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Observations on the distribution of meroplankton during a downwelling event and associated intrusion of the Chesapeake Bay estuarine plume

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We investigated the dispersal of larvae of benthic invertebrates and tested the hypothesis that larvae behaved as if they were passive particles. Observations were made off Duck, North Carolina, USA during a period of wind driven downwelling at the coast and an intrusion of estuarine water from the Chesapeake Bay. The plume of estuarine water (salinity < 30 psu) was strongest at the shoreward stations in the more northern transects. Wind driven shoreward surface flow converged at the seaward edge of the plume and downwelled. Offshore flow was present below the thermocline and caused the thermocline to bend downward and contact the bottom at between 5 and 10 km offshore.

In the zooplankton samples, we enumerated 33 taxa of larvae (17 taxa of bivalve veligers, 10 taxa of gastropod veligers, and 6 taxa of polychaete larvae). Using cluster analysis, larvae were separated into groups with similar patterns of distribution. If larvae were acting as passive particles then we hypothesized that: 1) Their distribution should remain tied to a water mass and 2) around a convergence or divergence, there should be no change in larval concentration. The distributions of larvae in Clusters 1, 4, 5, and 6 were consistent with the hypothesis that they were acting as passive particles. Larvae in Clusters 2 and 3, however, did not appear to be acting as passive particles. Larvae in Cluster 2 did not remain tied to a water mass. They entered the study area in the estuarine plume waters, but within 20 km they were nearly absent from the plume water and were found seaward of the plume and at greater depth. Larvae in Cluster 3 were most abundant in areas of converging currents where the shoreward flowing surface waters downwelled at the plume front or against the shore.

We hypothesized that larvae of organisms which as adults live in the intertidal or shallow subtidal zones would have more nearshore distributions than the larvae of adults that are broadly distributed across the shelf. We compared the depth of the habitat of the adult bivalves from which the bivalve larvae in the different clusters were derived. The results were consistent with the hypothesis; larvae with distributions closer to shore tended to come from adults found at shallower depths or in the intertidal zone.

INTRODUCTION

Many benthic invertebrates produce planktonic larvae. The size of the adult population of these organisms is dependent on the successful recruitment of their larvae. Hence, differential mortality during the period in which larvae are in the plankton can affect adult population sizes. Researchers have identified a number of processes that kill meroplankton and reduce recruitment (e.g. predation, starvation, disease, etc.) (Rumrill, 1990). Perhaps one of the most important processes controlling the rate of recruitment is the pattern of transport of larvae by ocean currents, so-called larval dispersal.

Depending on the species, larvae may spend anywhere from minutes to many months in the plankton before they leave the water column and settle into a benthic habitat.

Few larval types are strong enough swimmers to control their position in the ocean by swimming horizontally. For example, ciliated larvae have swimming speeds on the order of millimeters per second (Chia *et al.*, 1984), yet ocean currents are typically on the order of centimeters per second. The fact that larval swimming speeds are generally so much lower than the speed of ocean currents suggests that, while in the plankton, larvae are at the mercy of ocean currents. At the end of their development, larvae that have been carried to settlement sites may successfully recruit into adult populations. Those unlucky individuals that are not at settlement sites at the time when they must settle will be lost from the population. Hence, the rate of recruitment of larvae into a population may be controlled by the pattern of transport of larvae by ocean currents.

Are larvae, even slowly swimming ciliated larvae, truly at the mercy of ocean currents? Larval swimming speeds, while generally much slower than the speed of ocean currents, are fast enough that they can make relatively rapid changes in their vertical position in the water column. For example, even a bivalve veliger swimming at 1 mm s^{-1} may be able to swim through a 10 m column of water in <3 h. Ocean currents are often vertically sheared; their speed and direction change with depth. Researchers have suggested that by judicious selection of their depth, larvae may be able to exert some control over their horizontal movement [reviewed in Shanks (Shanks, 1995) and Bakun (Bakun, 1996)]. In a classic paper, Peterson *et al.* demonstrated that populations of different species of copepods were able to maintain their cross-shelf position in the face of energetic cross-shelf currents generated by upwelling and downwelling events (Peterson *et al.*, 1979). The particular cross-shelf position of a species was maintained by ontogenetic changes in depth. If ontogenetic changes in the depth of copepod nauplii, organisms that swim slowly, can affect the subsequent distribution of the adult population, then, perhaps, changes in the vertical position of meroplankters can affect their transport and distribution.

This or similar hypotheses have over the years inspired a number of papers, which have arrived at different conclusions. For example, Banse (Banse, 1986) presented data that suggested that a variety of polychaete and echinoderm larvae in Kiel Bay behaved as if they were neutrally buoyant particles; their distributions were tightly tied to the distributions of water masses. In contrast, Wood and Hargis (Wood and Hargis, 1971) found that oyster larvae in Chesapeake Bay did not act as passive particles so that due, presumably, to their behavior they were retained in the estuary. Models of larval dispersal have been designed which assume that larvae are passive particles (Jackson and Strathmann, 1981) or that by swimming they change their vertical distribution and can thus move into waters with different flow characteristics (Thiebaut, 1996). When modeling larval dispersal, the decision to view larvae as active or passive will have a profound effect on the results. The answer to the hypothesis is most likely dependent upon the species of larvae in question, the oceanographic characteristics of the study area, and, perhaps equally as important, the temporal and spatial scale of the observations.

The data reported here are part of the results of the 'Coastal Ocean Processes Study' (CoOP'94) (Butman, 1994). The purpose of the study was to investigate the nearshore cross-shelf dispersal of invertebrate larvae. During the course of the sampling (described below), the coastal ocean was dominated by the effects of the local winds. Winds from the southwest generated upwelling flow, while winds from the northeast generated downwelling (Cudaback and Largier, 2001). Intrusions of the Chesapeake Bay estuarine plume into the study area frequently occurred during downwelling events (Rennie *et al.*, 1999).

The work presented here describes sampling that took place during a northeast-wind-generated downwelling event and plume intrusion. The area sampled was ~30 km along shore by 20 km offshore, within which sampling was extensive, with 27 stations occupied along five transect lines (five or six stations per line). The oceanographic sampling adequately described the intruding plume as well as the nearshore reversal in the cross-shelf flow associated with the downwelling event. The associated biological sampling allowed us to describe the distribution of meroplankton relative to the oceanography. The sampling provided an opportunity to test the hypothesis that ciliated meroplankton were advected passively by ocean currents.

METHOD

The field work for this study took place during August 1994. Here we report the results of a grid of stations that was sampled on 24 August during a downwelling event and intrusion of Chesapeake Bay estuarine plume waters into the study area. The sampling grid was centered on the Army Corps of Engineers Field Research Facility (FRF) at Duck, North Carolina, USA (Figure 1). This section of coast is characterized by relatively simple submarine and coastal topography. It was hoped that this would minimize topographically induced alongshore variations in the oceanography. Transects were located ~20 and 10 km north (transects 3.0 and 3.5, respectively) and 8 and 17 km south (transects 4.5 and 5.0, respectively) of the transect centered on the FRF pier (transect 4.0). Transects were oriented roughly perpendicular to the coast and extended 20 km offshore. Transects 3.0, 3.5

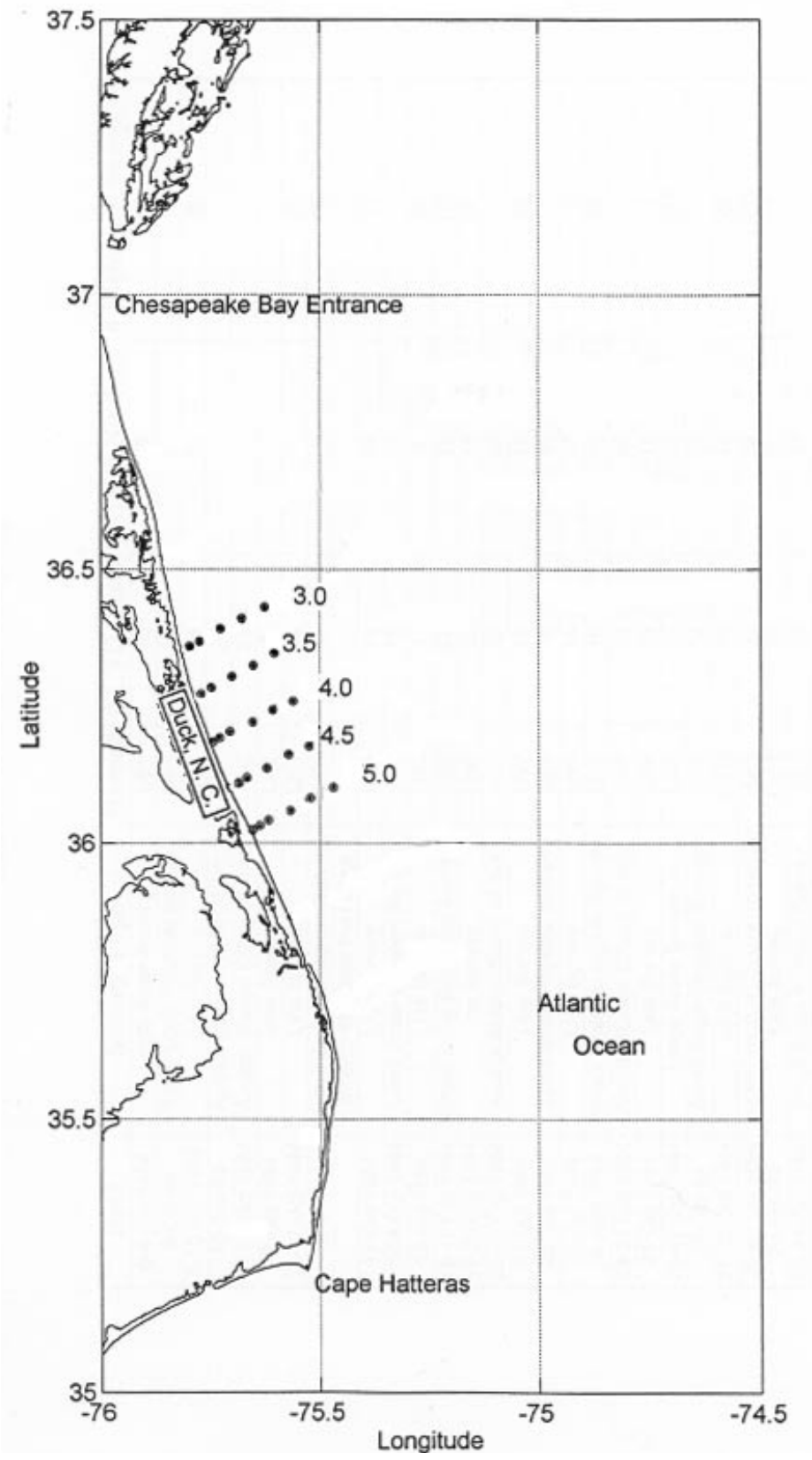

Fig. 1. Map of station locations.

and 4.5 consisted of five stations (~2, 4, 9, 14 and 19 km offshore), while transects 4.0 and 5.0 consisted of six stations (stations at the above distances plus a station at ~1 km offshore).

Sampling from the R/V 'Cape Hatteras' began at the most inshore station of transect 5.0 at ~00:00 h (GMT) on 24 August and the last station in the grid (transect 3.0, 19 km station) was sampled at 23:35 h (GMT) on the same day. Sampling along each transect started at the most inshore station. At each station, a SeaBird 911 conductivity–temperature–depth (CTD) cast was made. The concentration of chlorophyll was measured with a Wet Star *in situ* fluorometer mounted on the CTD. These measurements were not calibrated against extracted samples; hence, the values reported are rough estimates of the concentration of chlorophyll. The validity of these fluorescence data are discussed further by D'Sa *et al.* (D'Sa *et al.*, 2001). Simultaneously with the CTD cast, an Acoustic Doppler Current Profiler (ADCP) was used to measure the vertical profile of currents. The currents were measured with an RDI 1.2 MHz narrow-band instrument mounted on a catamaran that held the transducer at a depth of 0.4 m. Velocity profiles were made with a vertical resolution of 1 m and recorded at 1–2 Hz while the ship held position for the CTD cast. Surface water temperature and salinity were monitored while the ship was under way. A detailed description of the collection and processing of the physical oceanographic data can be found in Waldorf *et al.* (Waldorf *et al.*, 1995) and Rennie (Rennie, 1998).

In addition to sampling from the R/V 'Cape Hatteras', oceanographic and weather data were also collected by instruments mounted on offshore moorings and on the FRF pier (Alessi *et al.*, 1996; Cudaback and Largier, 2001). For this study, we have made use of data collected by instruments on the FRF pier and on the nearshore moorings along the 5 m isobath north and south of the pier. A SeaCat CTD was mounted on the FRF pier and on each mooring. The moorings were deployed at nominal distances of 15 and 30 km north and south of the pier: J0 at 32 km north, J1 at 17 km north, J2 at the pier, J3 at 16 km south and J4 at 25 km south.

Plankton samples were collected with a centrifugal pumping system. A 5-cm-diameter hose was connected to the CTD rosette and a deck-mounted pump. Output from the CTD provided information on the depth from which each sample was collected. Water from the pump was passed through a 100-μm-mesh net suspended in a large tub of water. The pumping rate was 227 l min^{-1} and 680 l were sampled at each depth. Sampling depths were selected based upon the water depth. At shallow depths (≤20 m), samples were generally collected ~2 m from the bottom and the ocean's surface, and half-way between these samples (Table I). At deeper stations, samples were generally collected ~2 m from the bottom and the surface, within the thermocline, and mid-way between the thermocline and the surface or the bottom (Table I). Samples were preserved in buffered formalin.

In the laboratory, the samples were washed free of formalin on a 53 μm sieve. After transfer to a 250 ml beaker, the sample, with the aid of an electronic balance, was made up to 200 ml (200 g). The sample was homogenized by vigorous random stirring and a 12 ml subsample was removed with a Stempel pipette (Peterson *et al.*, 1979; Omori and Ikeda, 1984). Subsamples were counted until at least 100 individuals of the most common organisms had been enumerated. This yielded a sample standard deviation (SD) of ~10% for the most abundant organisms and between 10 and 20% for the less common species (Venrick, 1978). To test the subsampling technique, we compared the number of organisms in four samples determined by subsampling and by counting the entire sample. No statistically significant differences (Mann–Whitney *U*-test, $P > 0.05$) were found between the number of organisms determined by the two methods, suggesting that the subsampling technique adequately described the samples.

The plankton samples were sorted under a dissecting microscope equipped with polarizing filters placed between the sample and the light source, and between the sample and the microscope lens. The filters were rotated until the shells of bivalves and gastropods appeared to 'glow' due to the birefringence caused by the crystalline structure of the shell (Gallager *et al.*, 1989). Lighting the samples in this way greatly decreased the sorting time. Bivalve and gastropod larvae were identified to genus and, when possible, to species using various identification guides (Thorson, 1946; Sullivan, 1948; Rees, 1950; Loosanoff *et al.*, 1966; Chanley and Andrews, 1971; Thiriot-Quievreuz, 1980, 1983; Gallager *et al.*, 1989). Polychaete larvae were identified to family using descriptions in Thorson (Thorson, 1946), Korn (Korn, 1960) and Bhaud and Cazaux (Bhaud and Cazaux, 1982). Trochophore stage polychaetes were identified to phylum only.

During the processing of the physical oceanographic data, current velocities were decomposed into alongshore and cross-shore components. Alongshore was defined as 20°W of true north. Contour plots of the distribution of the biological and physical data were made using the Noesys Transform contour plotting program with the Kriging option for gridding and interpolating.

RESULTS

Physical oceanography

Intrusions of low-salinity water were observed in the study area during weak or downwelling winds (Rennie *et al.*,

Table I: Depth (m) of plankton samples and station locations within the transect grid

Station # (distance alongshore, km)	Offshore distance of stations (km)					
	1	2	4	9	14	19
3.0	–	2	2	2	2	2
(0)		7	7	9	7	7
		10	14	13	11	11
				15	15	16
				17	19	21
3.5	–	3	3	2	2	2
(10)		7	19	12	8	7
		12	15	18	14	12
					17	17
					20	21
4.0	3	3	3	3	3	3
(20)	7	8	7	8	7	8
		13	12	14	11	13
			17	20	17	19
					24	24
4.5	–	3	3	3	3	3
(28)		8	9	11	7	7
		14	16	20	11	11
					15	17
					20	23
5.0	3	3	2	2	2	2
(37)	6	9	11	7	8	6
	9	14	20	11	13	9
				15	19	15
				18	24	21

1999). Originating as Chesapeake Bay outflow, these 'buoyancy current' pulses are composed of a mixture of Chesapeake Bay water with the ambient Mid-Atlantic Bight water. These pulses of southward flow appeared as a narrow band of low-salinity bay-influenced water along the shore. A day prior to the plankton sampling described here, and throughout the sampling, the wind was downwelling favorable. On 21 August, winds were from the south (upwelling favorable) and the density structure of the nearshore waters indicated that upwelling was occurring (Waldorf *et al.*, 1995). Late on 22 August, the wind began to blow from the northeast at ~5 m s^{-1}. This northeasterly wind continued through 25 August and downwelling circulation was observed, as described by Cudaback and Largier (Cudaback and Largier, 2001).

In the following presentation of results and their interpretation in the Discussion, it should be borne in mind that while the data are presented as if they were a snap shot of the system, they actually required nearly a day to collect. Currents in the study area, particularly against the shore, were vigorous. During the course of the sampling, water in the study could have moved, depending on its location, on the order of 20–50 km. This is a problem common to nearly all oceanographic and biological oceanographic surveys.

Data collected on 24 August (Figures 2 and 3) provide a good illustration of the low-salinity intrusion that occurred following the onset of downwelling winds. This low-salinity intrusion, defined here by salinity < 30 p.s.u., entered the study area on 23 August. It was observed initially at mooring J1 (17 km north of the FRF pier) at 09:04 h and arrived at the FRF pier at 15:04 h. The arrival

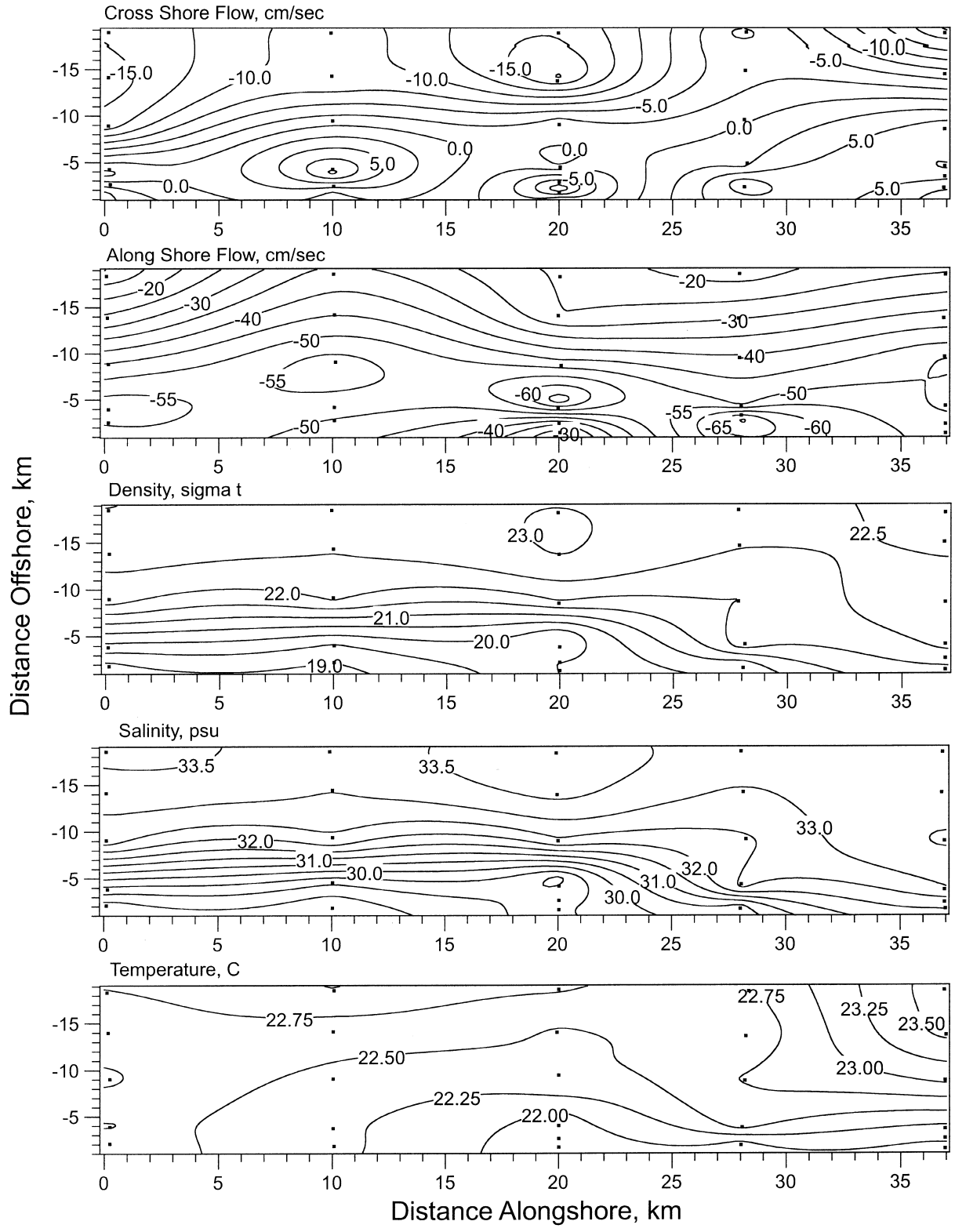

Fig. 2. Contour plots of surface values of physical oceanographic variables within the study area. Units are: cross-shore and alongshore flow in cm s^{-1} with negative values oriented onshore and to the south, respectively; salinity, p.s.u.; temperature, °C; density, σ_t. Station locations are indicated by black dots.

times suggest a propagation rate into the study area of ~0.75 m s^{-1} (Rennie *et al.*, 1999). Although sub-30 p.s.u. water was observed in the northern part of the shipboard survey on 24 August (lines 3.0, 3.5 and 4.0), such low salinities were not observed along either of the more southern transect lines (lines 4.5 and 5.0; Figure 2). Water of salinity <30 p.s.u. was not observed at either of the moorings south of the pier until late on 24 August (mooring J3) or early on the 25th (mooring J4) (Rennie *et al.*, 1999). Looking at the low-salinity intrusion in cross-section (Figure 3), we found the lowest salinity (~27.5 p.s.u.) at the most nearshore station along transect 3.0. By transect 4.0, the lowest salinity water was ~29 p.s.u. Nearshore, this low-salinity intrusion was in contact with the bottom. Offshore, where the low-salinity water formed a surface layer, an intense salinity gradient was observed (halocline). Similarly, at the offshore extent of the low-salinity surface water, salinity increased rapidly (Figures 2 and 3), forming a salinity front. Rennie *et al.* discuss the shape and downstream evolution of the plume in more detail (Rennie *et al.*, 1999).

Surface waters were between 22 and 23.5°C, with the warmest water found at the surface at the offshore edge of transect 5.0 (Figures 2 and 4). The bay-influenced waters did not exhibit a temperature signature relative to the surface coastal waters (Figures 2 and 4), as noted by Cudaback and Largier (Cudaback and Largier, 2001). Hence, the contrast in density (Figures 2 and 5) was solely due to the difference in salinity. Over the shelf, seaward of ~10–15 km, the water column was characterized by a strong thermocline (Figure 4). Temperature across the thermocline ranged from 22.5 to 18°C and the intensity of the temperature gradient was strongest (~1°C m^{-1}) away from the coast. The thermocline was bent downward and contacted the bottom between ~5 and 12 km from shore (Figure 4). Seaward of ~5 or 10 km, density appeared to be primarily controlled by changes in temperature (Figures 4 and 5).

Throughout the study area, flow was to the south (Figures 2 and 6). Velocity tended to increase shoreward and there were no obvious differences in alongshore flow across the thermocline. On transects 3.0–4.0, the highest flows were roughly centered on the offshore edge of the plume at distances of ~5 km from shore (Figures 2 and 6), with velocities from 0.55 to 0.65 m s^{-1}. The highest velocity (0.75 m s^{-1}) was found nearshore, but subsurface, on transect 4.5 (Figures 2 and 6). Farther south, on transect 5.0 there is no nearshore or frontal maximum in alongshore velocity, but just a general broad flow coinciding with the cross-shelf gradient of salinity/density over the innermost 10 km. The salinity data (Figure 2) suggest that the head of the low-salinity intrusion was located between transects 4.0 and 4.5, with the velocity maximum on line 4.5 possibly representing the very head of the buoyancy current. These low-salinity waters formed a separate water mass, isolated from the shelf waters by a frontal system.

Seaward of the salinity front, flow above the thermocline was towards the shore and below the thermocline it was away from the shore (Figures 2 and 7). This represents a strong downwelling circulation with velocities of up to 0.2 m s^{-1}, although the strength of this cross-shore circulation varied between transects. Averaging over this small-scale variability, the downwelling circulation in the region exhibited a general velocity of order 0.1 m s^{-1}. The front appeared to be an axis of convergence in near-surface cross-shore flow, with divergence observed nearshore within the low-salinity water (see Figure 7, transects 3.0, 3.5 and 5.0). There is no clear divergence below the front and the cross-shore convergence along the front, if continuous as it appears, must be balanced by a divergence in the alongshore flow, as suggested by Figure 2 and consistent with lateral entrainment of shelf waters in the coastal buoyancy current. The most intense cross-shore convergence was observed on line 4.5, in the vicinity of the maximum in alongshore velocity. Strong offshore flow through the whole water column and out to ~5 km offshore appears to represent a local deviation in the intense alongshore flow. Such meandering is the likely explanation for much of the variability in cross-shore flow between transects.

Note that the ADCP current data were not de-tided. The tidal currents, however, were relatively small (Lentz *et al.*, 2001). The M2 tide was the strongest constituent and the amplitude varied over the extent of the survey. Alongshelf velocities due to the M2 component of the tides varied from 3 cm s^{-1} at the coast to 5 cm s^{-1} at ~18 km offshore. Cross-shelf velocity varied from 0 at the coast to ~3 cm s^{-1} at ~18 km offshore. At 5–10 km offshore, where the ADCP data indicated there were strong convergences, the cross-shelf tidal currents were 1–2 cm s^{-1}, small relative to the measured currents. In addition, the cross-shelf gradients in the tidal currents were very small, negligible compared to the observed convergences and divergences.

The uncorrected data from the *in situ* fluorometer indicated that chlorophyll concentration ranged from ~1 to 3 μg l^{-1}. The lowest concentrations were found above the thermocline between ~5 km from shore and the outer edge of the transects (Figure 8). High concentrations were found below the thermocline and within the nearshore waters influenced by the Chesapeake Bay outflow (Figure 8). In the offshore waters, the distribution of high chlorophyll was tightly bound by the upper edge of the thermocline (~22°C) and the nearshore edge of this layer was found where the thermocline contacted the bottom

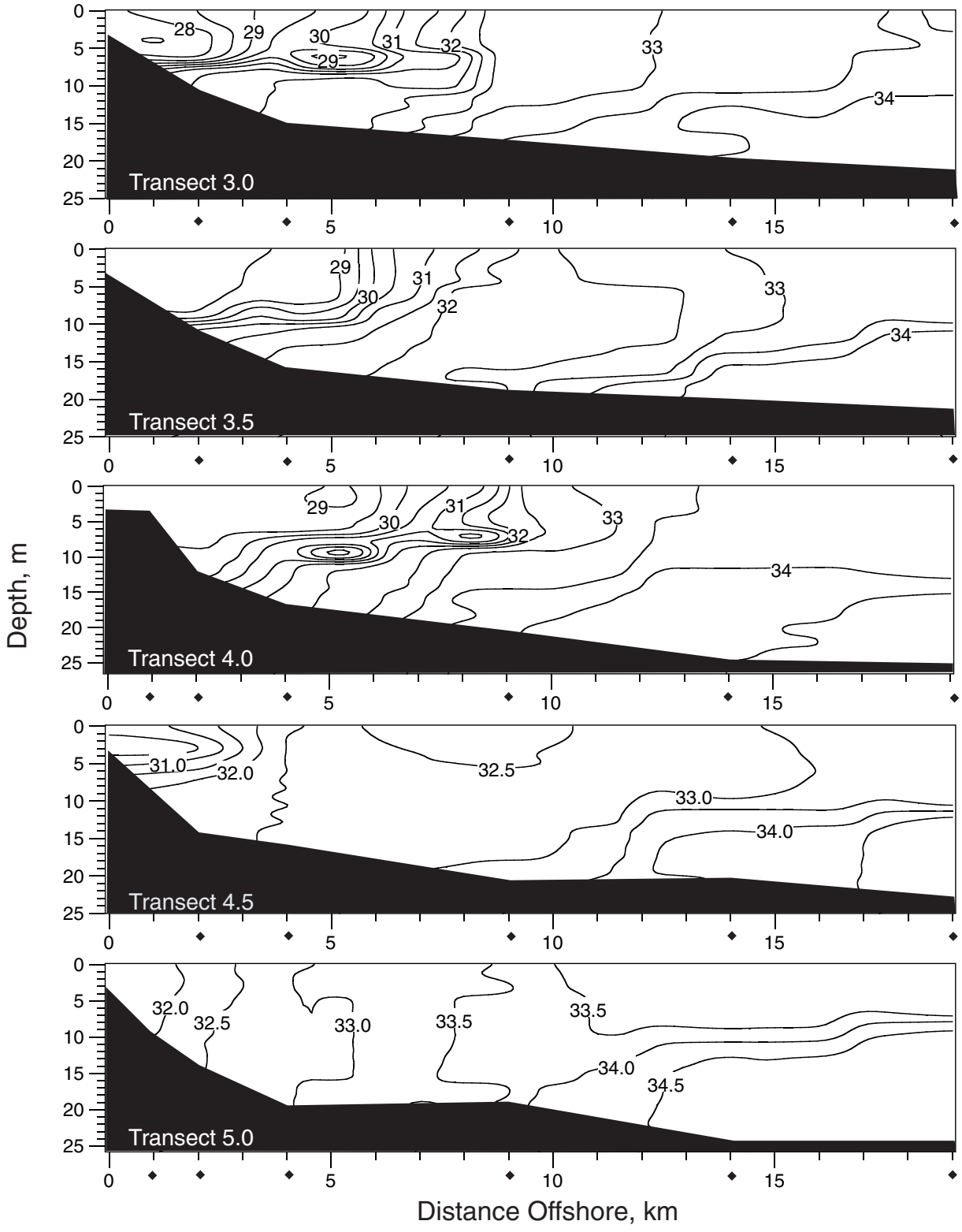

Fig. 3. Contour plots of salinity (p.s.u.) along the transect lines. The black diamonds along the horizontal axes indicate station locations.

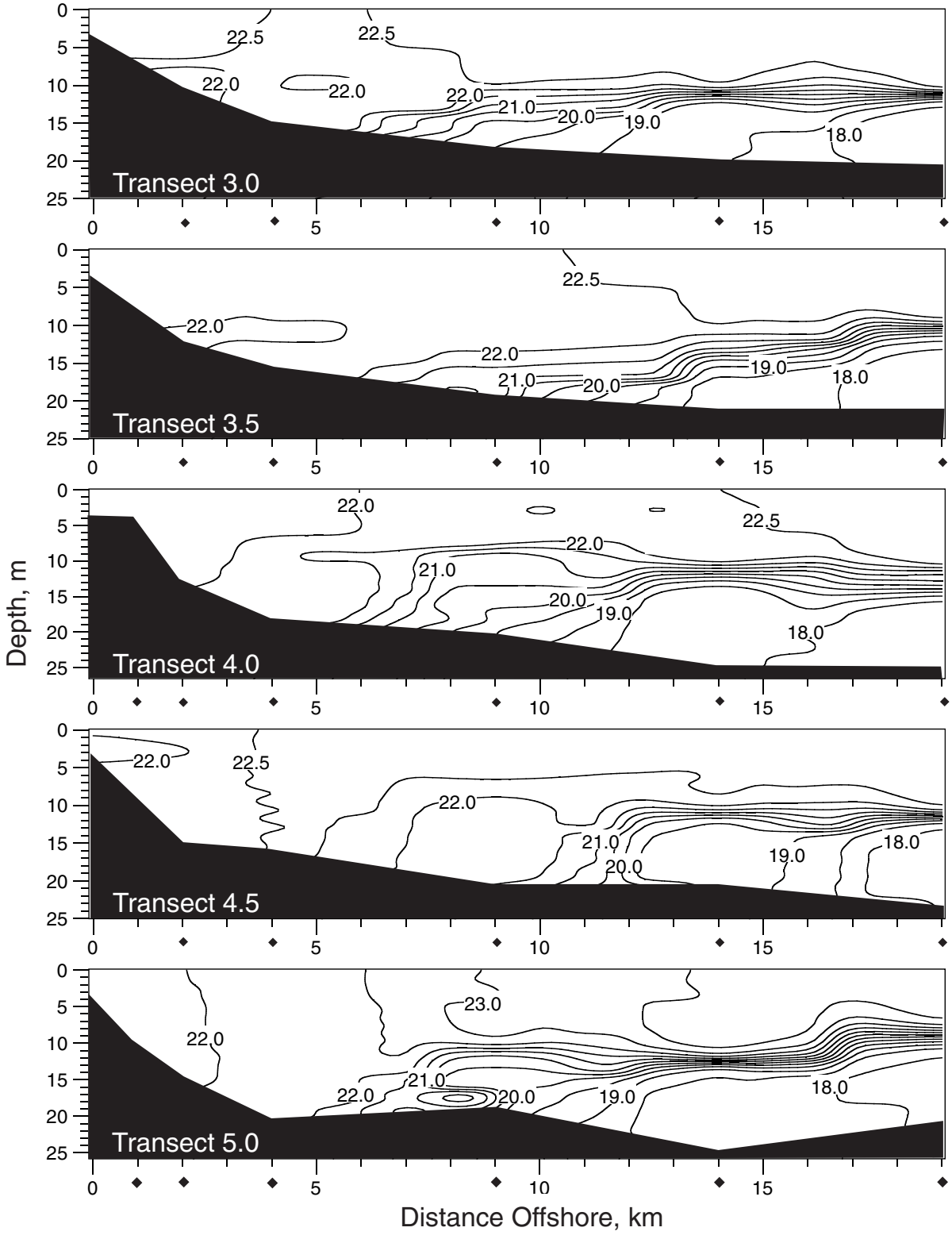

Fig. 4. Contour plots of temperature (°C) along the transect lines. The black diamonds along the horizontal axes indicate station locations.

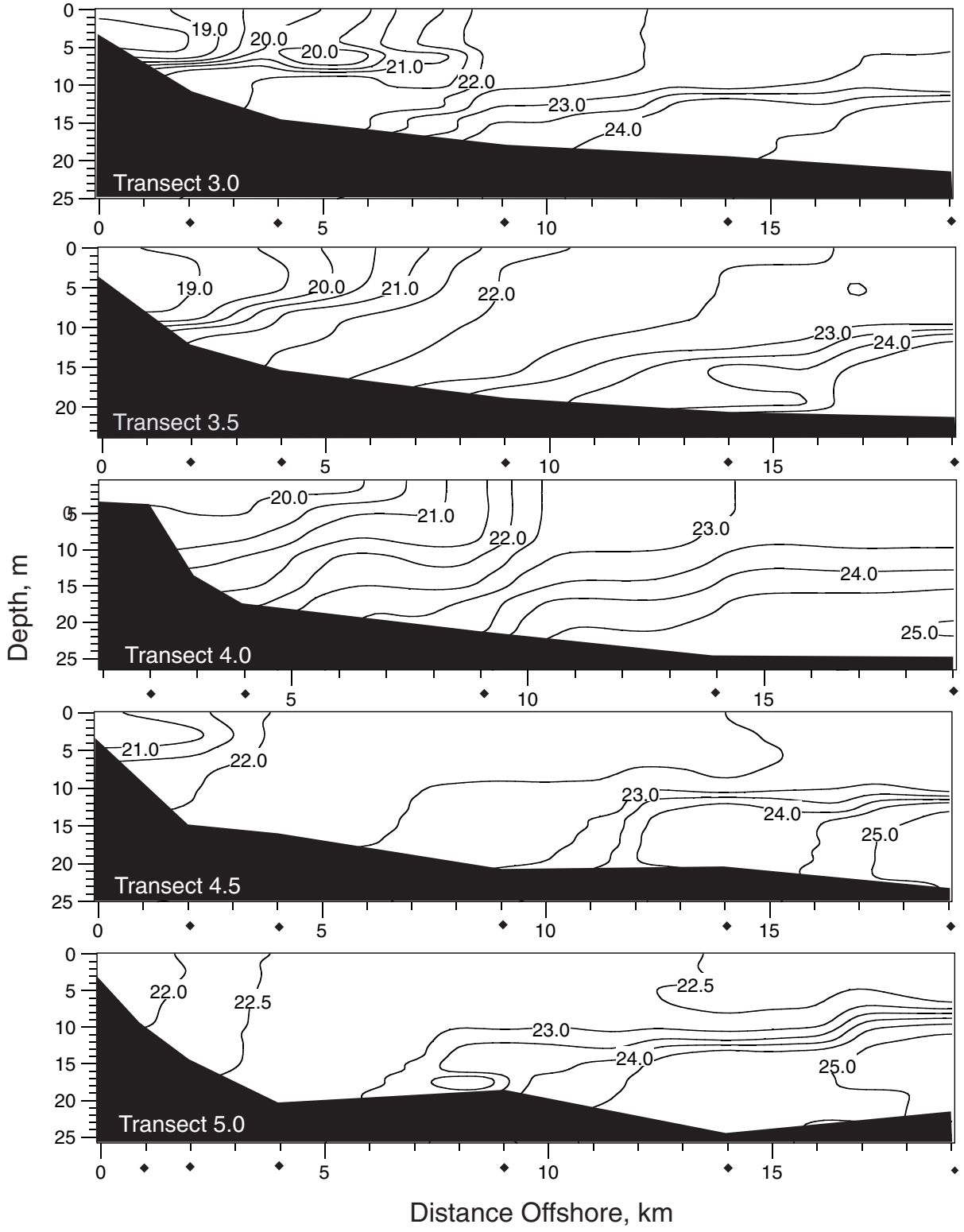

Fig. 5. Contour plots of density (σ_t) along the transect lines. The black diamonds along the horizontal axes indicate station locations.

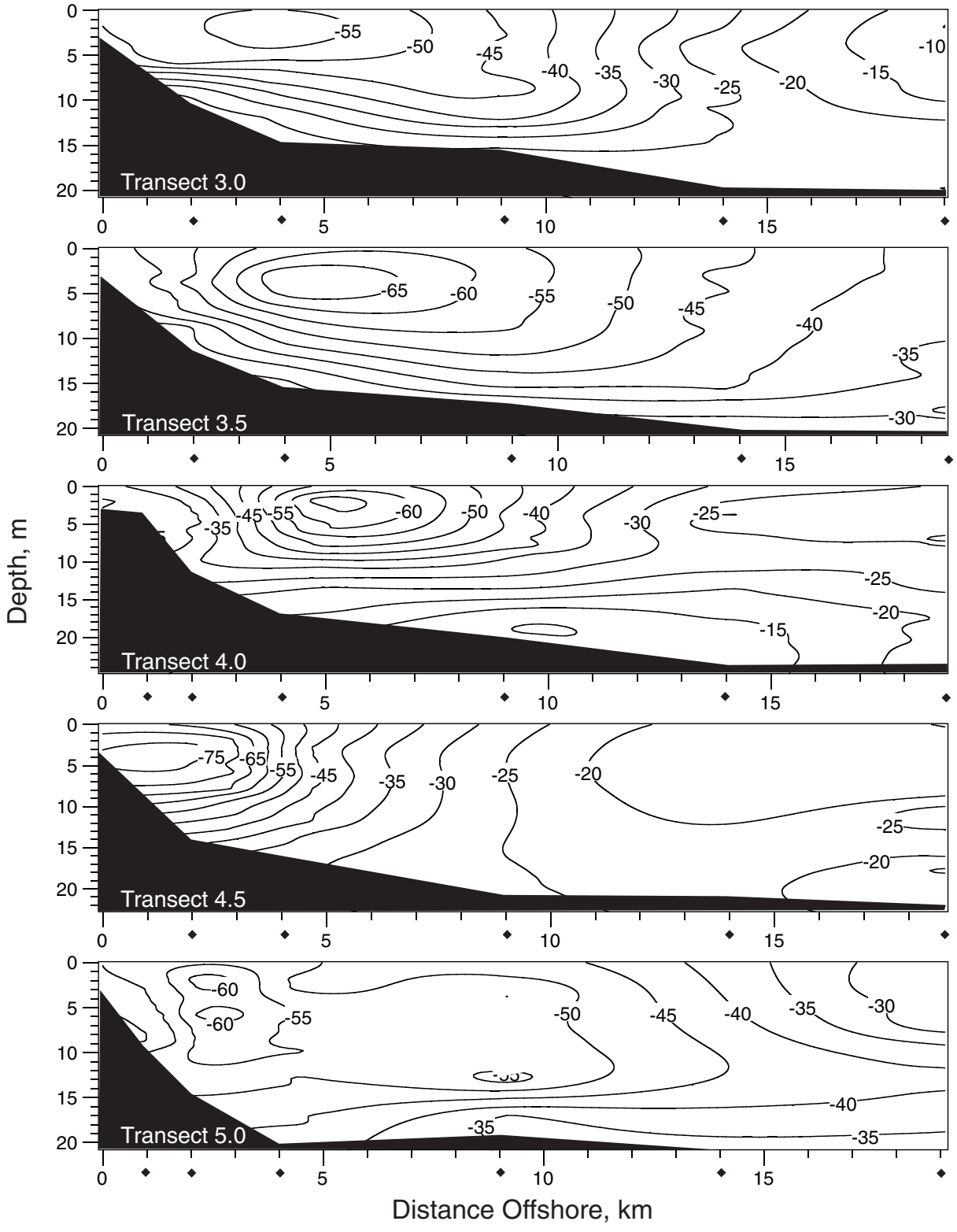

Fig. 6. Contour plots of alongshore flow (cm s^{-1}) along the transect lines. Negative values indicate flow to the south. The black diamonds along the horizontal axes indicate station locations.

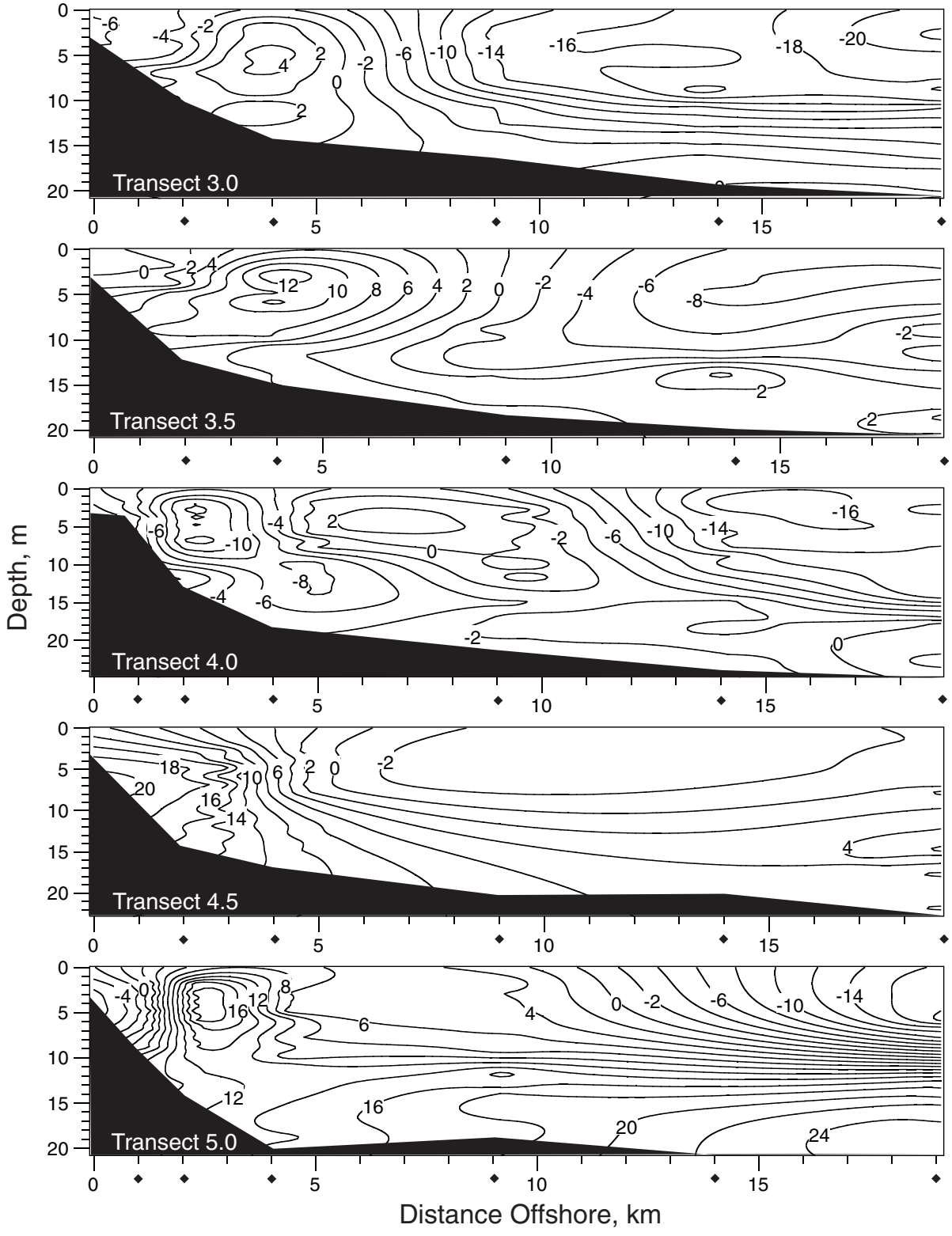

Fig. 7. Contour plots of cross-shore flow (cm s^{-1}) along the transect lines. Negative values indicate onshore flow. The black diamonds along the horizontal axes indicate station locations.

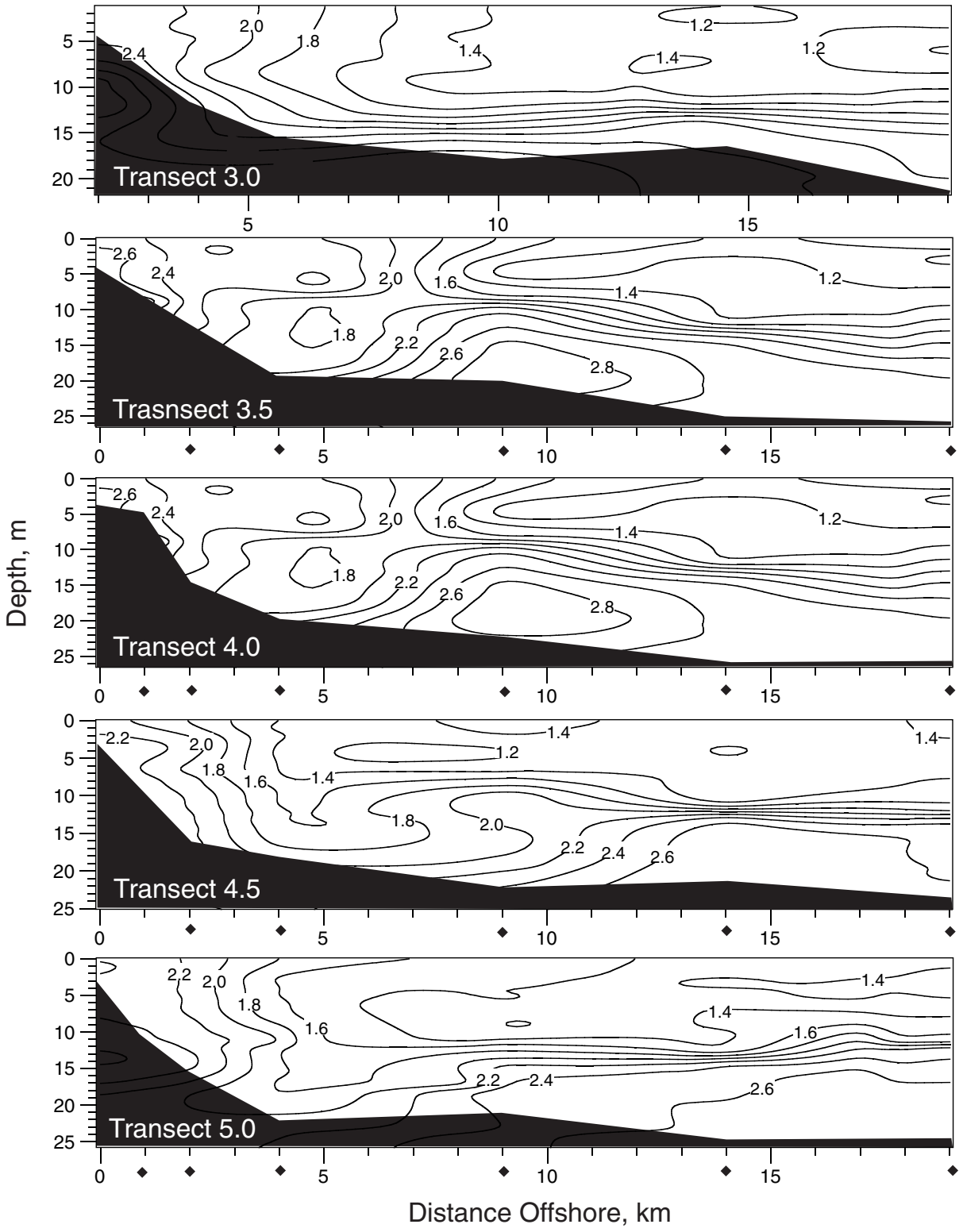

Fig. 8. Contour plots of chlorophyll fluorescence (uncorrected values, μg l^{-1}) along the transect lines. The black diamonds along the horizontal axes indicate station locations.

(Figures 4 and 8). In the nearshore waters, high chlorophyll concentration appears more geographically defined, rather than attached to a specific salinity or temperature. In the three most northern transects (transects 3.0, 3.5 and 4.0), the outer edge of this high-chlorophyll zone was associated with salinities of ~30 p.s.u., while in the two southern transects (transects 4.5 and 5) the outer edge of the high-chlorophyll zone was found at salinities of ~32–32.5 p.s.u. (Figures 3 and 8). In the waters between the chlorophyll maximum nearshore and that below the thermocline, we found intermediate concentrations of chlorophyll. This distribution of chlorophyll may have been caused by the downwelling of surface water low in chlorophyll, which then mixed with the high-chlorophyll nearshore and subthermocline water. The distribution of the waters with intermediate chlorophyll concentrations may be used to delineate downwelled surface waters.

Larval distributions

We counted a total of 14 656 bivalve larvae. We were able to identify 17 different bivalve genera or species in our samples. Three types of bivalve larvae, *Mytilus edulis*, *Barnea* sp. and *Tellina* sp., accounted for 79% of the bivalve larvae identified. An additional 13% were due to four additional organisms: *Spisula solidissima*, *Anadara* sp., *Mulinia lateralis* and *Ensis directus*. Approximately 3% of the bivalve larvae could not be identified. We did not attempt to identify the early developmental stages of larval bivalves (the so-called 'D' stage larvae). Probably due to our use of 100-μm-mesh nets, very few D stage larvae were caught.

We counted a total of 7755 gastropod larvae from 10 genera. Three genera, *Odostomia*, *Bittium* and *Littorina*, made up 79% of the catch. Approximately 7% of the gastropod larvae could not be identified.

We counted a total of 4827 polychaete larvae. Trochophores made up 25% of the catch. The remainder of the catch was composed of five families, with spionids and phyllodocids accounting for 72% of the catch.

Overall, we were able to identify larvae in 32 taxa. Inspection of the data suggested that there was a relatively small number of general distribution patterns to which the different taxa might be assigned. We sorted organisms into groups using the cluster analysis statistical package in Statistica. Two different techniques were used. The first technique separated larvae into groups based on their spatial distribution. The concentrations of larvae were standardized such that the mean equaled zero and the SD equaled one. Using the Wards Method, the larvae were grouped into clusters by their Euclidean distance. This analysis (as well as several of the other clustering algorithms) suggested that the larvae could be broken up into six clusters (Figure 9). The second technique formed clusters based on the relative affinity of larvae to location or water type. Correlations were calculated between larval concentrations and the physical variables (temperature, salinity, alongshore velocity, cross-shore velocity, offshore distance, alongshore distance and depth) and chlorophyll concentration. This correlation matrix was then used in the cluster analysis. Using the Wards Method, the larvae were grouped into clusters by their correlation coefficients with the physical variables. This analysis indicated that there were five clusters of larvae (Figure 10; Clusters A–E).

The outcome of these two analyses were quite similar. Clusters 2 and 4 were identical to Clusters E and D, respectively. The only difference between Clusters 3 and C was that Cluster C contained *Littorina* sp., while Cluster 3 did not. Clusters 1 and A consisted of 11 and 10 larval types, respectively. They shared eight larval types. Cluster 1 contained *Littorina* sp., *Caecum* sp. and *Aequipectin* sp., while Cluster A did not. Cluster A also included two organisms from Cluster 6: *Nassariu* sp. and Orbiniidae. Cluster B consisted of the organisms found in Cluster 5 plus *Aequipectin* sp. and *Caecum* sp. from Cluster 1. About 80% of the larvae that composed the numbered clusters were found in lettered clusters composed of similar members. Given the strong similarity between the two sets of clusters, we will concentrate the following presentation of the results on the numbered clusters, though in some of the statistical analysis the lettered clusters will also be used.

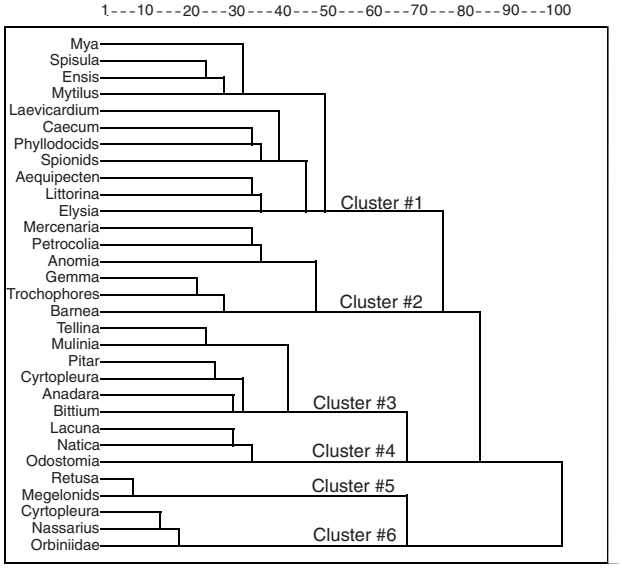

Fig. 9. Results of the first cluster analysis, which separated larvae into groups based on their spatial distribution. The concentrations of larvae were first standardized such that the mean equaled zero and the SD equaled one, and then using the Wards Method the larvae were grouped into clusters by their Euclidean distance.

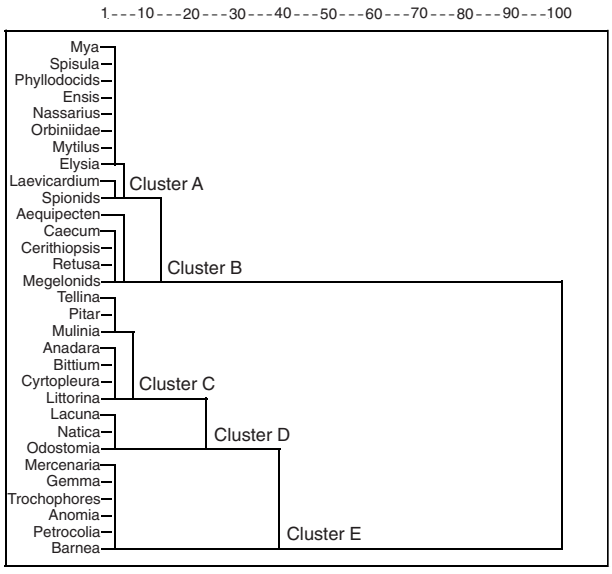

Fig. 10. Results of the second cluster analysis in which clusters were based on the relative affinity of larvae to location or water type. For this analysis, correlations were calculated between larval concentrations and the physical variables (temperature, salinity, alongshore velocity, cross-shore velocity, offshore distance, alongshore distance and depth) and chlorophyll concentration. This correlation matrix was then used in the cluster analysis. Using the Wards Method, the larvae were grouped into clusters by their correlation coefficients with the physical variables and chlorophyll concentration.

Cluster #1

Cluster #1 was composed of 11 different taxonomic groupings: the bivalves *Mya arenaria*, *S. solidissima*, *E. directus*, *M. edulis*, *Laevicardium mortoni* and *Aequipecten* sp.; the gastropods *Caecum* sp., *Littorina* sp. and *Elysia* sp.; and polychaetes in the families Phyllodocidae and Spionidae (Table II). Organisms in this cluster tended to be abundant and were caught at nearly all of the stations (average 92%; Table II). They tended to increase in abundance at the more southern end of the grid (positive correlations with alongshore distance; Table II). The concentrations of individuals in this group were, in general, significantly positively correlated with depth, salinity, density, chlorophyll fluorescence, and cross and alongshore flow (Table II). Furthermore, larval concentrations were negatively correlated with temperature (Table II). This combination of correlations suggests that these organisms tended to be found below the pycnocline. The distribution of *E. directus* will be used as an example of the distribution pattern of organisms in this cluster.

In transect 3.0, the highest concentration of *E. directus* was found in the waters adjacent to shore and in or under the Chesapeake Plume waters, suggesting that some *E. directus* entered the study area in the plume waters (Figure 11). However, the fact that *E. directus* larvae were caught at all of the stations in the sample grid (Table II) suggests that *E. directus* larvae were generally distributed and that the plume waters were not the only source for these larvae. *Ensis directus* larvae were absent from the plume waters in transect 3.5. In transects 3.5–5.0, *E. directus* larvae were found primarily in the waters below the 22°C isotherm (compare Figures 4 and 11) in association with the water containing the higher chlorophyll concentrations (compare Figures 4 and 8).

Cluster #2

Cluster #2 consisted of the bivalves *Gemma gemma*, *Mercenaria mercenaria*, *Petricola pholadiformis*, *Anomia* sp. and *Barnea* sp., and polychaete trochophores (Table II). Except for trochophores, none of these larvae were particularly abundant (concentrations < 200 m^{-3}) and they were absent from many of the stations (Table II). Trochophores were abundant at some locations (maximum concentration 3633 m^{-3}) and were caught at all stations (Table II). In general, the concentrations of these organisms were significantly negatively correlated with alongshore and cross-shelf distances, suggesting that the highest concentrations were found at the northern end of the grid and nearshore. Furthermore, all of these organisms were significantly negatively correlated with salinity and all but *P. pholadiformis* had significant negative correlations with density. The highest concentrations of these organisms tended to be found in lower salinity water. Taken together, these results suggest that these organisms were entering the study area with the intrusion of the Chesapeake Bay plume waters. The distribution of *M. mercenaria* will be used as an example of the general pattern displayed by the organisms in this cluster.

High concentrations of *M. mercenaria* larvae were found within 4 km of shore along transect 3.0 (Figure 12). This area of high concentration corresponded roughly to the distribution of water with salinity ≤29.5 p.s.u. (Figure 3) and density of ~19.5–20 σ_t (Figure 5). However, at ~2 km from shore, there were high numbers of larvae caught in higher salinity water (>30 p.s.u.) immediately below the plume waters. On transect 3.0, few *M. mercenaria* were caught seaward of 5 km. Along transect 3.5, the highest concentrations of *M. mercenaria* larvae were found deeper, farther offshore, and in water with higher salinities than had been seen in transect 3.0. There were two locations with concentrations >100 m^{-3}; one was located ~4 km from shore where the salinity was ~30.5 p.s.u. and the second was ~9 km from shore associated with a salinity of ~32.5 p.s.u. No *M. mercenaria* were caught seaward of 14 km along transect 3.5. Along transect 4.0, some *M. mercenaria* larvae were caught near the bottom of the water column at distances of 9 and 19 km from shore (Figure 12). No or very few *M. mercenaria* larvae were caught along transects 4.5 and 5.0 (Figure 12).

Table II: Organisms in numbered (column 1) and lettered (column 2) clusters (see text for explanation)

	Phys. cluster present	% stations with organisms (range, no. m^{-3})	Along-shore dist.	Cross-shore dist.	Depth	Cross-shore flow	Along-shore flow	Salinity	Density	Temp.	Fluor.
Cluster #1											
Mya arenaria	A	96 (4–122)	0.3422		0.2834	0.3670		0.1957	0.2372	–0.2606	0.2711
Spisula solidissima	A	100 (6–494)	0.3591		0.4595	0.3541		0.2811	0.3514	–0.4115	0.3075
Ensis directus	A	100 (8–354)			0.5454	0.2986	0.2290	0.2481	0.3412	–0.4629	0.4681
Mytilus edulis	A	100 (3–1144)	0.2176		0.3318	0.3837				–0.2848	0.4018
Laevicardium mortoni	A	57 (4–123)	0.3803		0.2367		0.2602	0.3047	0.3568	–0.3687	
Caecum sp.	B	81 (4–123)	0.3841	0.2313		0.3062		0.2145	0.2037		
Phyllodocids	A	100 (4–2062)	0.2073		0.3018		0.2138		0.2150	–0.2285	0.2518
Spionids	A	100 (3–1269)		0.2595	0.3847		0.2724	0.2179	0.2948	–0.3956	0.2514
Argopecten sp.	B	54 (4–134)	0.2504			0.3386					
Littorina sp.	C	100 (6–346)	0.2418								
Elysia	A	96 (4–80)			0.2046	0.2181					0.2076
Cluster #2											
Mercenaria mercenaria	E	58 (4–206)	–0.2809	–0.2189				–0.3152	–0.2503		0.2568
Petricolia pholadiformis	E	50 (4–37)						–0.2266			0.2600
Anomia spp.	E	77 (3–49)						–0.3143	–0.2791		
Gemma gemma	E	38 (3–49)	–0.2211	–0.3039				–0.3762	–0.3235		0.2602
Trochophores	E	100 (4–3633)	–0.2546	–0.2969				–0.4401	–0.3869		0.2506
Barnea sp.	E	44 (4–74)	–0.2925			0.2148		–0.2709	–0.2210		0.3078
Cluster #3											
Tellina sp.	C	100 (6–2504)	0.3401	–0.6550		0.4390	–0.4624	–0.3688	–0.3917	0.3139	
Mulinia lateralis	C	92 (4–417)	0.2364	–0.5549		0.3370	–0.2294	–0.3207	–0.3091		0.2332
Pitar sp.	C	73 (3–147)		–0.2123			–0.2635				
Cyrtopleura costata	C	100 (11–4591)	0.4022		–0.2920	0.2077	–0.2886			0.3293	–0.2618
Anadara sp.	C	96 (4–196)		–0.2877			–0.2637	–0.2435	–0.2548	0.1955	
Bittium sp.	C	96 (4–2602)	0.2224	–0.3669	–0.2673		–0.3462	–0.2516	–0.3007	0.3223	
Cluster #4											
Lacuna	D	96 (4–66)		0.2016							–0.2637
Natica	D	100 (3–683)		0.2927	–0.2600					0.2955	–0.3588
Odostomia	D	100 (4–922)	0.2001	0.2557	–0.4547	–0.2409				0.4053	–0.5412
Cluster #5											
Retusa sp.	B	58 (3–159)									
Magelonids	B	65 (3–976)									
Cluster #6											
Cerithiopsis sp.	B	50 (3–107)									
Nassarius sp.	A	23 (3–263)									
Orbiniidae	A	23 (4–173)				0.2663	–0.2466				

The percentage of the stations where these organisms were caught and the range in concentration (no. m^{-3}) are presented in columns 2 and 3, respectively. The remaining columns in the table present the results of correlations between the concentration of an organism and the physical variables or chlorophyll fluorescence. Only significant ($P < 0.05$) r values are presented.

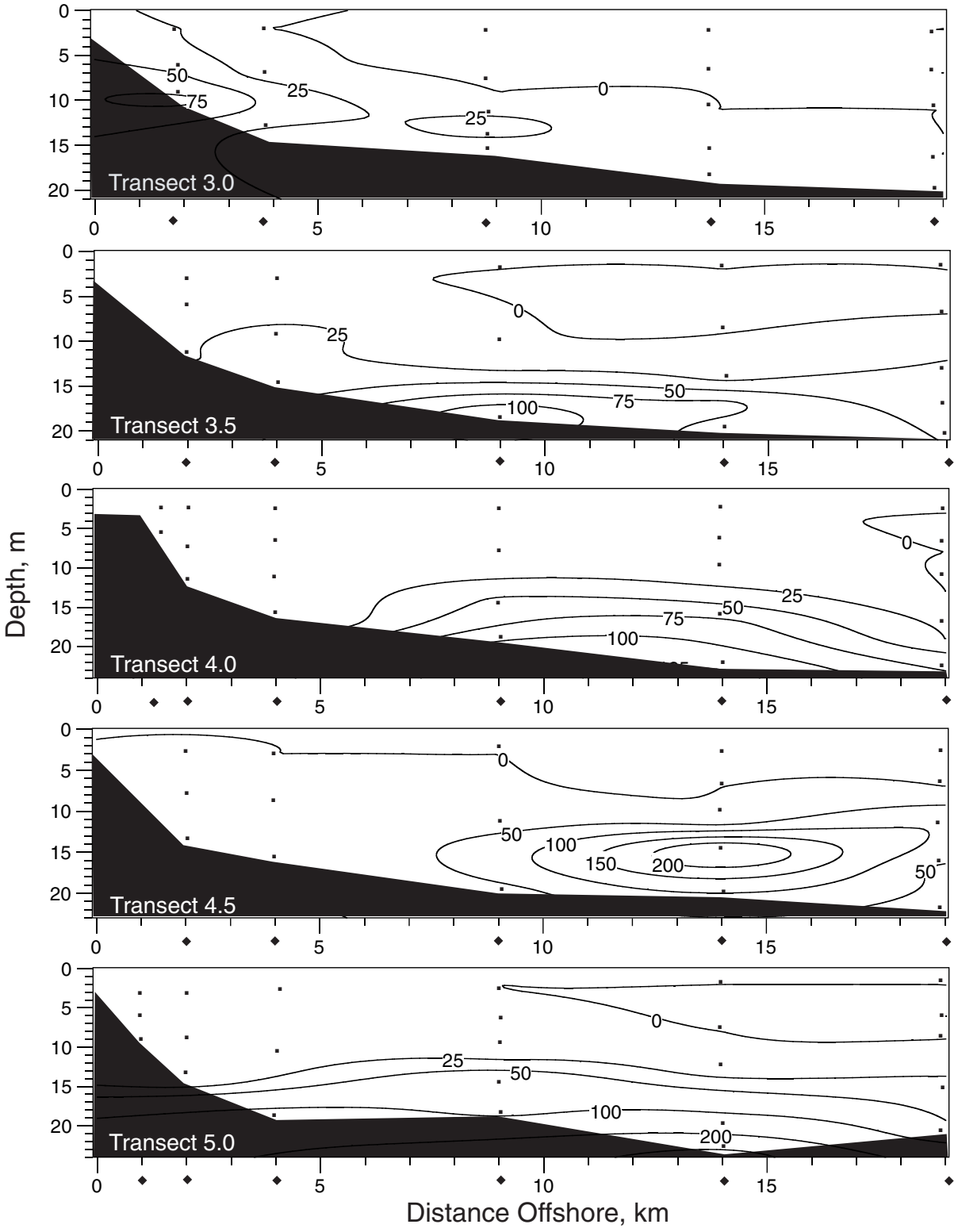

Fig. 11. Contour plots of *E. directus* concentrations (no. m^{-3}), an example of a Cluster #1 or Cluster A larva, along each of the transect lines. The black diamonds along the horizontal axes indicate station locations. Sample depths at each station are presented in Table I.

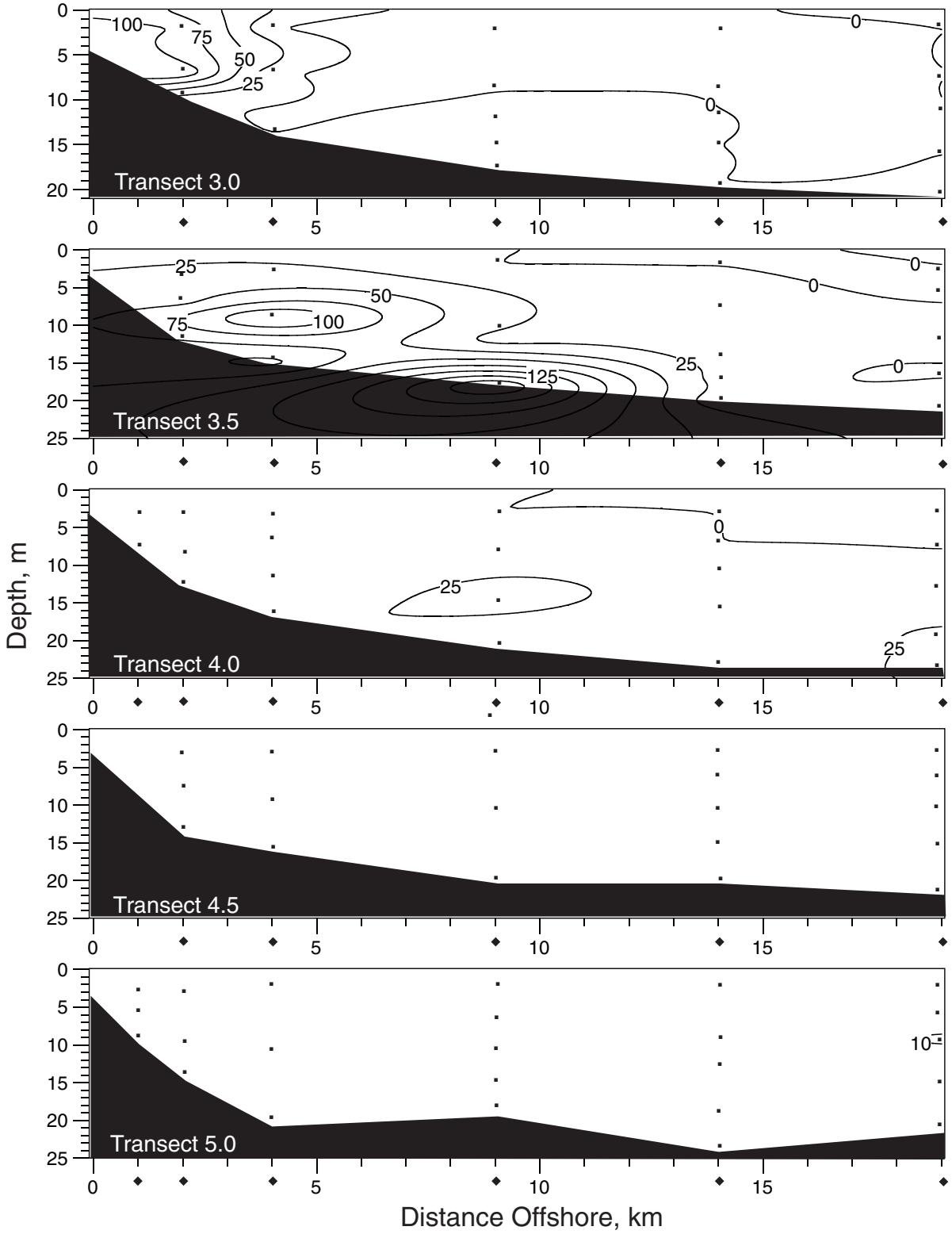

Fig. 12. Contour plots of *M. mercenaria* concentrations (no. m^{-3}), an example of a Cluster #2 or Cluster B larva, along each of the transect lines. The black diamonds along the horizontal axes indicate station locations. Sample depths at each station are presented in Table I.

Cluster #3

Cluster #3 consisted of the bivalves *Mulinia lateralis*, *Tellina* sp., *Anadara* sp., *Pitar* sp. and *Cyrtopleura costata*, and the gastropod *Bittium* sp. Organisms in this cluster were amongst the most abundant. They were caught at most or all of the stations within the grid, suggesting that while they may have been present in the plume water they were also a component of the general shelf zooplankton community (Table II). Their abundance tended to be significantly positively correlated with distance alongshore and negatively correlated with distance offshore, suggesting that they increased in number to the south and were most numerous near the coast. Their numbers tended to be significantly negatively correlated with depth, salinity and density, and positively correlated with temperature (Table II). This combination of significant correlations suggests that they tended to be found in the water above the pycno-cline. Lastly, their abundance tended to be significantly positively correlated with cross-shelf flow and negatively correlated with alongshore flow. In other words, higher numbers tended to be found in offshore flow and in areas of highest southward flow. The distribution of *Tellina* sp. will be used to describe the general pattern of distribution of organisms within this cluster.

Along transect line 3.0, *Tellina* sp. was caught at all of the stations, but it was most highly concentrated (~500 m^{-3}) in plume waters with salinities < 29 p.s.u. (Figure 13). At and just seaward of the plume front, we found concentrations between 200 and 100 m^{-3}. Seaward of waters with salinities < 32.5 p.s.u., larval concentrations were <100 m^{-3}. Along transect line 3.5, the highest concentrations of *Tellina* sp. were centered on the pycnocline under the plume and between 2 and 6 km offshore. Seaward of the 30 p.s.u. isohaline, larval concentrations of between 200 and 50 larvae m^{-3} extended offshore above and below the pycnoline. Even fewer *Tellina* sp. larvae were present in the plume waters along transect 4.0. The highest concentrations of *Tellina* sp. were found immediately under the plume waters (Figure 13). Extending offshore and centered on the thermocline, *Tellina* sp. was found at concentrations of from 50 to 100 m^{-3}. Right next to shore along transect 4.5 was a thin lens of water with salinity < 31.5 p.s.u. Within these waters, the concentration of *Tellina* sp. larvae was ~400 m^{-3}. Below and offshore of the 31.5 p.s.u. isohaline we found an ~8-km-wide zone of waters in which the concentration of *Tellina* sp. was >800 m^{-3} and rose as high as 1200 m^{-3}. Concentrations of ~100–200 *Tellina* sp. m^{-3} were found above the pycnocline from 9 km offshore to the seaward edge of transect 4.5 (Figure 9). Lower concentrations were found below the pycnocline. In transect 5.0, very high concentrations of *Tellina* sp. larvae (e.g. as high as 2000 m^{-3}) were found above 12 m depth and landward of 9 km. Concentrations decreased seaward of 9 km. Along transects 3.5–5.0, the highest concentrations of *Tellina* sp. were found associated with the low-chlorophyll waters that were downwelled between the plume and the area where the thermocline contacted the bottom (compare Figures 8 and 13).

Cluster #4

Cluster #4 was composed of the gastropods *Lacuna* sp., *Natica* sp. and *Odostomia* (Table II). Organisms in this cluster were moderately abundant and they were present at nearly all of the stations. Significant positive correlations were found between offshore distance and temperature, and significant negative correlations were found between depth and chlorophyll fluorescence. Taken together, this combination of significant correlations suggests that organisms in this cluster tended to be found primarily offshore and above the pycnocline. *Natica* sp. will be used as an example of the distribution of organisms in this cluster.

In general, the highest concentrations of *Natica* sp. were found above the pycnocline and at the outer edge of the transects (compare Figures 14 and 5). The lowest concentrations of *Natica* sp. were found along transects 3.0, 4.0 and 5.0 (concentrations <50 m^{-3} along transects 3.0 and 4.0, and <200 m^{-3} along transect 5.0; Figure 14) where the onshore flow above the pycnocline was highest (Figure 7). The highest concentrations (400–600 m^{-3}; Figure 14) were found along transects 3.5 and 4.5, where, in contrast, the onshore flow was weakest (< –5 cm s^{-1}; Figure 7).

Clusters #5 and #6

The organisms in Clusters #5 and #6 had very restricted distributions. Cluster #5 was composed of the gastropod *Retusa* sp. and polychaete larvae in the family Magelonidae (Table II). They were present at ~60% of the stations. They were found at low concentrations at most stations. In fact, the only place where they were abundant (159 *Retusa* sp. m^{-3} and 976 magelonids m^{-3}, respectively) was along transect 5.0 at 9 m depth at the 19 km station. Water at this location was amongst the warmest in the entire grid (~23.5°C; Figure 4). Cluster #6 was composed of the gastropods *Cerithiopsis* sp. and *Nassarius* sp., and larval polychaetes in the family Orbiniidae. Larvae in this cluster were caught at less than half of the stations in the grid and, like the organisms in Cluster #5, they were only abundant at one location. In this case, they were abundant only at 20 m depth, 14 km offshore along transect 4.5. In neither of these clusters were there significant relationships between the distributions of the larvae and the physical variables.

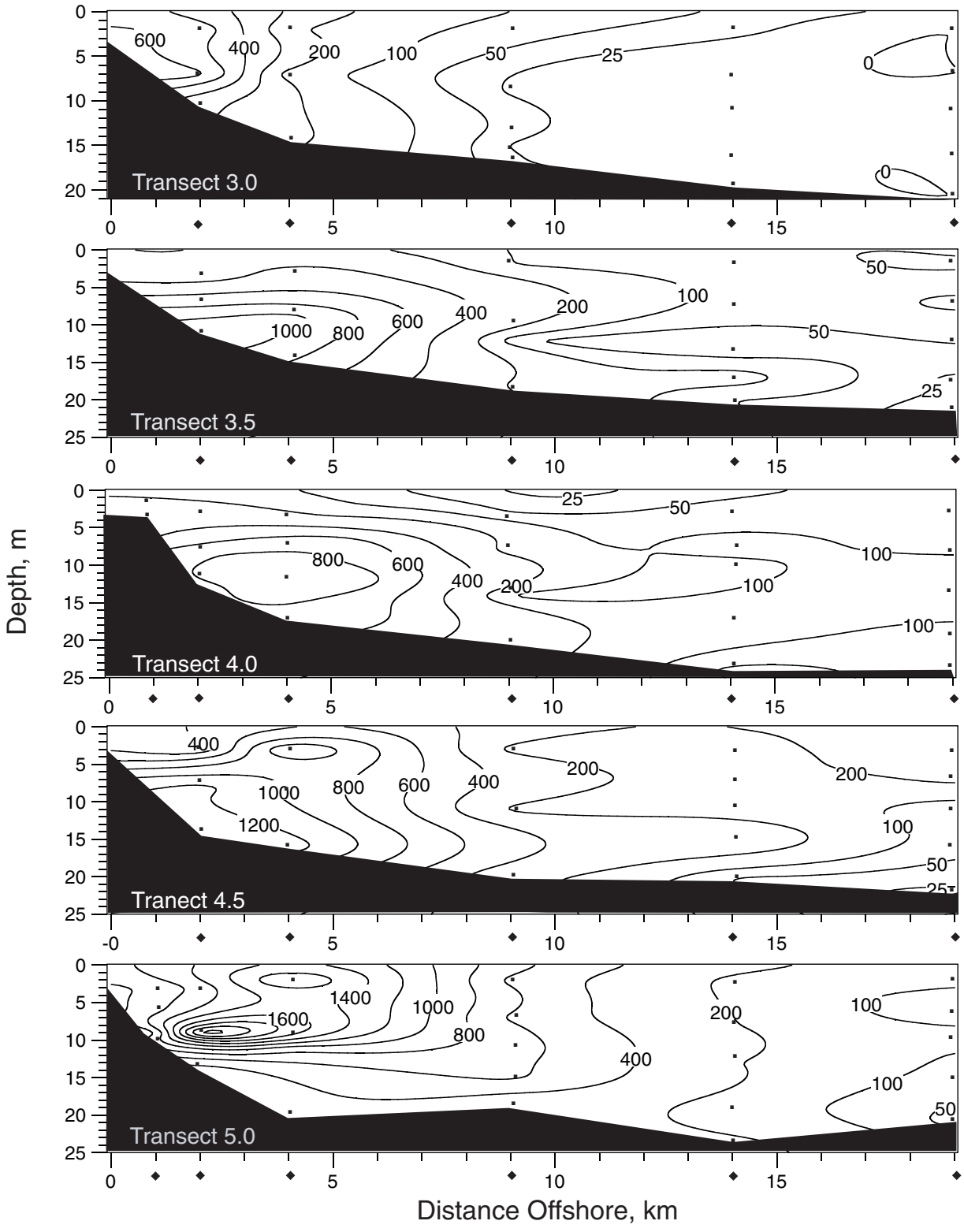

Fig. 13. Contour plots of *Tellina* sp. concentrations (no. m^{-3}), an example of a Cluster #3 or Cluster C larva, along each of the transect lines. The black diamonds along the horizontal axes indicate station locations. Sample depths at each station are presented in Table I.

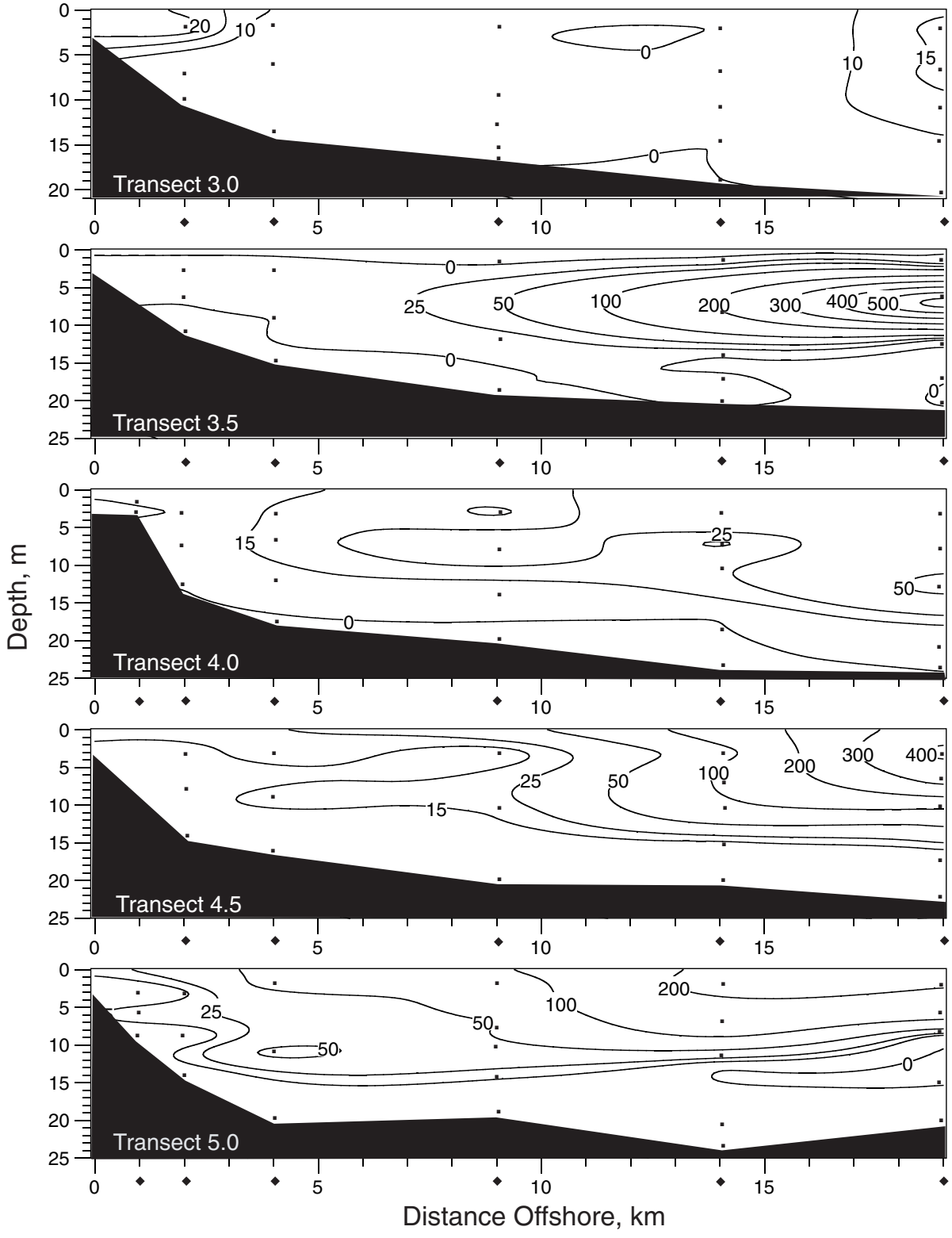

Fig. 14. Contour plots of *Natica* sp. concentrations (no. m^{-3}), an example of a Cluster #4 or Cluster D larva, along each of the transect lines. The black diamonds along the horizontal axes indicate station locations. Sample depths at each station are presented in Table I.

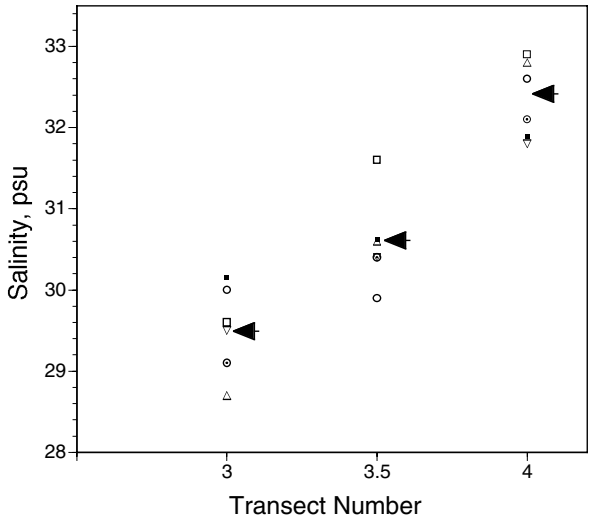

Fig. 15. Comparison of the average salinity at which larvae in Cluster 2 were found along transects 3.0, 3.5 and 4.0. The larvae in Cluster 2 were *M. mercenaria* (open squares), *Gemma gemma* (open circles), *Anomia* spp. (downward-pointing triangles), *Petricolia pholadiformis* (upward-pointing triangles), *Barnea* sp. (closed squares) and polychaete trochophores (open circles with a center dot). The average salinity at which all of the larval types within the cluster and along each transect is indicated by the arrows symbol. The salinity at which the larvae were found increased significantly with distance down the coast (ANOVA: d.f. = 2,15, F = 43.908, $P < 0.00001$).

DISCUSSION

In this study, we attempted to test the hypothesis that ciliated larvae act as passive particles. Using data on the distribution of larvae, there are two ways in which we might test this hypothesis. First, if larvae act as passive particles, then their distribution should be tied to a water mass (Okubo, 1994). In a study restricted in space and time, such as this one, transect-to-transect changes in the distribution of a water mass should be matched by changes in the distribution of larvae in that water mass. Use of this criterion to define larval behavior as passive could be confounded by either the input of new larvae from spawning or their removal by predation or settlement. Owing to the size of the mesh in the plankton net used in this study, few early stage larvae were caught and, thus, the input of spawned individuals will not confound the analysis. Sampling of the entire grid of stations took less than a day, suggesting that mortality due to predation should also not confound the analysis. Lastly, only a small proportion of the larvae were at a stage of development competent to settle (L. Brink, unpublished data), suggesting that this source of variation in larval abundance is also probably of minimal influence. Given the small spatial and temporal coverage of this study, if larvae were dispersed as functionally passive particles at this temporal scale, then their distribution should be tied to a water mass. A second way in which we can determine whether larvae are acting as passive particles is by observing how the distribution of the larvae changes around convergences and divergences. Around a convergence or divergence, larvae acting as passive tracers will simply follow the water streamlines and there will be no change in their concentration (Franks, 1992). In contrast, relatively strong-swimming larvae (e.g. swimming speeds > vertical current speeds) will be swept into a convergence zone where, if they attempt to maintain their depth, they will become concentrated (Franks, 1992; Bakun, 1996). These two criteria will be used to judge whether larval types in each of the clusters were acting as passive particles.

Clusters #1 and 4 were made up of larvae that tended to be found in the waters below and above the pycnocline, respectively. The shoreward limit to the distribution of larvae in Cluster #1 was found roughly where the pycnocline contacted the bottom (compare Figure 5 with Figure 11). The several larval types that made up Cluster #4 were generally found above the pycnocline and no closer to shore than ~10 km. Under the downwelling conditions that prevailed during the sampling, the distribution of the larvae in these two clusters was roughly tied to water mass types and, furthermore, there was little indication that they were concentrated in convergence zones. These observations suggest that larvae in Clusters #1 and 4 were acting as passive particles.

The organisms in Cluster #2 (Table II) appear to have entered the study area in the plume waters sampled in transect 3.0, but the subsequent change in their distribution suggests that these larvae may have actively crossed the halocline and front associated with the plume waters. Looking at just those transects that contained plume waters (e.g. transects 3.0, 3.5 and 4.0 contained waters with salinity ≤ 30 p.s.u.), the average salinity at which Cluster #2 organisms were found increased significantly southward (one-way ANOVA, F = 43.908, $P < 0.0001$; Figure 15). Along transect 3.0, the average salinity at which they were found was between 29 and 30 p.s.u. (i.e. the plume waters), but by transect 4.0 the average salinity had risen to between 31 and 33 p.s.u. (Figure 15). In addition, with the progression from transect 3.0 to 4.0, the location of high concentrations of these larvae was found at greater depths and farther offshore. Cluster #2 larvae were not tracking the water mass in which they apparently entered the study area.

The change in the distribution of Cluster #2 organisms is exemplified by the distribution of *M. mercenaria* larvae. Between transects 3.0 and 3.5, salinity in the plume rose slightly, due to mixing with shelf waters (Figure 3). At the same time, the concentration of *M. mercenaria* went from 50–100 m^{-3} in the plume waters of transect 3.0 to ~25–50

m^{-3} in the plume waters of transect 3.5 (Figure 12). In other words, between transect 3.0 and 3.5, the plume waters increased slightly in salinity but the concentration of *M. mercenaria* decreased by ~50%. The 'missing' *M. mercenaria* appear at two locations along transect 3.5, both seaward of the plume and at greater depths than they were found on transect 3.0. The southward decrease in the concentrations of Cluster #2 larvae in the plume waters coupled with the concurrent increase in their concentrations seaward of the plume and at greater depths suggest that these larvae may have left the plume waters, perhaps by swimming downward through the halocline marking the lower edge of the plume. These data suggest that the larvae in Cluster #2 were not acting as passive particles; their distributions did not remained tided to a water mass. This was true even over the relatively small spatial scales represented by the distance between transects 3.0 and 3.5 (10 km).

The larvae in Cluster #3 also appear not to have acted as passive particles. Unlike the larvae in Cluster #2, there is no indication that the larvae in Cluster #3 were moving from one water mass to another. The highest concentrations of Cluster #3 larvae, as exemplified by the distribution of *Tellina* sp., tended to be found landward of the location where the thermocline contacted the bottom (compare Figures 4 and 13) and where cross-shelf flow at the surface switched from onshore to offshore and/or roughly under the water with the highest southward flow (compare Figures 6 and 7 with 13). This is the area in which downwelling of the surface waters was occurring. This can be seen most clearly in the distribution of the waters containing low chlorophyll (Figure 8). In the zone of downwelling, these low-chlorophyll waters were pulled downward between the halocline beneath the plume waters and the top of the thermocline. It is in these downwelled waters that we found the highest concentrations of Cluster #3 larvae (compare Figure 8 with Figure 13). The areas in which Cluster #3 larvae were concentrated were characterized by convergent flows. The high concentrations of Cluster #3 larvae in these areas of convergent flow suggest that they were not acting as passive particles, but, due to their swimming behavior within the convergent flow, they became concentrated there.

The pattern of significant correlations between the abundance of larvae in Cluster #3 and the physical variables (Table II) suggests that these larvae were generally found above the pycnocline. At these depths, they would tend to be swept into convergence zones where the vertical currents would carry them downward. In order for organisms to become concentrated in a convergence zone, they must attempt to maintain their 'preferred' depth by successfully swimming against the downwelling current in the convergence (Franks, 1992). Vertical current speeds in these areas were on the order of 0.01 cm s^{-1} (Cudaback and Largier, 2001), speeds slower than the observed swimming speeds of bivalve veligers, which fall in the range 0.1–1 cm s^{-1} (Mileikovsky, 1973; Cragg, 1980; Chia *et al.*, 1984; Mann *et al.*, 1991). Laboratory experiments have demonstrated that some types of veliger exhibit high barokinesis to pressure increases of as little as 0.5 bar (Cragg, 1980; Mann *et al.*, 1991). High barokinesis is one way in which an organism can maintain a 'preferred' depth. Laboratory observations indicate that at least some types of veligers have the necessary swimming speeds and behavior to become concentrated in convergence zones.

In summary, the distributions of the larvae in Clusters #5 and 6 (Table 11) were so limited that it is not possible to determine whether they were passive tracers of water movement. The distributions of the organisms in Clusters #1 and 4 are consistent with the hypothesis that they were acting as passive particles. They tended to remain tied to water mass types and they did not have a tendency to become concentrated in convergence zones. In contrast, the larvae in Clusters #2 and 3 were apparently not acting as passive particles. The larvae in Cluster #2 did not remain tied to a water mass type and the highest concentrations of larvae in Cluster #3 were found in convergence zones.

Few studies have collected the data necessary to test the hypothesis that the larvae of benthic invertebrates act as passive particles. Banse made observations in Kiel Bay, a body of water subject to estuarine exchange between the Baltic and Danish coastal waters (Banse, 1986). He found that a variety of larval polychaetes and echinoderms remained tied to particular water masses, suggesting that during their dispersal they were acting as passive neutrally buoyant particles. Pedrotti and Fenaux made observations on the dispersal of echinoderm larvae in the Ligurian Sea (Pedrotti and Fenaux, 1992). The offshore extent of the distribution of these larvae was set by an offshore upwelling front, results consistent with the hypothesis that the larvae were acting as passive particles. The data presented in these two papers suggested that larvae were acting as passive particles.

Mann, working in Chesapeake Bay, found that oyster larvae moved passively through a frontal system and associated convergence zone (Mann, 1988). Farther down the estuary and closer to the sea, however, the larvae were found at shallower depths and in a different water mass, suggesting that in this part of the estuary they may not have been acting as passive particles. Thiebaut studied the distribution of the larvae of the polychaete *Pectinaria koreni* in relation to the Seine River plume (Thiebaut, 1996). The distribution of *P. koreni* larvae appeared to have been tied to the distribution of Seine River plume waters,

suggesting that they were acting as passive particles. However, they also appeared to have been concentrated at a presumably convergent front associated with the edge of the plume, suggesting that, at least within a convergence zone, the larvae may not have been acting as passive particles. Shanks *et al.* found that a variety of larval invertebrates were highly concentrated around the convergence zone generated by an upwelling front that was moving shoreward following the end of upwelling winds (Shanks *et al.*, 2000). Furthermore, there is a large body of evidence suggesting that a variety of larval invertebrates and fish are concentrated and transported shoreward by the convergences generated by large internal waves [reviewed in (Shanks, 1995)]. Larvae found concentrated in convergence zones are not acting as passive particles.

As in the study reported here, the results from these previous investigations are mixed. Many types of larvae do appear to act as passive particles; their distributions suggest that they track the movement of a water mass and they do not become concentrated at convergence zones. In contrast, some larval types at times do not act as passive particles; their distributions do not track a water mass and/or they can become highly concentrated at convergence zones.

It is tempting to compare the distributions of the larvae to the habitats in which they are found as adults. One might hypothesize that the larvae of organisms that, as adults, live in the intertidal or shallow subtidal zones might have a more nearshore distribution than do those of adults that are broadly distributed across the shelf. Several factors limit our analysis. We identified polychaete larvae only to family; hence, the habitat of the adults that spawned these larvae is unknown. We identified gastropod larvae to genus and that, in most cases, also means we do not know the habitat of the adults. Because the adult habitat of the larval polychaetes and gastropods is unknown, we cannot use them to test this hypothesis.

Was there a difference in the depth of the habitat of the adult bivalves from which the bivalve larvae in the different clusters were derived? Using Theroux and Wigley (Theroux and Wigley, 1983), we determined the average depth of occurrence of the adult bivalves in Clusters 1–3 and in the very similar Clusters A–C. The average depth of occurrence of the adults from these clusters was significantly different (see the legend to Figure 16). The water depth at which adults of larvae in Clusters 1 and A were found averaged 29 m (SD = 18 m) and 34 m (SD = 16 m), respectively (Figure 16). Larvae in these clusters tended to be found below the pycnocline in deeper waters (generally >15 m depth) and farther from shore (generally >5 km offshore), waters that are adjacent to their future adult habitat. The water depth at which adults of Clusters 3 and C larvae were found averaged 12 m (SD = 7 m) and 10 m (SD = 8 m), respectively (Figure 16). Their larvae tended to be most abundant relatively close to shore (generally <5 km from shore) in shallower waters (generally <15 m depth); these larvae were also found in waters adjacent to their future adult habitat. Larval bivalves in these two clusters tended to be found in waters adjacent to the habitat into which they would eventually settle. This is similar to Grosberg's finding that the vertical depth distribution of barnacle cyprids was similar to the depth distribution of the adults (Grosberg, 1982). The cyprids were also found in waters adjacent to the adult habitat.

The average depth of adults in Clusters 2 and B was 19 m (SD = 31 m). From an inspection of Figure 16, it appears that the adult depth of *Anomia* sp. is an outlier. Recalculating the average depth of adults in Clusters 2 and B without *Anomia* sp., we find average adult depths of 5 m (SD = 2 m) and 9 m (SD = 7 m), respectively. These larvae appear to have entered the study area in the intruding plume waters, but by transects 3.5 and 4.0 they were at low concentrations in the plume waters and were found deeper and farther offshore. This shift in larval distribution would probably not have affected the chances of *Anomia* sp. finding a settlement site as the

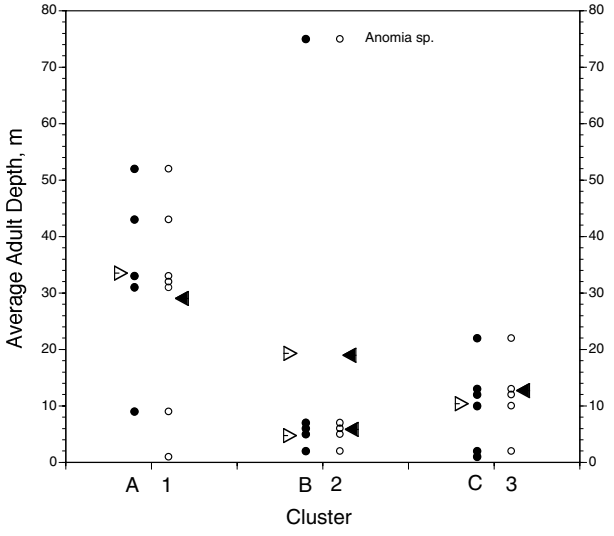

Fig. 16. The average depth of occurrence of the adults of the larvae in Clusters 1, 2 and 3 (open circles; cluster average open arrow) and Clusters A, B and C (closed circles; cluster average black arrow). There was substantial overlap in the members of the numbered and lettered clusters (see Table II). The average depth of occurrence of adults was determined from Theroux and Wigley (Theroux and Wigley, 1983). In Clusters B and 2, there are two sets of arrows. One set was calculated using the entire data set and the other was calculated excluding *Anomia* spp. An ANOVA indicated that the overall average depth of occurrence of the adults in the lettered clusters was significantly different (d.f. = 2,11, $F = 27.22$, $P < 0.0001$). If *Anomia* spp. was excluded from the data set, then the overall average depth of occurrence of the adults in the numbered clusters was also significantly different (d.f. = 2,13, $F = 5.03$, $P = 0.024$).

adults of this species are found across the continental shelf (Theroux and Wigley, 1983). The same may not be true for the other species in Cluster 2 or B. These species as adults tend to be found in estuaries or in the intertidal zone (Theroux and Wigley, 1983). The deeper distributions of larvae found in the more southern transects may have placed them in waters unfavorable for future successful settlement.

In summary, we collected an extensive set of biological and physical oceanographic data on a grid of transects during a downwelling event with associated intrusion of a plume of Chesapeake Bay estuarine waters. The meroplankton community sampled in these waters could be broken down into clusters of organisms with similar distributions. Two clusters were composed of just a few taxa and they were found in abundance in small patches; little could be said about their distribution. There was a cluster that was found predominantly above the pycnocline and a second cluster that was most common below the pycnocline. The tight association between the water mass and the larval distributions is consistent with the hypothesis that these larvae were behaving as passive neutrally buoyant particles. We found a cluster that appeared to enter the study grid with the estuarine plume waters. They were tightly coupled to the plume in the more northern transect, but in the transects to the south they were no longer associated with the plume; they were found at greater depths, seaward of the plume in saltier waters. This change in distribution suggests that they may not have been acting as passive particles; by their behavior, they moved from one water mass, the plume water, into an adjacent one. The last cluster consisted of organisms that were most abundant in the convergence zone that formed between the plume waters and the downwelling surface layer. Their consistently high concentration in the convergence zone suggests that they were also not acting as passive particles; only actively swimming organisms or buoyant particles can become concentrated in a convergence (Franks, 1992).

Whether larvae act as passive or active particles will profoundly affect their dispersal. The results of this and previous studies suggest that one cannot model the dispersal of invertebrate larvae, even ciliated larvae, by simply assuming that they are acting as passive particles; larvae, even ciliated larvae, do not necessarily track a parcel of water. The dispersal path of larvae does not necessarily equal the movement of water in which they are found.

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