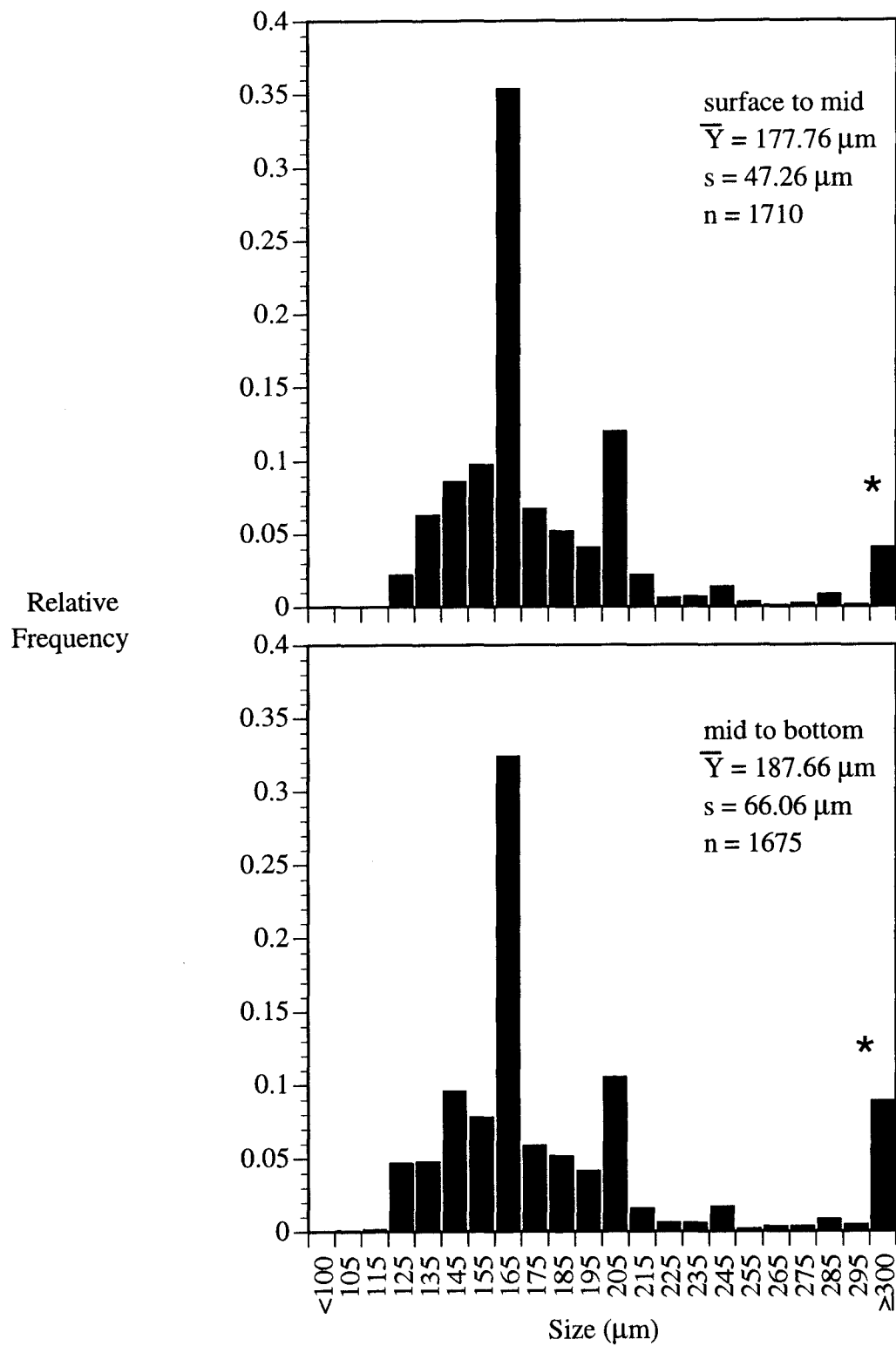
Cyrtopleura costata

FIGURE 46. Size Frequency Histograms for Larvae of the Bivalve *Spisula solidissima*. Asterisks Represent Average Size at Settlement. Sizes Shown Indicate the Mid-Point of the Range for Each Size Bin.

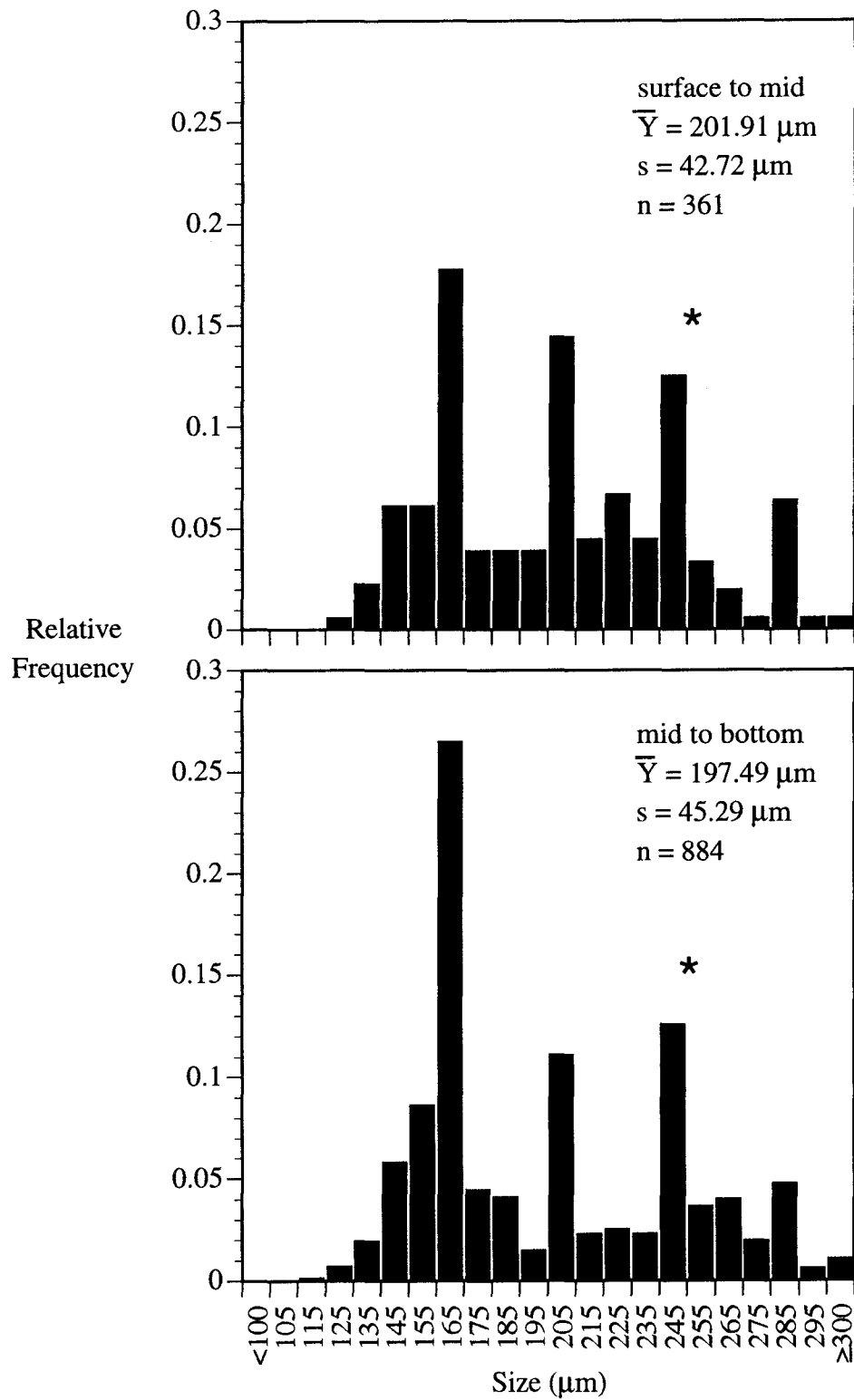
Spisula solidissima

FIGURE 47. Size Frequency Histograms for Larvae of the Bivalve *Mya arenaria*. Asterisks Represent Average Size at Settlement. Sizes Shown Indicate the Mid-Point of the Range for Each Size Bin.

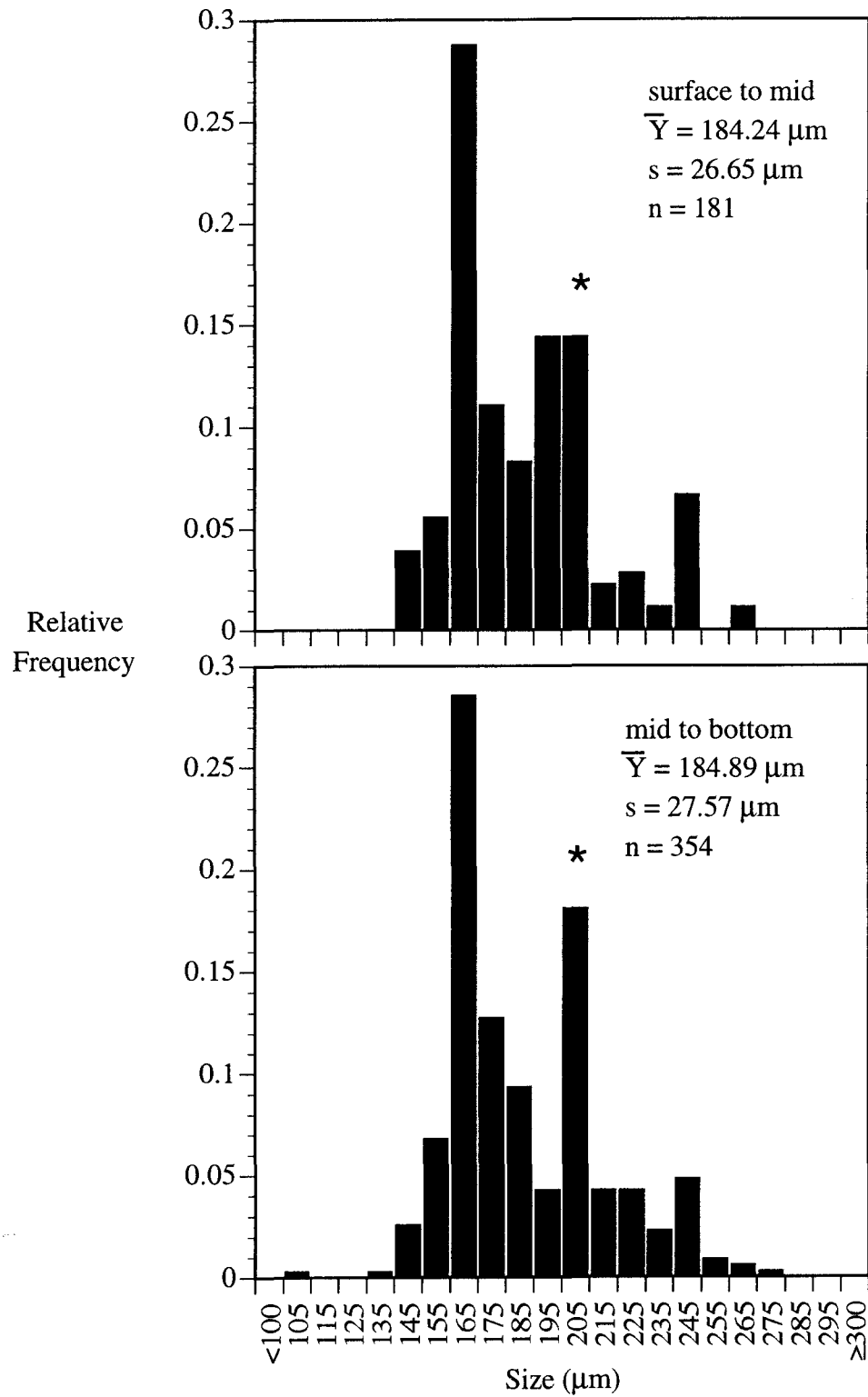
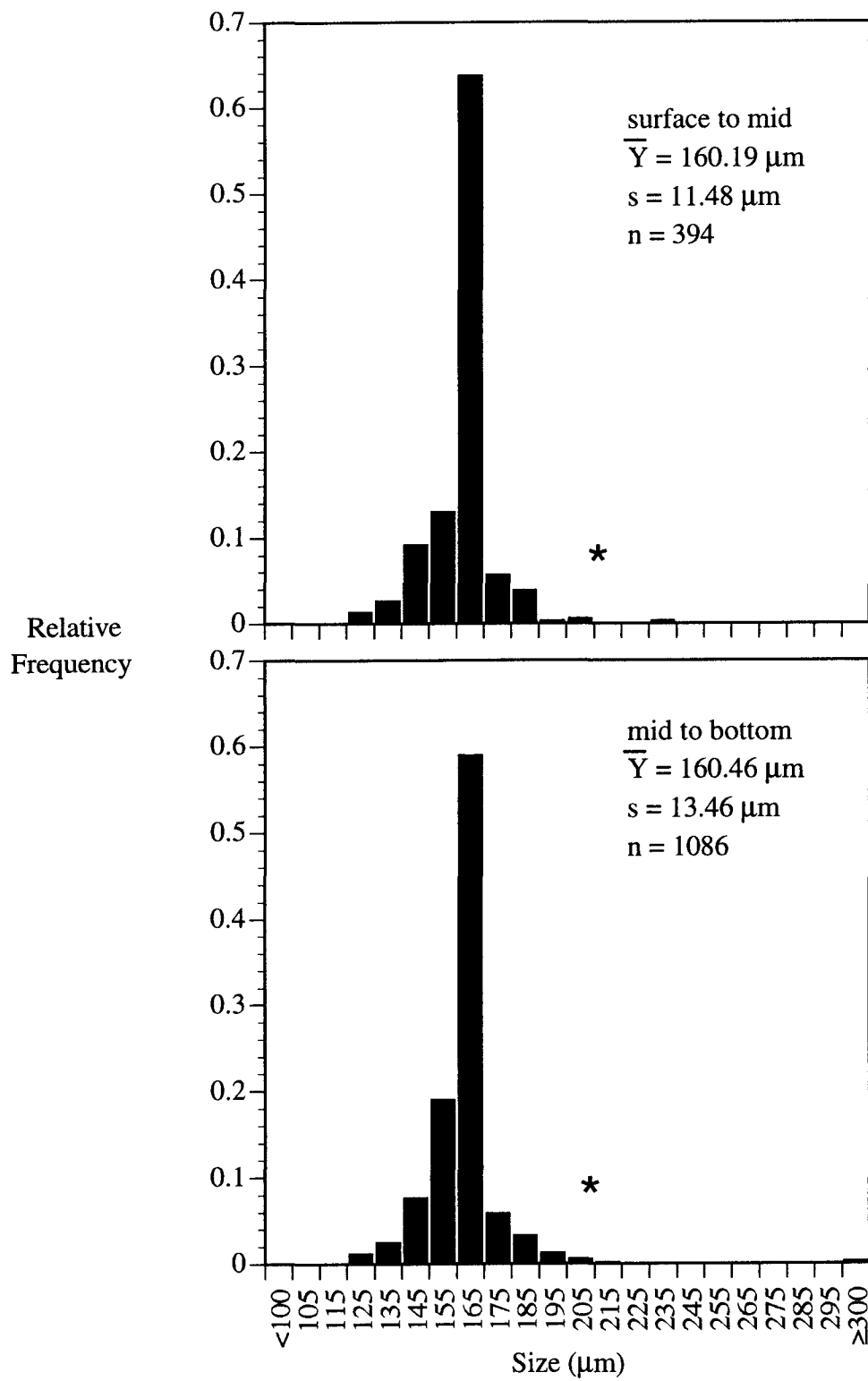
Mya arenaria

FIGURE 48. Size Frequency Histograms for Larvae of the Bivalve *Mulinia lateralis*. Asterisks Represent Average Size at Settlement. Sizes Shown Indicate the Mid-Point of the Range for Each Size Bin.

Mulinia lateralis

Discussion

Much of the research on vertical migration has been carried out in either lab settings or in freshwater lakes or seaside embayments (Hardy & Bainbridge, 1954; Enright & Hamner, 1967; Mills, 1983; Alldredge & King, 1985; Forward, 1985; Lampert & Taylor, 1985; Pennington & Emler, 1986; Levy, 1990; Tremblay & Sinclair, 1990b; Bollens *et al.*, 1992; Barile *et al.*, 1994; Zeng & Naylor, 1996). In these studies, such physical phenomena as the ebb and flow of the tides, upwelling and downwelling, and vertical mixing did not play a role in the migratory behavior of the organisms. A stable water mass was the backdrop for these studies. But continental shelf waters are usually not stable. Changes in wind direction and speed lead to changes in the strength and depth of the pycnocline, vertical mixing, and dramatic changes in current speeds and direction.

Over the course of the 23 hour sampling period, no diel vertical migrations were observed within the sampling area. A few larval types, namely *Odostomia sp.*, *Bittium sp.*, and the spionid larvae, were encountered in the upper half of the water column after dusk (Figs.38, 39, & 42, respectively). But had a typical diel vertical migration occurred, the larvae would have been at depth during the day, would have ascended into surface waters at night, and then migrated back down to depth with the approach of dawn. On the contrary, most larvae were present in high concentrations only during certain periods of time, and were virtually absent from the water column the remainder of the time. The abrupt physical oceanographic changes which occurred during the 23 hour sampling period appeared to have overshadowed any possibility of diel vertical migrations.

Both *Spisula solidissima* and *Littorina spp.* (Figs.33 & 36, respectively) larvae occurred in relatively high numbers prior to the shift in wind and current directions. After the switch their concentrations decreased by more than 50%. *Spisula solidissima* larvae appeared to be descending from surface waters during the morning of the 22nd, perhaps after residing at the surface during the previous night. Once near the bottom, larvae were

transported out of the study site by shoreward-moving bottom waters. *Littorina spp.* larvae also appeared to have been making a descent from surface waters during the morning of 22 August, but once they reached approximately 7 m, they were then in the midst of a shoreward-moving current, and were likely to have been transported in that direction. The decrease in the numbers of *Littorina spp.* larvae that were sampled during the remainder of the study was probably due to the larvae being upwelled and transported north in the alongshore current.

Cyrtopleura costata was found at relatively low concentrations prior to the change in currents (Fig.32). However, once the reversal in current direction occurred, their larval numbers dramatically increased. *C. costata* larvae showed an increase in concentration in the upper half of the water column about the time that the currents changed direction, suggesting that larvae were transported into the study site with shoreward-moving surface waters. From this time on, larvae were concentrated between the 23.9 and 24.7 isopycnals. Larvae were forced progressively deeper as these isopycnals were forced towards the bottom as lower density surface waters moved in near the surface. By 0630 hrs, when the water column was nearly uniform with respect to density, larvae had once again accumulated in the upper half of the water column and larval densities near the bottom were very low. One of two things may have been happening: the larvae may have been swimming vertically into surface waters, thereby avoiding the offshore-moving bottom waters, or the larval cloud at the surface at 0630 hrs is a group of larvae that had just been transported into the study site by shoreward-moving surface waters. It seems likely that a combination of the two events occurred. Undoubtedly some of the larvae present near the bottom at 0130 hrs were transported offshore by the current, while a portion of the larvae present near the surface at 0630 hrs were probably transported to that spot by the surface current. However, between those two times, a small cloud of larvae appear to be swimming upwards out of the shoreward-moving bottom current.

Spionid larvae, like *Cyrtopleura costata* larvae, were found in relatively low concentrations prior to the change in current direction (Fig.42). The relatively high density cloud of spionid larvae at 2330 hrs and the virtual absence of larvae at all other times suggests that these larvae were transported briefly into the area by surface currents, being trapped in the frontal zone between downwelling waters and low density onshore-moving surface waters. These larvae continued to move either shoreward or in the alongshore direction and out of the study site.

The high density cloud of *Odostomia sp.* larvae sampled after midnight would also appear to have been brought into the area by the same surface currents (Fig.38). Other than the small cloud of larvae seen at 1730 hours at 10 m, very few *Odostomia sp.* larvae were encountered in the water column. It appears as though larvae were transported into the sampling area as low density surface waters began to move shoreward with the onset of downwelling.

With each of the five larvae just mentioned (*Cyrtopleura costata*, *Spisula solidissima*, *Littorina spp.*, *Odostomia sp.*, and spionid larvae) the highest densities of larvae were found in shoreward-moving waters (Figs.32, 33, 36, 38, & 42, respectively). In four of these five cases (*C. costata*, *S. solidissima*, *Littorina spp.*, and *Odostomia sp.*) the adult habitat is known to be in either an estuary or the intertidal zone (Abbott, 1974) (without being able to identify the spionid larvae to at least genus, it is difficult to determine their adult habitat). If in fact these larvae are actively vertically migrating, either by sinking or swimming, into these shoreward-moving currents, this would be a means of being retained close to shore and thus close to the adult habitat.

The cues that a larva responds to in order to know when to migrate into these shoreward currents are a mystery. It has been suggested that larvae can respond to changes in current velocities and turbulence (Carriker, 1951). Perhaps the change in current velocities between two water masses (for instance onshore-moving surface waters and

offshore-moving bottom waters) could signal some larvae to sink or swim into these shoreward currents. Here we have a scenario analogous to selective tidal stream transport. Rather than swimming up and down with the ebb and flow of the tide however, some larval types may be responding to current velocities and altering their vertical position accordingly so as to be transported shoreward or towards the mouth of an estuary.

The vast majority of larvae, however, had distributions that appeared to closely follow the density contours. These larvae can be broadly grouped into two categories: those which tended to remain within a narrow density range over the course of the 23 hours, and those which avoided density extremes, such as the low density surface waters or high density bottom waters.

The majority of larvae of the bivalves *Tellina agilis* and *Mulinia lateralis* were found between the 24.1 and 24.9 isopycnals (Figs.31 and 35, respectively). Water density is directly related to temperature and salinity, so by remaining within a narrow density range, the larvae may be avoiding temperatures and salinities that could prove disadvantageous. For instance, a larva that swims into low density waters (corresponding to low salinity and high temperature) may find itself in estuarine plume waters, far from the adult habitat. Some larval types may be unable to survive in water that is perhaps too warm or too saline. Therefore, larvae may be using density to "monitor" their vertical position within the water column.

Salinity has typically been suggested to act as the cue regulating swimming behavior of many small plankters (Latz & Forward, 1977; Hidu & Haskin, 1978; Mann *et al.*, 1991). Swimming speeds have been shown to be altered by salinity gradients, with larvae usually accumulating at the salinity interface. But in none of the above-mentioned research were density gradients considered. In lab experiments when larvae are found to alter their swimming behavior or vertical position in response to salinity or temperature changes, it is assumed that the change in larval behavior is directly related to the changes in salinity or

temperature. But with changes in temperature and salinity come changes in density, and unless density can somehow be ruled out as the cause of the behavioral change, then density must be considered as a possible cause of the behavioral change.

Harder (1968) showed that the copepod *Temora longicornis* accumulated at steep salinity and corresponding density gradients. But when a salinity gradient was constructed without a density gradient, no accumulation occurred. Through the addition of sucrose to a homogeneous saline solution, Harder was able to form a density gradient without any change in salinity. In this case, copepod aggregation at the density interface occurred. This strongly suggests that these copepods were orienting to density and not salinity. Because density is directly related to temperature and salinity, water density may be an indirect indicator to larvae of the physical characteristics of a water mass, providing larvae with information on both temperature and salinity. This information in combination with changes in pressure and/or current velocities, may allow a larva to determine where it is within the water column and adjust its vertical position accordingly. By changing its vertical position, a larva may find itself in a water mass that is traveling in a direction different from that of the water mass that it was previously in. The larva's transport is thereby going to be affected.

There does not appear to be any correlation between a larva's association with particular density isopycnals and the location of the adult habitat. While *Bittium sp.* is an estuarine gastropod (Smith, 1964) and finding it in lower density surface waters seems likely both *Mya arenaria* and *Hydrobia sp.*, also estuarine organisms (Smith, 1964), were found primarily in higher density waters (Figs. 34 and 37, respectively). Of course tolerance to different salinity and temperature regimes is undoubtedly a species-specific response. It could very well be that *Bittium sp.* larvae are unable to tolerate water that is much colder or saltier than found in the estuary, which would explain why they were distributed as they were. But the data gives no indication that in general, a larva's position

within the water column is related to its adult habitat.

The bivalve length-frequency data was inconsistent between species, but some interesting trends were still apparent. Size frequency distributions within each species were very similar between the two sampling depths, indicating that the same cohort was probably being sampled between depths. All five bivalve species had similar modes in their length frequency distributions, indicating that spawning times and growth rates may be similar among species.

Only two of the five species of bivalve larvae sampled showed any significant difference between the sizes of larvae sampled in the upper half of the water column and those sampled in the lower half. The mean size of *Tellina agilis* and *Cyrtoleura costata* larvae were significantly different between the surface and bottom, and in both cases, the mean size was larger for those larvae sampled near bottom (Figs.44 and 45, respectively). Histograms for both species indicate that a slightly higher percentage of competent larvae were found in the lower half of the water column.

Tellina agilis and *Cyrtoleura costata* are both bivalves that are found within the littoral zone (Smith, 1964). Those larvae which were found to be at or near settlement size within the lower half of the water column may have actively swam or sunk towards the bottom in preparation for settlement and metamorphosis.

There is also the possibility that some of the post-settlement sized larvae that were sampled in the lower half of the water column were byssus thread drifters, post-settlement larvae which have released byssus threads and became resuspended within the water column. This is known to be a common way for post-larval bivalves and gastropods to further their dispersal (Lane *et al.*, 1985; Martel & Chia, 1991; Cummings *et al.*, 1993). However, for byssus drifting to occur, it may be necessary for there to be relatively high bottom current velocities. The exact current velocities at which resuspension of bivalve and gastropod larvae can occur once byssus threads have been released is unknown. During

the course of the 23 hour sampling period, bottom speeds did not exceed 9 cm sec^{-1} . At this velocity, larval bivalves may have been able to become resuspended by releasing byssus threads. It may also be that these larger larvae, those which were at or above their average settlement size (Loosanoff *et al.*, 1966; Chanley & Andrews, 1971), were larvae that had not found suitable settlement sites and were able to delay metamorphosis.

CHAPTER III

SUMMARY OF FINDINGS AND CONCLUSIONS

Major Findings

Three hypotheses were investigated in this thesis. These hypotheses were: 1) planktonic larvae of benthic invertebrates act as passive particles transported and dispersed solely by physical means, 2) there is no difference in the distributions of planktonic larvae from differing adult habitats, and 3) a larva's vertical position within the water column is unrelated to its size or competency to settle. The first hypothesis was the principal supposition addressed and as such I would like to address it last.

Larval Distributions vs. Adult Habitat

Aside from the polychaete larvae whose adult habitat is unknown, the meroplanktonic larvae fell into two broad categories with respect to their adult habitat: 1) those found primarily in the estuary, and 2) those found primarily in the littoral zone. To say that there were no differences in the two groups' distributions would be an over generalization. In both the cross-shelf transport study and the vertical migration study, larvae of some estuarine organisms (e.g. *Bittium sp.* and *Cyrtopleura costata* (which is also found littorally)) were not found in abundance in the higher density waters, remaining near the surface in lower density waters. However, this was not true for all the estuarine larvae. The same is true for the larvae whose adult habitat was the littoral zone. While most of these types of larvae did not occur in the lower density waters of the surface, there were cases in which larvae of littoral organisms were found near the surface or in the low density

Chesapeake bay plume. It would appear that a better statement to make concerning a meroplanktonic larva's distribution in relation to its adult habitat is that in general, larvae tend to occur in waters of densities and salinities which are more similar to those of the adult habitat.

Size Frequencies

The size frequency data were in most cases inconclusive. Most types of bivalve larvae showed no variation of size with depth. The exceptions were *Cyrtopleura costata* and *Mya arenaria*. On each of the four sampling days *C. costata* larvae were larger near the bottom. This size distribution may be due to a combination of factors: 1) the larger-sized larvae, those nearing settlement, may be actively sinking and/or swimming down towards the bottom in preparation for settlement, and 2) post-settlement larvae entering the water column by byssal thread drifting in response to high current velocities near the bottom. Although sample sizes were often quite low, *Mya arenaria* larvae showed no significant differences in mean size between sampling depths on all four days. As many large larvae were found near the surface as were encountered near the bottom. Because the adult habitat of *M. arenaria* is primarily in the estuary, their larvae may not settle over the shelf, which may explain why larger larvae were not found closer to the bottom. Ontogenetic differences in vertical distributions may be a species-specific response dictated by the location of the adult habitat.

Passive vs. Active Transport

By adjusting their vertical positions within the water column based upon the surrounding density of water, the majority of larvae showed some degree of control over their horizontal transport. By swimming and/or sinking out of or into waters of particular

densities, larvae may be able to avoid being transported away from the adult habitat. At other times larvae were seen to remain in a single location despite the currents moving past them. For instance, larvae may have swam against downwelled waters in order to remain near the surface against the coast. As long as vertical current speeds were not too high, larvae could swim vertically against the direction of the current, thereby maintaining their relative position within the water column.

Some types of larvae appeared to show no behavioral influence over their dispersal, however. Some of the polychaete larvae acted like passive particles being pushed back and forth across the shelf at the mercy of the currents. These are larvae whose swimming speeds are surprisingly slow. As a result, swimming vertically against vertical currents may not work for these organisms as a way to alter their transport.

Perhaps the most concise conclusion to draw from the data presented in this thesis is that the transport of marine larval invertebrates is neither solely a passive nor an active process, but rather that the transport of these larvae is a combination of both physical oceanographic events and behavioral changes on the part of the larvae.

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