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Differences in fine-scale structure and composition of zooplankton between mixed and stratified regions of Georges Bank

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Abstract—Transects were made with the Video Plankton Recorder (VPR) in different water masses on the southern flank of Georges Bank in May 1992. CTD-data, chlorophyll fluorescence, and attenuation were measured simultaneously. Images were recorded at a rate of 60 fields per second, as the instrument was towed at 2 m s^{-1} (4 knots). Tapes from high and low magnification cameras (imaging volumes of 0.62 ml and 33 ml, respectively) were analyzed with respect to the distribution of copepods and other grazers, as well as invertebrate predators. This paper describes the differences in patterns of occurrence of important zooplankters in well-mixed and stratified waters on the Bank and in Slope Water south of these stations. Planktonic taxa were sampled over the same range of scales as the fluorescence and hydrography, allowing direct visual comparisons of the spatial distributions of these variables. Late copepodites of *Calanus finmarchicus* were strongly concentrated near the surface in the stratified area, while a dense belt of *Limacina* sp. and *Oikopleura* sp. occurred below the pycnocline. Other fragile forms were also found to be dominant. Colonies of hydroid polyps were very abundant at the mixed station, especially deeper in the water column, indicating that they may have been transported up from the bottom. Colonies of the diatom *Chaetoceros socialis* were abundant in the cold bottom water in the stratified region and also in the mixed area. These colonies may have been in the process of sedimenting out of the water column, as similarly sized and shaped marine snow was abundant in the same area. In the Slope Water, acantharia and *Trichodesmium* were found in the chlorophyll maximum above the pycnocline. Other important genera encountered were: *Pseudocalanus*, *Oithona*, *Centropages*, *Obelia*, *Pleurobrachia* and *Sagitta*. Taxa that occurred in all three areas were often differently distributed with respect to depth and physical parameters, indicating that vernal stratification is an important structuring factor of plankton populations.

INTRODUCTION

The distribution of planktonic organisms in the sea, as in other habitats, is determined by environmental characteristics and interactions with other organisms. It is important to determine spatial relationships as a means to understand the interactions between organisms, and between the organisms and their physical environment. In the sea, however, we normally do not see plankton, because of their minute size and transparent appearance, but also because their habitat is inaccessible to us. Until recently, we have used point or integrative sampling methods to collect plankton and to determine their distribution and abundance. The refinement of acoustic methods (echo sounding) has helped us to detect swarms of plankton, especially in broad-scale studies (e.g. Wiebe and Greene, 1994). However, we are still struggling to combine a high degree of spatial

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resolution with accurate species information. The towed Video Plankton Recorder (VPR; Davis *et al.*, 1992a, 1992b) allows us to see small, undisturbed plankton in their natural habitat, and simultaneously collect information on environmental parameters, such as salinity, temperature, and chlorophyll fluorescence. A high sampling frequency—30–60 images per meter tow path—gives contiguous images along the tow path at low magnification (Camera 2) and an image every few (~3–4) centimeters for high magnification (Camera 4). This makes the method useful also for studies of micro- and fine-scale distribution (μm–km scale; Haury *et al.*, 1978) of planktonic organisms and detritus all the way up to the air–sea interface. Fragile species, such as ctenophores and some protozoans, which cannot be identified in net samples, or which are dissolved in preservatives, can be identified in video images.

This paper presents distributional data from three tows made during a VPR instrument testing cruise to Georges Bank in May 1992. This cruise also was used as a platform to conduct pilot VPR sampling for the Global Ocean Ecosystem Dynamics (GLOBEC) Georges Bank Program. We describe fine-scale distribution patterns for some of the important zooplankton species observed in short transects at three different locations on the southern flank of the bank. These tows represent the mixed, shallow area on top of the Bank, the stratified area in slightly deeper waters, and an area on the slope of the Bank, affected by warmer water from the Gulf stream.

MATERIALS AND METHODS

Video Plankton Recorder transects were made at three locations on the southern flank of Georges Bank on 21–22 May 1992 from R.V. *Endeavor*, cruise no. 237 (Fig. 1). Tow 3 was made at 41°20′N, 67°28′W in mixed, shallow water (40–45 m) at *ca* ~13:00 h. Tow 4 was made at 17:30–18:30 h in stratified water (*ca* 80–90 m deep) at 40°55′N, 67°18′W. Tow 5 was made in deeper Slope Water (140–160 m depth) at 40°34′N, 67°13′W beginning at midnight. The instrument was towed up and down 3–5 times, in "tow-yos", as the ship moved at $2\ m\ s^{-1}$ (4 knots). Video recordings were made at four different magnifications; the data from two cameras were used in this analysis. These cameras had fields of view (FOV) of 4.5×6.0 mm and 24.5×34.0 mm, respectively, with focal depths of 23 mm and 40 mm. The corresponding sample volumes were 0.62 ml and 33 ml, respectively. The focal depth was calibrated against a standard tape. Only objects perceived by the investigator as being in focus, i.e. within the sample volume, were analyzed. The higher magnification was suitable for the identification of small copepods, pteropods, invertebrate larvae, and large diatoms. Older stages of *Calanus*, appendicularians, chaethognaths, small medusae, and ctenophores were better represented in the lower magnification.

The image data were analyzed by manually scrolling through the tapes using a dynamic tracking VTR (Betacam sp) and identifying items in focus to nearest taxon. Video overlay permitted the selection of taxon from a list on-screen and digitization of size using a mouse. This information was written to an ASCII file along with a time code and a short comment using Matlab (Mathworks, Inc.) software running on an 80486 PC. Time codes were input from the video via a time code reader (Horita Inc.) connected to the serial port of the PC and using a PASCAL routine (called from within the Matlab program) to read in the data. A total of *ca* 1.26×10^5 FOV was analyzed for Tow 3, 2.10×10^5 for Tow 4 and 3.93×10^5 for Tow 5. Most of these FOVs were empty of organisms.

Data were sorted and organized using Excel for Windows. Further data processing and

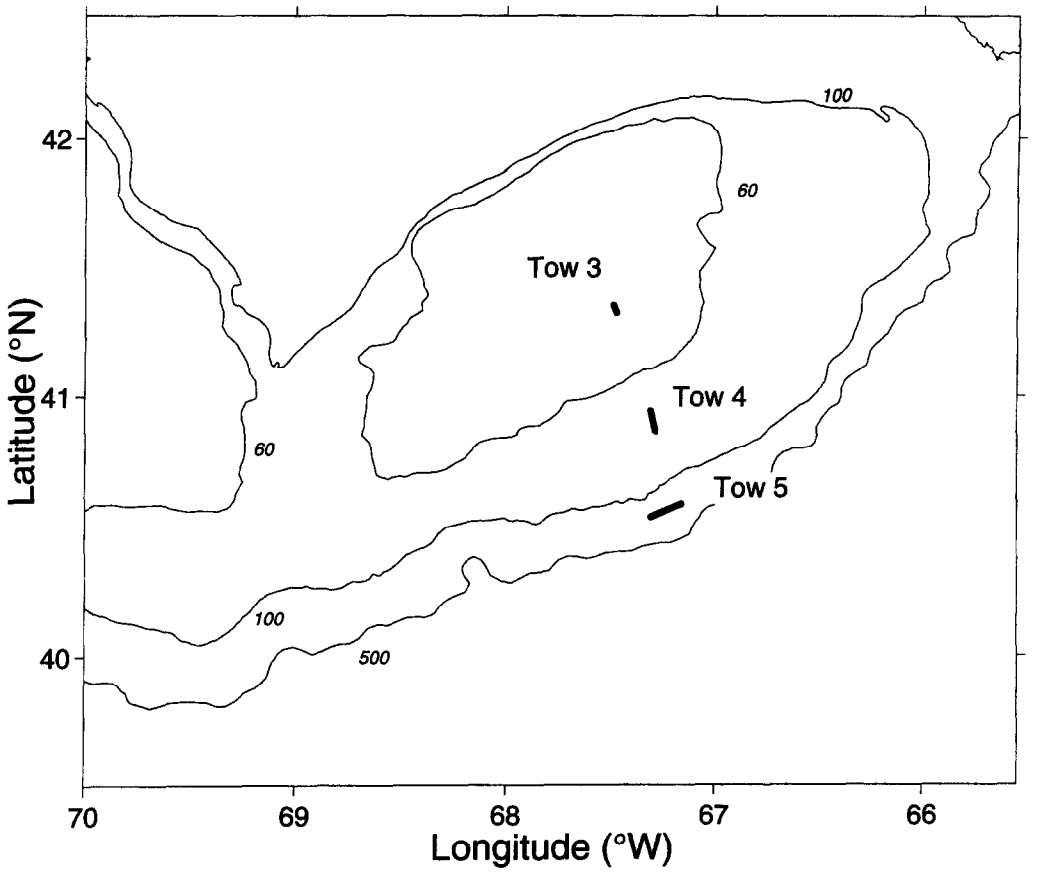

Fig. 1. Georges Bank, 21–22 May 1992. Video Plankton Recorder Tows 3, 4 and 5. Lines for transects are based on positions at the start and end of each of the tows. Depth contours are in meters.

graphic representation were carried out in Matlab for Windows. Data on zooplankton occurrence were transformed to abundance data by binning sightings into 1 m depth bins along the tow path.

Two dimensional gridding (i.e. depth and distance) was done using a custom gridding program written in FORTRAN, which employed an inverse square spline method. The NCAR Zgrid operator (∇^2–$3\nabla^4$) was used for gridding. The gridded data were then contoured in Matlab, employing a smoothing routine. Organism data were square-root transformed in order to make optimal use of the color axis. These graphs should be viewed as a means to visualize the spatial distribution of plankton rather than as statistically accurate pictures. In sparse data sets, e.g. ctenophores and chaetognaths, individual animals can be seen as bright spots surrounded by dark blue.

RESULTS

Environmental characteristics

The mixed station (Tow 3) had a nearly constant temperature of 6.5–6.7°C and salinity of 32.4–32.5‰ (Fig. 2A), while chlorophyll fluorescence increased toward the bottom (Fig. 2A, B). The stratified station (Tow 4) featured a pycnocline at 10–18 m, where temperature shifted from ~6°C in the surface to below 4°C in deeper waters and salinity increased from 31.7‰ in surface waters to 32.3‰ in deeper waters. Chlorophyll fluorescence increased below the pycnocline. An intrusion of slightly colder water was seen at mid-depth in the last portion of Tow 4. The low temperatures at this station were the residue of Scotian shelf water extending south to George's Bank earlier in spring 1992 (Bisagni *et al.*, 1996). The slope station (Tow 5) had water of higher temperature and salinity and a pycnocline at 30 m depth. Water above the pycnocline was 14.4–16°C and had a salinity of 34.8–35.3‰ (Fig. 2). Chlorophyll fluorescence had a maximum from 25–40 m, around the pycnocline. Shelf water of lower temperature (*ca* 5°C) and salinity (32.5‰) was mixed into the last part of Tow 5 (Fig. 2), with a shallower pycnocline and chlorophyll maximum.

General distribution patterns in the three areas

At the mixed station (Tow 3), most zooplankton were distributed throughout the water column in patches (Fig. 3). Many of the species were the same as in the stratified station (Tow 4), but in lower abundances (Table 1). Invertebrate predators also were dispersed throughout the water column, while the hydroid colonies that were specific for this area, were more abundant towards the bottom. Tow 4 (the stratified station) displayed a distinct layering of different zooplankton species (Fig. 4), albeit in wide bands. In general, there was an upper belt of herbivorous copepods, a wide belt of pteropods and appendicularians around the pycnocline (in the cold water intrusion), and a dense belt of marine snow and diatom colonies below the pycnocline. Omnivorous small copepods were dispersed all through the water column, but tended to be less abundant below the pycnocline (Fig. 4). The slope station (Tow 5) had a strong concentration of zooplankton in the warm layer above the pycnocline (Fig. 5), while there was mostly marine snow in the deeper layers of the water column (Fig. 9C).

Distribution of microplankton

Colonies of the diatom *Chaetoceros socialis*, forming lumps up to a few millimeters in size, were found in all three tows. Highest densities were observed at the mixed station. *C. socialis* formed a dense belt below the pycnocline in Tow 4, intermingled with clouds of marine snow (Figs 6 and 9). In Tow 5, colonies of *C. socialis* occurred in considerably lower densities and primarily in the shelf water at the end of the tow (Table 1 and Fig. 6). The cyanobacterium *Trichodesmium* was common in the warm waters above the pycnocline in Tow 5.

Protozoa were observed in all tows. In both the mixed and stratified stations on the bank, tintinnids and *Globigerina*-type foraminifera were common (Table 1). Sarcodine acantharia were especially conspicuous above the pycnocline in the warm slope waters of Tow 5 (Fig. 5).

Table 1. *Georges Bank*, 21–22 *May* 1992. *Abundance of important zooplankton taxa and one form of phytoplankton, determined from transects made with the Video Plankton Recorder (VPR) at three locations*

Taxon phylum order/family (*genus*)	TOW 3 mixed location 54 m (mean ± SD)	TOW 4 stratified location 66 m (mean ± SD)	TOW 5 slope location 100 m (mean ± SD)	Camera no.
Bacillariophyta				
Chaetoceros socialis, colonies	5543±7727	1486±2951	6.72±41.0	4
Cyanophyta				
Trichodesmium	0	+	6.36±37.7	4
Sarcodina				
Acantharia	0	+	19.2±70.5	4
Foraminiferida, (*Globigerina*)	1772±4153	412±1408	+	4
Ciliophora				
Tintinnida	0	178±1020	3.9±26.7	4
Cnidaria				
Anthozoa, Ceriantharia	2.38±18.5	0	0	2
Hydrozoa, medusae	3.98±27.1	4.42±22.2	0.88±9.84	2
Obelia medusae	6176±7656	0	0	4
Hydroids, polyps	8079±16010	0	0	4
Hydroids, colonies	521±430	0	0	2
Ctenophora				
Cydippida(*Pleurobrachia*)	0	5.83±26.2	0.72±8.19	2
Lobata	0	4.03±21.0	+	2
Annelida				
Polychaeta (Spionidae larvae)	1075±3708	not counted	10.8±40.6	4
Mollusca, Gastropoda				
Pteropods (*Limacina*)	+	928±2779	2.85±22.5	4
Unident. veligers	9.85±47.2	0	0	2
Arthropoda, Crustacea				
Krill, decapod larvae	3.43±20.6	2.54±15.9	4.17±19.9	2
Amphipoda	0	11.6±14.1	+	2
Copepoda				
Calanus, all life history stages	18.3±15.7	682±2106	1.83±19.4	4
Calanus, older stages	12.2±48.6	88.6±174	23.6±65.0	2
Centropages	0	+	124±523	4
Metridia	0	+	1.18±8.94	4
Oithona spp. (incl. females)	148±1094	2348±3816	72.7±159	4
Oithona females with eggs	+	418±1506	10.2±15.9	4
Pseudocalanus sp. (incl. females)	428±1873	2395±3739	8.86±42	4
Pseudocalanus females w eggs	+	192±961	2.76±19.8*	4
Unident. cyclopoids (*Oncaea*)	0	283.9±1403	4.35±28.1	4
Nauplii	+	1971±3846	3.94±27.4	4
Unident. or rare copepods	278±1547	875±2223	17.9±61.4	4
Echinoderma				
Ophiopluteus w/flexible arms	0	239±1190	0	4
Metamorphosed form of previous	0	46.3±414	21.1±72.4*	4
Other pluteus larvae	0	129±787	+	4

(*continued*)

Table 1. *Continued*

Taxon phylum order/family (*genus*)	TOW 3 mixed location 54 m (mean ± SD)	TOW 4 stratified location 66 m (mean ± SD)	TOW 5 slope location 100 m (mean ± SD)	Camera no.
Chaetognatha				
Sagitta	11.9±60.6	1.14±9.34	2.06±13.1	2
Chordata, Appendicularia				
(*Oikopleura*)	1.95±15.5	75.3±122	176±335	2
Unidentified, camera 4	255±1411	953±2255	20.0±60.7	4
Unidentified, camera 2	9.57±40.9	10.7±31.4	18.3±26.0	2

Abundance has been calculated for each vertical section (leg) of the tows, and is given as numbers of individuals per m^3 (mean±SD; $n=10$ for Tows 3 and 4, $n=6$ for Tow 5). Maximum sampling depth is given for each tow. Camera 2 has a lower magnification than camera 4 and is therefore suitable for larger organisms. + denotes less than five observations in the transect. * denotes the use of camera 2 for a species which is usually counted in camera 4 images. In some cases, abundance estimates have been made with data from both cameras.

Distribution of herbivores and omnivores

Several species of meroplankton were prominent at the mixed station (Tow 3), e.g. veligers, and larvae of ceriantharia (burrowing anthozoans). Spionid polychaete larvae were very abundant and often shown perched on a piece of detritus in the video images. Other groups found here were appendicularians, small decapods, and copepods.

The stratified station (Tow 4) had the highest abundance of the small copepods *Pseudocalanus* and *Oithona* (*O. nana*, *O. similis* and *O. spirinostris* could be distinguished in many video images) and *Calanus finmarchicus*, as well as *Limacina* sp pteropods (Table 1 and Fig. 4). Appendicularians of *Oikopleura*-type were also common here. Other taxa observed here were the calanoids *Centropages*, *Microcalanus* and the cyclopoid *Oncaea*. A group of meroplankton, especially common in Tow 4, were echinoderm larvae (Fig. 7). A type of ophiopluteus with soft, flexible arms were abundant in the pycnocline and in the cold water intrusion. This form apparently metamorphosed in the the water column into a five-armed juvenile forms that occurred closer to the bottom (Fig. 7). The latter, star-shaped larvae also were found in Tow 5 (Table 1).

The highest densities of appendicularians were found in the warm slope waters of Tow 5 (Table 1 and Fig. 5). These were small (head width <0.5 mm) and occurred in densities up to several in one low-magnification (25×31 mm) FOV and were likely to have been another species than those occurring in the other tows. The most common copepods here were *Centropages*, *Metridia* and *Calanus*, followed by *Pseudocalanus* and *Oithona* in order of importance (Table 1). Pteropods were also common here.

Abundance of predators

Ctenophores, hydromedusae, and chaetognaths were the dominant predatory taxa on the Bank. At the mixed station (Tow 3), hydroid colonies were found in densities up to 2×10^6 colonies m^{-3}, with an average of seven live polyps (hydranths) in each colony (Table 1). The abundance of colonies increased towards the bottom (Fig. 3B), suggesting that they may

have been broken off from their natural substrate and mixed up into the water column. The hydroid colonies were not found in the two other tows. In the mixed transect, there were also numerous small *Obelia* hydromedusae with a diameter of ~1 mm, as well as chaetognaths (*Sagitta*). The cydippid ctenophore *Pleurobrachia* and lobate ctenophores (*Bolinopsis infundibulum* or *Mnemiopsis* sp.) were most abundant in the stratified area (Tow 4), as were hydromedusae other than *Obelia*. The lowest abundances of invertebrate predator species were found in the slope waters. Other predators in all three tows were unidentified decapod larva, amphipods, and krill. In the mixed area, a few fish larva were observed.

Association with temperature, chlorophyll and depth

Several of the zooplankton species important as grazers or omnivores were observed at all three locations (Fig. 8). However, the pteropod *Limacina* was almost completely absent from the mixed location (Tow 3), with only one observation in Camera 4. Appendicularians occurred in that tow, but without their typical vertically stratified distribution. Both groups had peak abundances around the pycnocline in Tow 4. In Tow 5, appendicularians were very abundant above the pycnocline, while pteropods were more scattered (Fig. 8). *Calanus* was highly concentrated in the surface of Tow 4 (stratified locality), but younger stages also occurred in deeper waters. In Tow 5, the highest abundance of this species was found deeper in the water column, a few meters above the pycnocline and chlorophyll maximum. *Pseudocalanus* was most abundant in the stratified waters, and was found throughout the water column, although egg-carrying females seemed to be closer to the surface. In the mixed area (Tow 3), these copepods were more evenly distributed with depth (Fig. 8). Both species of copepods were considerably less abundant in the warmer slope waters of Tow 5 (Fig. 8).

Evidence of sedimentation

Marine snow was especially dense below the pycnocline in the stratified Tow 4 (Fig. 9). Fresh and deteriorating colonies of the diatom *Chaetoceros socialis* were common in the same layers, and may have contributed to the marine snow (Fig. 9). The shed mucus houses of the appendicularian *Oikopleura* could be identified before they aggregated with other particles. These were distributed below the live appendicularians (Fig. 9). Other components of the marine snow were copepod exuviae and fecal pellets of appendicularians and copepods. Copepod exuviae were most common in the slope water and fecal pellets in the stratified waters of Tow 4.

DISCUSSION

In general, the patterns of distribution of the zooplankton species presented here, appeared to be associated with the stratification of water, rather than the availability of food (as measured in chlorophyll fluorescence). However, the correlation between chlorophyll and grazing plankters is made difficult by the fact that the tows were not made during the same time of day. Tows 3 and 4 were daytime tows, when vertically migrating copepods should have been distributed deeper than at night. In a few cases, however, there was a connection between zooplankton and chlorophyll; in Tow 5, there was a pronounced peak of fluorescence at ~30 m depth, just above the pycnocline in the warm slope water.

Acantharia and *Centropages* had peak concentrations in this region (Fig. 5). In this tow, *Calanus* had a peak of occurrence at ~20 m, just above the marked peak of fluorescence (Fig. 8). Tow 5 was made around midnight and may have represented the main feeding time of vertically migrating species.

Although we have information about the relative chlorophyll concentrations in the different areas, we know little of the composition of phytoplankton. In Tow 4, the large colonies of *Chaetoceros socialis* coincide with higher chlorophyll fluorescence below the pycnocline (Fig. 6). This is not the case for the same species in Tow 3 (Fig. 6). It is possible that the colonies were in different stages of their growth cycle or that smaller phytoplankton species were abundant there.

Colonies of *C. socialis* were first described over 100 years ago (Lauder, 1864; Gran, 1908), as spherical colonies containing coiled chains of cells in a gelatinous matrix. The species is very common in northern temperate and Arctic waters (Gran, 1908), and mass occurrences on George's Bank were described by Bigelow (1926). Many species of *Chaetoceros* form aggregates towards the end of a bloom, but before the chains become senescent, and finally sediment out in mass events (Alldredge and Gotschalk, 1989). These events are important for vertical flux and also may reduce food availability for pelagic grazers in spring (Alldredge and Silver, 1988; Alldredge and Gotschalk, 1989). It is conceivable that the mucoid colonies form as a stage in the life cycle of *C. socialis*, making further aggregation possible. The colonies we observed were often shaped as if composed of several spheres, which may have been aggregates of spherical colonies. An abundance of detritus particles with a similar, bulky and branched shape, but a fuzzier texture, suggest that part of the *C. socialis* population was indeed decaying (Fig. 9). It is possible that such large, and perhaps unpalatable, phytoplankon particles discourage herbivorous copepods from occupying the deeper part of the water column in this transect (Hansen *et al.*, 1991).

Higher quality phytoplankton food may have been located higher up in the water column, where values of fluorescence were lower. At this time of year the older copepodites of *Calanus* would be preparing for diapause (Miller *et al.*, 1991) and in need of an easily accessible food source. These stages were observed in the very uppermost stratum of the water column in Tow 4 (Fig. 8). The smaller copepods *Pseudocalanus* and *Oithona* were also abundant in the upper layers of the water column in Tow 4 (Figs 4 and 6). *Oithona* depends on high levels of food during early development (Uchima and Hirano, 1986), making it necessary for egg-carrying females to occupy regions rich in phytoplankton and tintinnids. Older stages of *O. nana* will consume a wide range of food, including copepod nauplii (Lampitt and Gamble, 1982), which were abundant above the pycnocline of Tow 4. Although *Pseudocalanus* is known to ingest a wide variety of foods (e.g. Poulet, 1976), the fatty acid composition of *P. acuspes* shows that mostly diatoms are ingested in spring or early summer (Norrbin *et al.*, 1990).

Copepod nauplii were abundant in Tows 4 and 5, but only two individuals were found in the mixed area (Table 1). Nauplii were exposed to potential predation from large invertebrates, such as chaetognaths, ctenophores, medusae, and krill, but also from omnivores like *Oithona* (Uchima and Hirano, 1986), sarcodines and foraminifera (Swanberg and Caron, 1991) and pteropods (Gilmer and Harbison, 1991), all of which were present in some or all of the regions (Table 1). Several potential sources of predation were especially prominent in the mixed region and may have been responsible for the almost complete absence of copepod nauplii in this transect; *Obelia* medusae (most were ~1 mm in diameter; a few larger), chaetognaths, and hydroid colonies. An *Obelia geniculata* of 2 mm

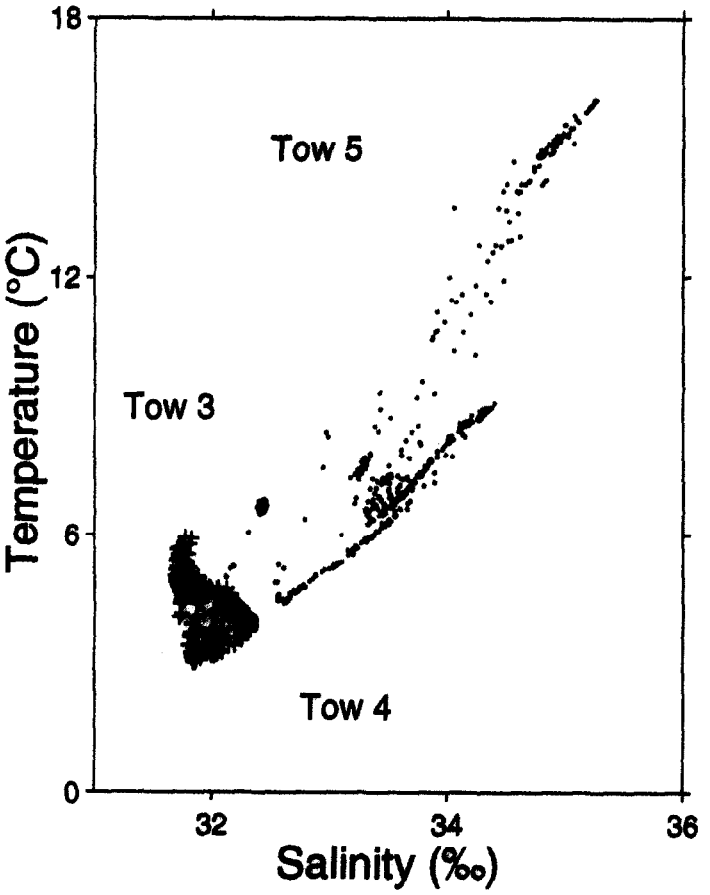

Fig. 2. (A) *T–S* diagram for salinity and temperature recorded by the VPR. Values are based on readings taken from the SEABIRD sensors mounted on the VPR tow-body. Tows are represented by different symbols; green dots for Tow 3, + for Tow 4 and black dots for Tow 5.

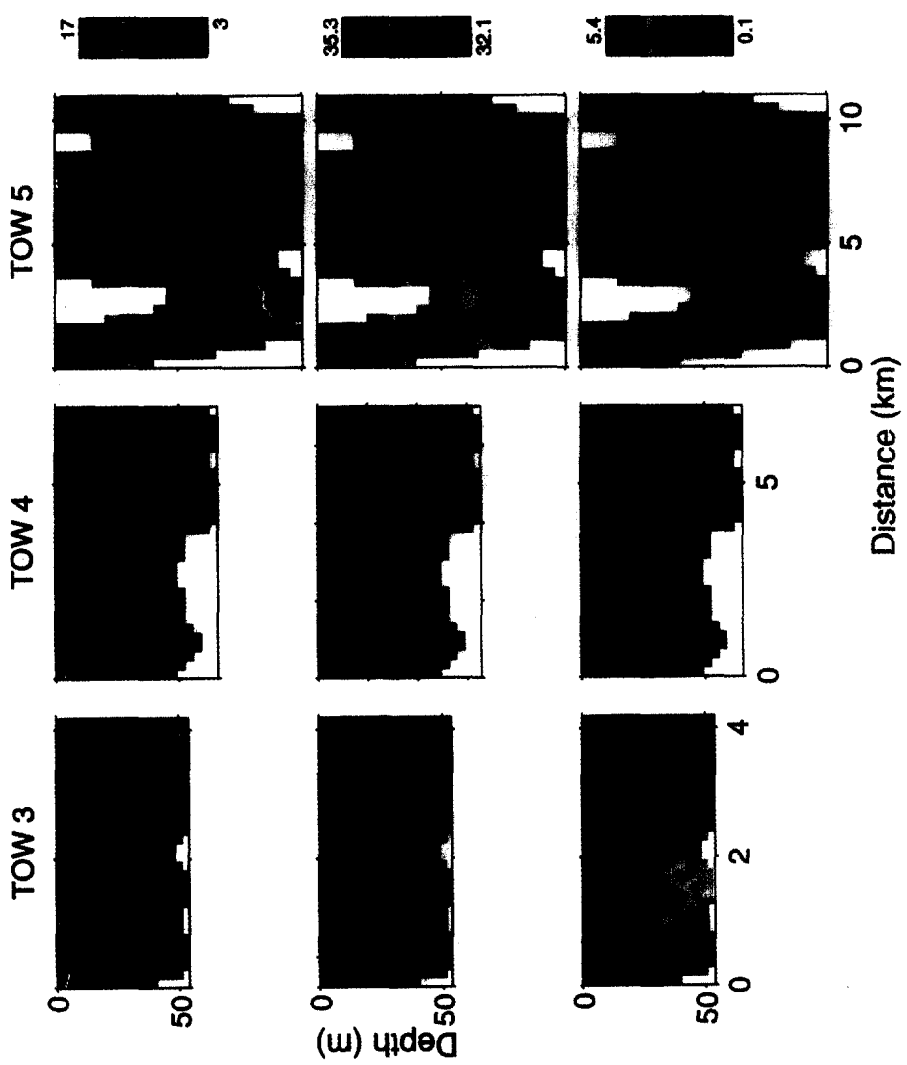

Fig. 2. (B) Environmental parameters along the VPR transects, Tows 3, 4 and 5. The scaling of each parameter is linear, and the same for all tows. *Temperature is shown in the upper row, salinity in the middle row and chlorophyll fluorescence in the bottom row. The tow path of the VPR is overlaid on* the temperature sections. Readings were taken every 4 s from the VPR, and have been gridded and smoothed to produce the figures. The horizontal scale has been translated from time to distance traveled through the water at a ship's speed of 2 m s^{-1} (4 knots).

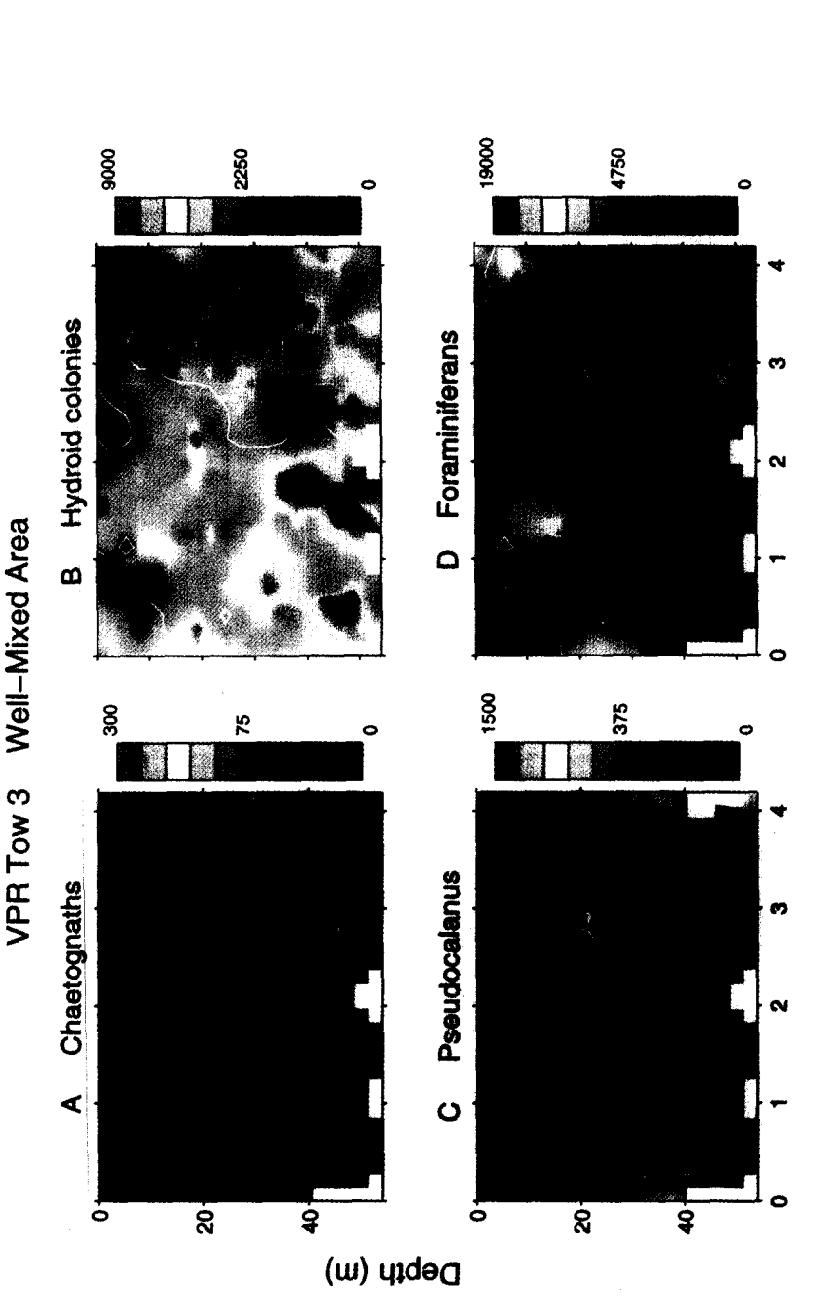

Fig. 3. Distribution of dominant zooplankton along the transect in the shallow, mixed area (Tow 3). Abundance data in 1-m depth bins were gridded using an inverse spline method, and contoured and smoothed in Matlab for Windows. To produce the color scale for abundance, data were square-root transformed. Scale bar shows 10 color levels of this quadratic scale, from 0 to a rounded, maximum number (individuals m^{-3}). See Fig. 2B regarding *x*-axis scaling. Temperature contours are overlaid on the color plot. (A) and (B) from camera 2, (C) and (D) from camera 4. For each taxon is given the total number of observations on which the plots are based. (A) Chaetognatha, 44 obs. (B) Hydroid colonies, 2325 obs. (C) *Pseudocalanus* sp., 37 obs. (D) Foraminifera of *Globigerina*-type, 137 obs.

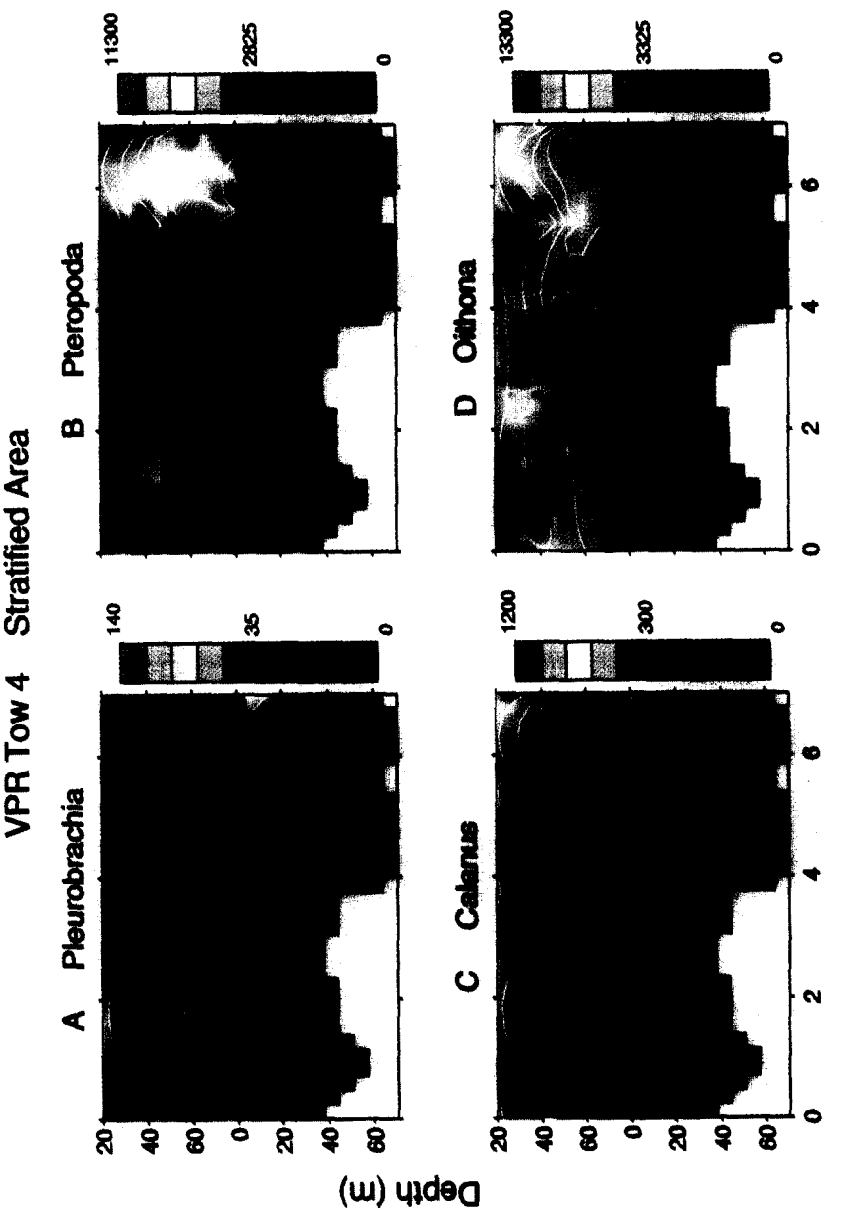

Fig. 4. Distribution of dominant zooplankton along the transect in the stratified shelf area (Tow 4). See Fig. 3 for an explanation of data transformation and scaling. Temperature contours are overlaid for comparison. (A) and (C) from camera 2, (B) and (D) from camera 4. (A) The ctenophore *Pleurobrachia*, 33 obs. (B) *Limacina* pteropods, 111 obs. (C) *Calanus finmarchicus*, 688 obs. (D) *Oithona* spp., 303 obs.

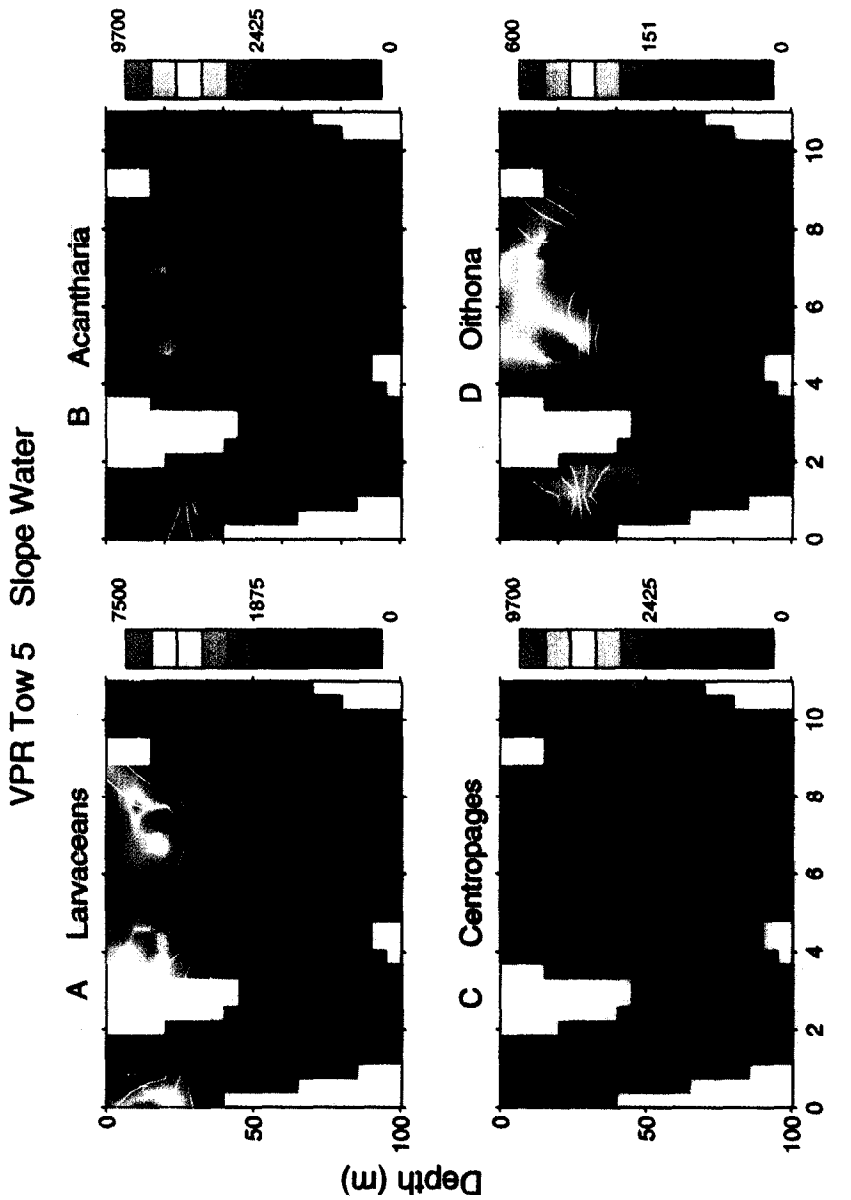

Fig. 5. Distribution of dominant zooplankton along the transect in the slope area (Tow 5). See Fig. 3 for an explanation of data transformation and scaling. All figures are based on data from camera 4. (A) Larvaceans, 116 obs. (B) Acantharia, 74 obs. (C) *Centropages* sp., 52 obs. (D) *Oithona* spp., 270 obs.

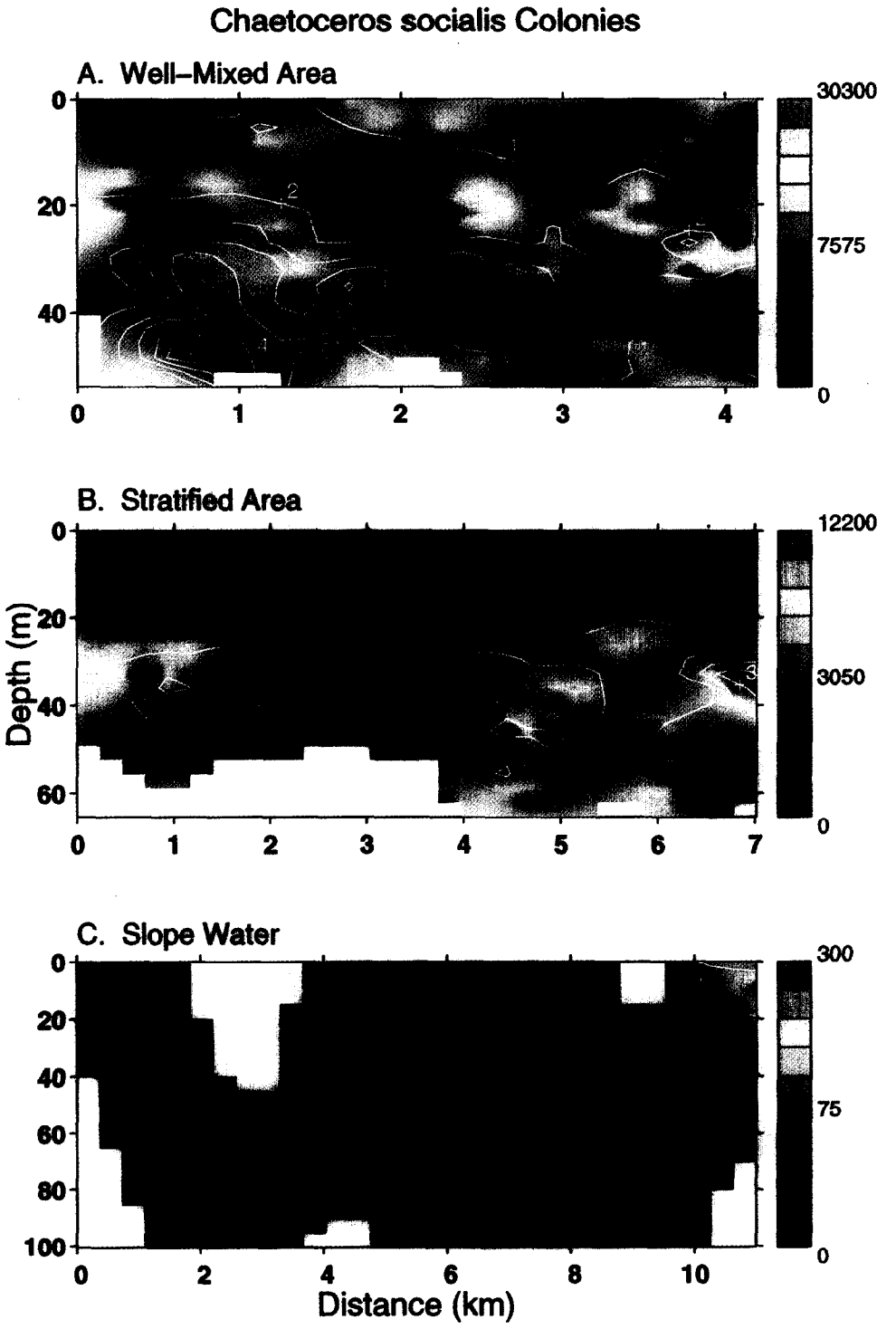

Fig. 6. Distribution of *Chaetoceros socialis* colonies in VPR Tows 3–5. Fluorescence contour lines are overlaid for comparison. See Fig. 3 for an explanation of data transformation and scaling. (A) Tow 3; (B) Tow 4; (C) Tow 5.

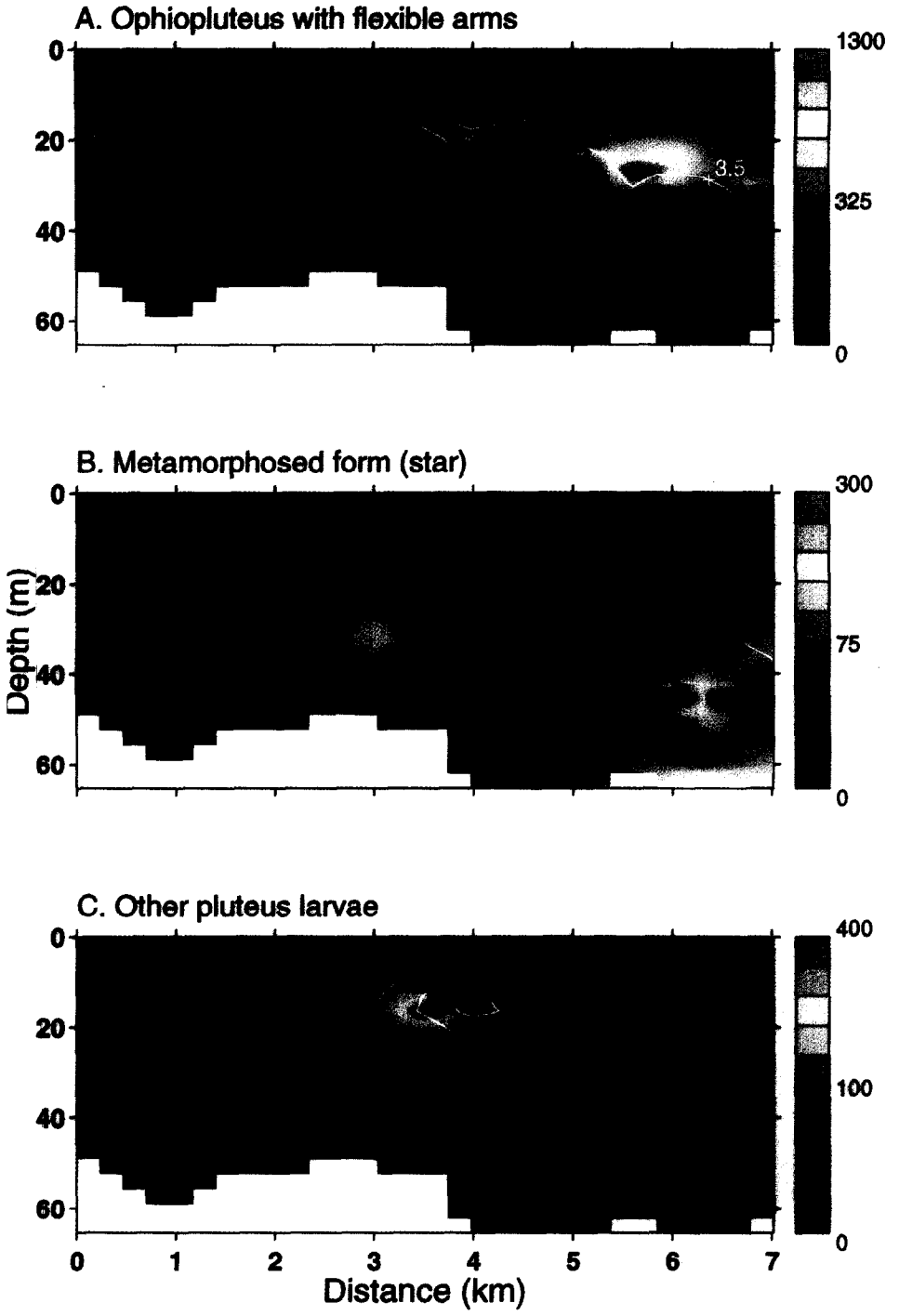

Fig. 7. Distribution of some forms of echinoderm larvae in Tow 4. See Fig. 3 for an explanation of data transformation and scaling. Temperature contours are overlaid for comparison. (A) Ophiopluteus with flexible arms, 30 obs. (B) Metamorphosed form of the ophiopluteus in previous pane, 7 obs. (C) Other pluteus larvae, 15 obs.

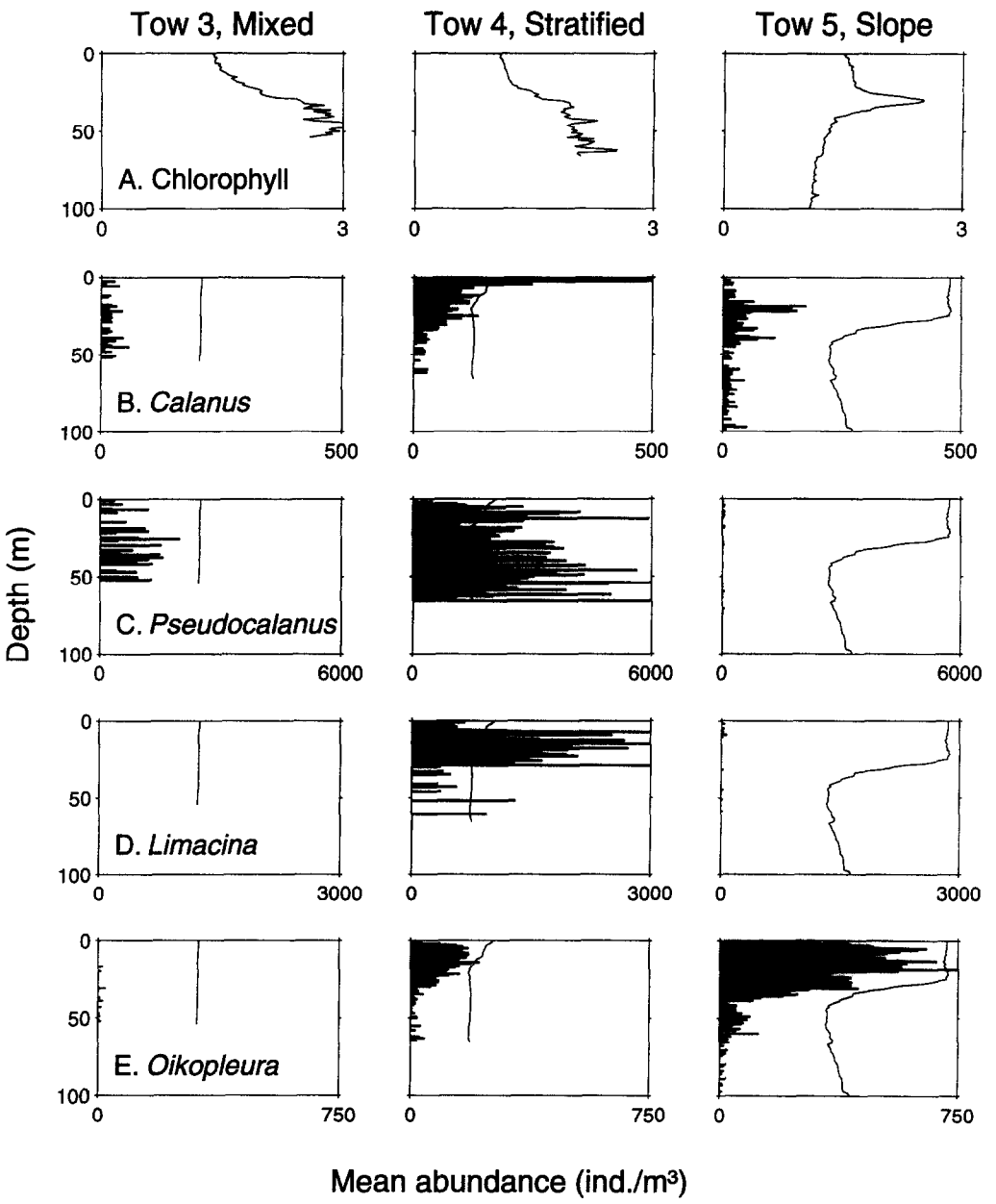

Fig. 8. Depth distribution of important zooplankton species, temperature and chlorophyll observed in VPR tows in mixed, stratified and slope waters. All data are averaged over 1 m depth bins in the up and down legs of each tow. For Tow 5, data for the last up-tow, in colder shelf water, are omitted. Standard deviation is omitted for the sake of clarity, but was generally of the same order as the average. A mean temperature curve is included in each histogram to show the stratification on each locality. Only Tow 5 reaches 100 m depth; Tows 3 and 4 are plotted down to 50 m and 65 m, respectively. (A) Chlorophyll fluorescence reading (V); (B) *Calanus finmarchicus* (camera 2); (C) *Pseudocalanus* sp. (camera 4); (D) *Limacina* pteropods (camera 4); (E) appendicularians (cf. *Oikopleura*; camera 2).

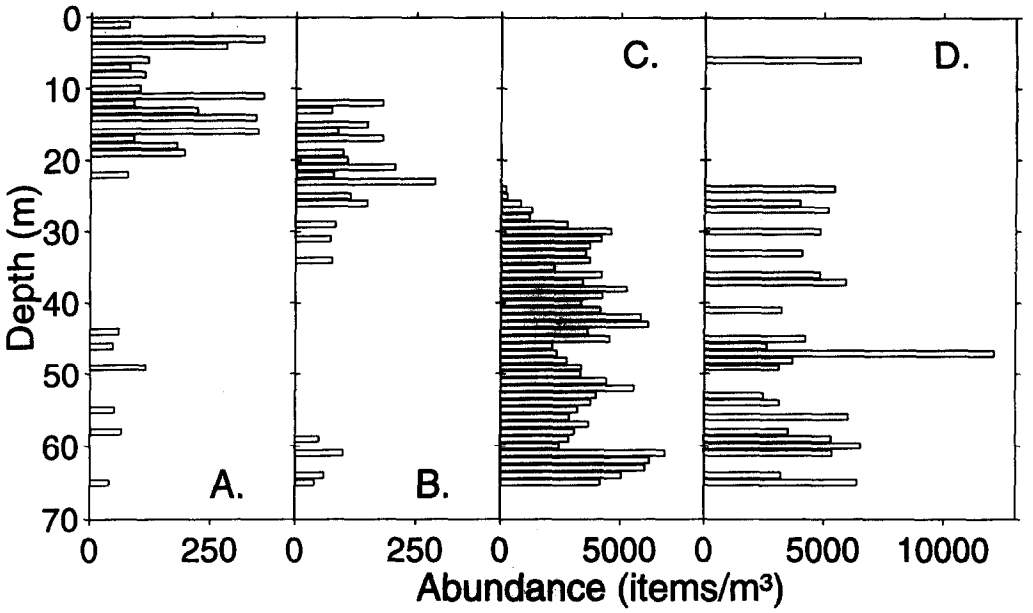

Fig. 9. Depth distribution in one vertical leg of Tow 4 in the stratified area of Georges Bank. Note that the abundance scale for panes (A) and (B) is somewhat exaggerated in relation to the last two panes. (A) and (B) are based on data from camera 2, (C) and (D) on camera 4. (A) Appendicularians; (B) shed mucus houses of appendicularians; (C) marine snow (up to a few millimeters in size); (D) *Chaetoceros socialis* colonies.

diameter may have a clearance rate of $0.41\,day^{-1}$ when feeding on nauplii (Fulton and Wear, 1985), giving a potential daily clearance of $113\,m^3\,m^{-2}$ surface area in the mixed area (Tow 3). The population of *Sagitta* could be expected to ingest somewhat less than 3000 copepodites $m^{-2}\,day^{-1}$ (Øresland, 1987) in the mixed area and one-tenth of that in the stratified area. The hydroid colonies may have had an even larger predation impact in the mixed region (Madin *et al.*, 1996).

A major group which was found in only one VPR image in the mixed region was *Limacina*, a thecosomatous pteropod. Members of this genus feed using delicate, invisible feeding nets (Gilmer and Harbison, 1986), which may be sensitive to the turbulence in the mixed area. A small degree of turbulence is reported to cause ingestion of the feeding web in pteropods of this genus (Gilmer and Harbison, 1986). *Limacina* is believed to be highly important for vertical flux (Bathmann *et al.*, 1991). Members of this genus generally sit and wait for falling particles or motile prey, making a distribution in a dense layer around the pycnocline, such as in Tow 4 (Figs 4 and 6) advantageous. *Limacina* has a wide-spread distribution in cold-water rings and eddies (Wormuth, 1985; Beckmann *et al.*, 1987), where it grows from a small seed population to abundances far higher than in the water surrounding these gyres, and ultimately sediment out in massive events (Bathmann *et al.*, 1991). The population of *Limacina* on Georges Bank may have been such a trapped population, multiplying primarily within the limits of the Bank. It was abundant, with a strongly structured distribution in the stratified tow in the shallow area, while a scattered population was found in the deeper slope water of Tow 5. It was also present in Great South Channel, west of the Bank (Gallager *et al.*, 1996). Describing the distribution of this group is

important in the context of acoustic abundance estimates, since it has a very high level of acoustic back-scatter (Stanton *et al.*, 1994).

Limacina's companion in the pycnocline of the stratified area (Tow 4) was the appendicularian *Oikopleura* (Fig. 8). This group may be a significant structuring component of the ecosystem and important for vertical flux, because of its ingestion of a very wide size range of particles. Smaller particles may stick to the filtering unit in the mucus houses of the appendicularians, which are shed at least daily, while the larger fraction ends up in dense fecal pellets with a high sinking rate (Bedo *et al.*, 1993). The shed houses may be the basis of much of the loose aggregates of marine snow, to which other particles adhere, and which provide the basis for bacterial activity and the regeneration of nutrients. Evidence of such a process were observed in many video images.

In summary, the VPR has allowed us to observe the distributions of dominant planktonic taxa, many of which were fragile, on the same scales as the hydrography and chlorophyll fluorescence. The various taxa appeared to have different affinities for particular hydrographic conditions. A further processing of this data set will be used to explore the micro-scale distribution of zooplankton species and the association between groups of organisms.

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