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Distribution of plankton, particles, and hydrographic features across Georges Bank described using the Video Plankton Recorder☆

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Abstract

It is well known that plankton abundance is highly variable over a broad range of scales. Conventional sampling with nets, pumps, and bottles is discrete and covers only a small portion of the total variance spectrum. Development of the Video Plankton Recorder (VPR) has enabled us to quantify the abundance of seston and plankton, including delicate taxa, over a range of scales from centimeters to hundreds of kilometers. During the 1994–1995 GLOBEC Georges Bank field years, three VPR surveys were conducted across the bank from the Slope Water in the south to the Gulf of Maine in the north, a distance of $\sim$ 200 km. The surveys, conducted in June 1994, January 1995, and March 1995, intersected at least four distinct water types (Slope Water, stratified bank water, well-mixed bank water, Gulf of Maine water) and crossed several frontal boundaries (shelf break front, tidal front, Gulf of Maine front). The Video Plankton Recorder was equipped with temperature, conductivity, fluorescence, and transmissivity probes in addition to two video cameras, permitting comparison of the plankton and particle distributions with the physical fields. Only data collected using the low-magnification camera are considered here. A combination of analytical methods including temperature–salinity–plankton plots and statistical analyses (spatial variance spectra, principle component analysis, and correlation analysis) revealed that the distribution of taxa and particles were associated with particular water mass types but that smaller-scale variability in plankton abundance did not appear to be tightly coupled to or correlated with hydrography. The distributions and seasonal progression in abundance of *Calanus finmarchicus*, the most abundant plankton taxon, revealed a deep dwelling population in the Slope Water and shallower populations on the bank and in the Gulf of Maine in January with abundance becoming increasingly greater on the bank in March and June. The data indicate that physical advection of water mass types and intrinsic plankton was important to the establishment of *Calanus* populations on Georges Bank. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Both physical and biological processes produce the distributions of plankton and particles observed on Georges Bank. Physical mechanisms such as advection, frontal isolation, tides, and the establishment of stratification determine water mass and plankton distribution, modify environmental conditions in various regions of the bank, and influence the input, retention, or loss of water and populations from the bank (immigration and emigration). Biological processes such as growth, reproduction, and mortality act within the physical environment to further modify abundances and distributions. One of the goals of the US GLOBEC Georges Bank research program is to identify and describe these biophysical mechanisms and their impact on zooplankton populations in this region (GLOBEC, 1992).

Georges Bank is characterized by complex circulation and hydrography (e.g., Hopkins and Garfield, 1981; Flagg, 1987; Butman et al., 1987), with characteristic water types present at different geographic locations. Georges Bank Water on the crest of the bank is separated from Gulf of Maine Water to the north and Shelf Water on the southern flank of the bank by tidal mixing fronts (northern and southern tidal mixing fronts). The Shelf Water and Slope Water found along the southern edge of the bank are separated by the prominent Shelf–Slope Front. Both Gulf of Maine Surface Water and Shelf Water are modified seasonally by increased insolation during the spring and summer, which leads to the development of stratification. In contrast, Georges Bank Water on the crest remains well-mixed throughout the year. These seasonally varying conditions of vertical structure also modify the strength of the density structure of the tidal mixing fronts, particularly along the southern edge of the crest, such that the southern tidal mixing front may not be distinct in hydrographic data during the winter when little contrast in vertical structure exists between the Shelf Water and Georges Bank Water. Episodic events such as storms, interactions with Gulf Stream rings, or anticyclonic eddies in the Slope Water transport water masses and plankton populations onto or off of Georges Bank (e.g., Ramp et al., 1983; Churchill et al., 1986; Houghton et al., 1986; Flagg, 1987; Garvine et al., 1988; Garfield and Evans, 1989; Lewis et al., 1994) Injections of Scotian Shelf Water also occur on the eastern end of the bank onto the southern flank (e.g., Bisagni et al., 1996).

The mean circulation on Georges Bank is dominated by anticyclonic flow around the margins of the crest outside of the tidal mixing fronts (e.g., Bumpus, 1976; Butman et al., 1987; Limeburner and Beardsley, 1996). This flow is narrowly focused along the northern flank of the bank but more diffuse across the southern flank. The strength of the current varies seasonally, with more intense flow and higher velocities occurring following the development of density stratification during spring and summer. The system becomes a partially closed gyre during late spring and summer, with recirculation occurring from the southern flank to the northern edge along the western end of the bank (e.g., Butman and Beardsley, 1987; Limeburner and Beardsley, 1996). The observed currents on the bank are impacted strongly by tidal currents, which may obscure the prevailing anticyclonic circulation if such data are uncorrected for the tidal signal (e.g., Moody et al., 1983; Candela et al., 1992).

These variable hydrographic and circulation patterns, in conjunction with individual life histories, are important to the distribution of plankton populations across the bank since advection and the modification of the physical environment (e.g., development of stratification) are critical towards determining the ultimate distribution of a taxon. The general seasonal cycle of zooplankton taxa across Georges Bank has been described (e.g., Bigelow, 1926; Davis, 1987). The copepod *Calanus finmarchicus* (and congeneric species; herein "*Calanus*") in particular has received considerable attention as it can be a dominant component of the total zooplankton biomass during winter and spring (e.g., Bigelow, 1926; Davis, 1987; Meise and O'Reilly, 1996) and its young are believed to be a significant food source for larval cod and haddock (Kane, 1984; Buckley and Lough, 1987). Abundances and distributions of *Calanus* on the bank vary throughout the year. *Calanus finmarchicus* establishes strong populations on Georges Bank during January 1995, developing to a biomass peak in late spring (May–June; Davis, 1987; Meise and O'Reilly, 1996). Abundances on the bank diminish during the warm summer months, and populations must be reestablished during the following winter through recolonization (e.g., Davis, 1987; Meise and O'Reilly, 1996). It is believed that populations on the bank originate in the Gulf of Maine to the north and are advected onto the bank at the northeast corner (Northeast Peak) (e.g., Meise and O'Reilly, 1996; Durbin et al., 1997, unpublished data; Hannah et al., 1998). Advection subsequently spreads populations of the copepod along the southern flank and to the southwestern corner of the bank; some retention on the bank may occur in recirculation along the southwestern edge (e.g., Limeburner and Beardsley, 1996; Manning and Beardsley, 1996; Durbin et al., 1997, unpublished data). Because of its importance to the ecosystem, including as a food source for larval cod and haddock, this species was selected as one of the target species for the US GLOBEC Georges Bank program (GLOBEC, 1992).

The present study quantified the distributions of plankton and particles (e.g., marine snow) and the associations of these distributions with the physical environment (temperature, salinity, velocity) from transects across Georges Bank conducted in three different months during 1994 and 1995 as part of the GLOBEC Georges Bank Program. The transects were surveyed using the Video Plankton Recorder (VPR; Davis et al., 1992a), which produces high-resolution descriptions of plankton distributions. The VPR describes plankton abundances and community compositions that are similar to those observed using conventional net systems, such as the multiple opening/closing net and environmental sensing system (MOCNESS; Wiebe et al., 1976, 1985) for abundant taxa, although the VPR may not differentiate different species or different life stages within a species (e.g., Benfield et al., 1996). For regions with a low diversity of copepods, such as Georges Bank, the instrument is able to differentiate between certain copepod genera and species. The VPR is more effective than conventional net systems at describing the abundances and distributions of fragile, gelatinous taxa since the instrument samples non-invasively (e.g., Davis et al., 1992b; Benfield et al., 1996; Gallager et al., 1996; Norrbin et al., 1996). Furthermore, far greater spatial resolution (< 1 m) of both biological and physical fields is achieved using the VPR than with conventional net systems (e.g., Davis et al., 1992b; Gallager et al., 1996).

The specific goals of the study were to (1) describe the distributions of dominant plankton taxa and particles across Georges Bank, (2) identify associations between the plankton distributions and hydrographic characteristics and water masses, (3) document changes in these distributions and associations throughout the winter–spring period, (4) describe the dominant spatial scales of patchiness of the dominant plankton and physical mechanisms that impact such patchiness, and (5) identify potential avenues of on-bank or off-bank flux of plankton populations.

2. Methods

Three 180–200 km long transects across the northeast region of Georges Bank were conducted during 15–16 June, 1994 (R/V Columbus Iselin) and 18–19 January, 1995 and 6–8 March, 1995 (R/V Endeavor). Each transect extended from the Slope Water south of Georges Bank to the Gulf of Maine (Fig. 1). The two transects conducted in 1995 followed a straight line while the 1994 transect contained a turn near the midpoint. The transects conducted in 1995 also were accomplished in two segments, with some time interval (16 h, January 1995; 25 h, March 1995;) between each leg. As a result, time is not continuous across these transects. The Video Plankton Recorder (VPR) was towed at 2 m/s (~ 4 knots), undulating continuously from surface to near bottom (towyo) (Fig. 2). For these surveys, the VPR was equipped with 2–4 cameras, temperature and conductivity probes, fluorometer, and transmissometer. The present study examines the distributions of plankton obtained from the camera with a field of view of ~ 37 × 24 × 40 mm (W × H × D) (the actual field of view and volume imaged differed slightly (~ 1 mm) for each cruise), producing an imaged volume of ~ 35 ml. This magnification is suitable for imaging copepods of 1–2 mm prosome length, such as late copepodites of *Calanus finmarchicus*, but not for identifying naupliar stages, early copepodites, or for effectively enumerating the abundances of very small copepods such as *Oithona* spp. Environmental data were collected at 0.25 Hz (June 1994) or 0.5 Hz (January 1995, March 1995) Hz; video images were recorded at 60 fields per second (fps).

Video tapes were analyzed for plankton abundances using a semi-automated method (Davis et al., 1996). In-focus images were extracted from the video tapes and saved to disk as tiff files using an Imaging Technologies Series 151 Image Processor and a Sun Sparc 20 workstation. The images were identified by hand to particle type, taxon, or species and measured using a custom routine

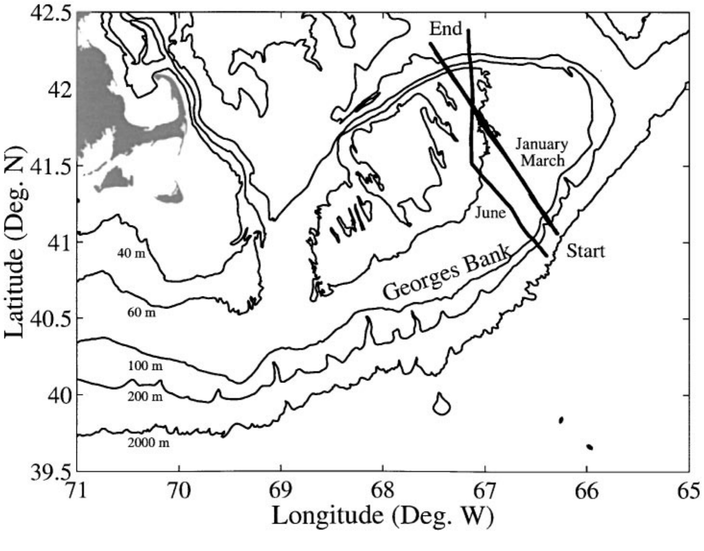

Fig. 1. Location of three cross-bank transects. The June 1994 (CI9407) transect was conducted on the R/V Columbus Iselin and the January 1995 (EN259) and March 1995 (EN262), transects were conducted on the R/V Endeavor. Note that the transects from 1995 followed a straight course across the bank while the 1994 transect consisted of two legs.

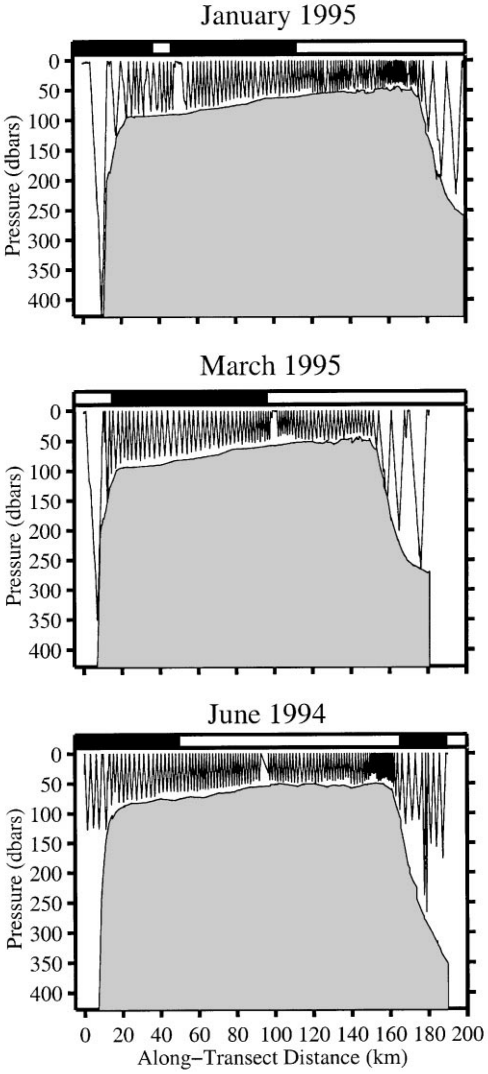

Fig. 2. Towyo path of the instrument through the water as a function of along-transect distance. Along transect distance for the three transects was calculated from the geographic starting location of each transect, rather than a common starting point. The instrument was deployed to approximately 10 m off of the bottom during most towyos. Periods of night (black) and day (white) indicated across the top of each graph.

written in MATLAB (Mathworks, Inc.; see Davis et al., 1996). The size measurement of each particle or organism was obtained by manually identifying two locations on each image; for copepods, the width of each individual was measured (the animals were rarely oriented parallel to the field of view and hence an accurate length measurement could not be obtained). The number of images extracted and examined (28,906, 72,262, and 41,681 for January 1995, March 1995, and June 1994, respectively) were somewhat greater than the numbers identified (14,401, 38,575, 29,462) as some portion of the extracted images were not in focus and hence not within the imaged volume. Twenty taxa, species, or particle types were identified routinely; only the most abundant are discussed here. Life stage was not differentiated for the copepods. Plankton and particle observations were merged with environmental and navigational data by binning the observations for each category into the time intervals at which the environmental data were collected using routines written in MATLAB (see Davis et al., 1996); concentrations were calculated utilizing the total volume (liters) imaged during that period. For less-abundant categories, usually only a single organism was observed during each time interval so that the resulting concentrations are close to presence or absence data rather than covering a range of values.

Although data were collected during three separate months, it is important to note that the June data were collected during 1994, a year prior to January 1995 or March 1995 data. In the present study, we consider the months in the temporal sequence of January 1995, March 1995, and June 1994 in order to examine seasonal patterns although the months were not surveyed chronologically. We describe features typical of the physical and biological distributions and mechanisms on Georges Bank for each month.

Principal component analysis was utilized to identify potential associations between hydrography, fluorescence, particulate concentration (represented by light attenuation), the abundance of *Calanus finmarchicus* (the most abundant taxon), and the concentration of marine snow and to describe the mesoscale spatial distribution of variability in these fields (e.g., Mariano et al., 1996). For these analyses, data first were standardized to the standard deviation of each variable, producing variances of 1.0 in the standardized data, prior to calculation of the eigenvalues and the variable mean was subtracted from each observation prior to calculation of the principal components. For the June 1994 data, the temperature and salinity data from the southern end of the transect were quite noisy, either because of the presence of very warm, salty Gulf Stream water that had been advected to the bank edge or because of spurious readings by the temperature or conductivity sensors. Hence, observation times with a temperature greater than 13°C were excluded from the principal component analysis. Correlation coefficients also were calculated between these variables in order to identify co-varying characteristics on a point-by-point basis. Because of the very high sample size ($>$ 23,553 or greater), most correlation coefficients calculated were "significant" ($r_{0.05(2),1000} = 0.062$) and the correlation coefficients were utilized to identify data pairs for which a high proportion of the observed variation was correlated (Zar, 1984). The highly discrete distributions (presence/absence) of the less-abundant taxa were not appropriate for both analyses (principal component analysis, correlation) and meaningful results could not be obtained.

Velocities measured using an acoustic Doppler current profiler (150 kHz) were collected during the January 1995 cruise on the R/V Endeavor and were archived into a database at Brookhaven National Laboratory (C.N. Flagg, pers. comm.) (Acoustic Doppler current profiler data were not available from the March 1995 and June 1994 cruises). These data were used to explore the potential advection or flux of *Calanus* around and on or off of the bank. Acoustic Doppler current profiler velocities first were detided to remove the signature of the tidal ellipse from the data (Candela et al., 1992 and pers. comm.). Flux estimates were calculated by binning the *Calanus* abundance data to the time-depth bins of the ADCP vectors, multiplying each component of velocity by the average *Calanus* concentration for that depth and time bin, and resolving the components into a flux vector.

Power spectra for temperature, salinity, density, fluorescence, and the abundance of *Calanus* were computed to compare the scales of variability between the plankter and conservative properties (e.g., Platt and Denman, 1978). For reference, the spectrum for pressure also was computed. The 0.25 or 0.5 Hz data first were binned into 1-min intervals. The data then were normalized by subtracting the mean and dividing by the standard deviation. The MATLAB routine PSD then was used to compute the power spectrum density.

3. Results

3.1. Water masses and physical distributions

The different water masses present across the transect were identified using T/S plots (Fig. 3). Comparisons of the T/S plots from the different months revealed seasonal changes in water mass properties. The T/S diagrams for January 1995 and March 1995 were similar while that of June 1994 was distinctly different because of the establishment of stratification along the Georges Bank southern flank and in the Gulf of Maine. Both Upper (14°C, 35) Slope Water and Lower (4–6°C, 35) Slope Water were observed south of the bank (blue) during all three months (e.g., Flagg, 1987). Note that little or no Lower Slope Water was observed in the March 1995 and June 1994 data, in part because the sampling did not extend to depths greater than 350 m (March 1995) or 125 m (June 1994). Upper Slope Water was continuous with Shelf Water along a mixing curve gradient of temperature (6–14°C) and salinity (33–35); this mixture of water masses was found south of and in the Shelf–Slope Front. The exceptionally high salinity and temperature (14.5°C, 35.8) observed in the Slope Water during March 1995 and the considerable variability seen during June 1994 in the Slope Water probably resulted from interaction of near-bank waters with a Gulf Stream Ring or meander. Water along the southern flank (green) exhibited a narrow range of temperature/salinity characteristics during both January 1995 and March 1995. The T/S minimum at 4°C, 32.25 observed during March 1995 may have resulted from an influx of Scotian Shelf Water onto Georges Bank from across the Northeast Channel (e.g., Bisagni et al., 1996; D. Mountain, pers. comm. and unpublished data). Water across both the southern flank and the crest of the bank (yellow) was colder during March 1995, following winter heat loss and cooling, than during January 1995. Water on the crest of the bank, between the northern and southern tidal mixing fronts (yellow), exhibited almost constant temperature and salinity along a transect (7°C, 33.2, January 1995; 4–6°C, 32.5–33, March 1995; 9.5°C, 32.6, June 1994), as is characteristic of a well-mixed water mass (Georges Bank Water) (e.g., Hopkins and Garfield, 1981; Flagg, 1987). North of the northern tidal mixing front (red), both Intermediate (6–8°C, 33.5) and Bottom (8°C, 35) Maine Water were observed during all three months. Note that the properties of Maine Bottom Water and Lower Slope Water converge; it is thought that Maine Bottom Water along the northern edge of the bank may originate from Slope Water that enters the Gulf of Maine through the Northeast Channel (as Deep Channel Water) (Ramp et al., 1986; Loder et al., 1997; Smith et al., 2001). This may have important consequences to the distribution of plankton species, since deeper living species may be input to the Gulf of Maine from the Slope Water. The June 1994 T/S diagram is complicated by the establishment of stratification following heating and the subsequent development of surface water including Maine

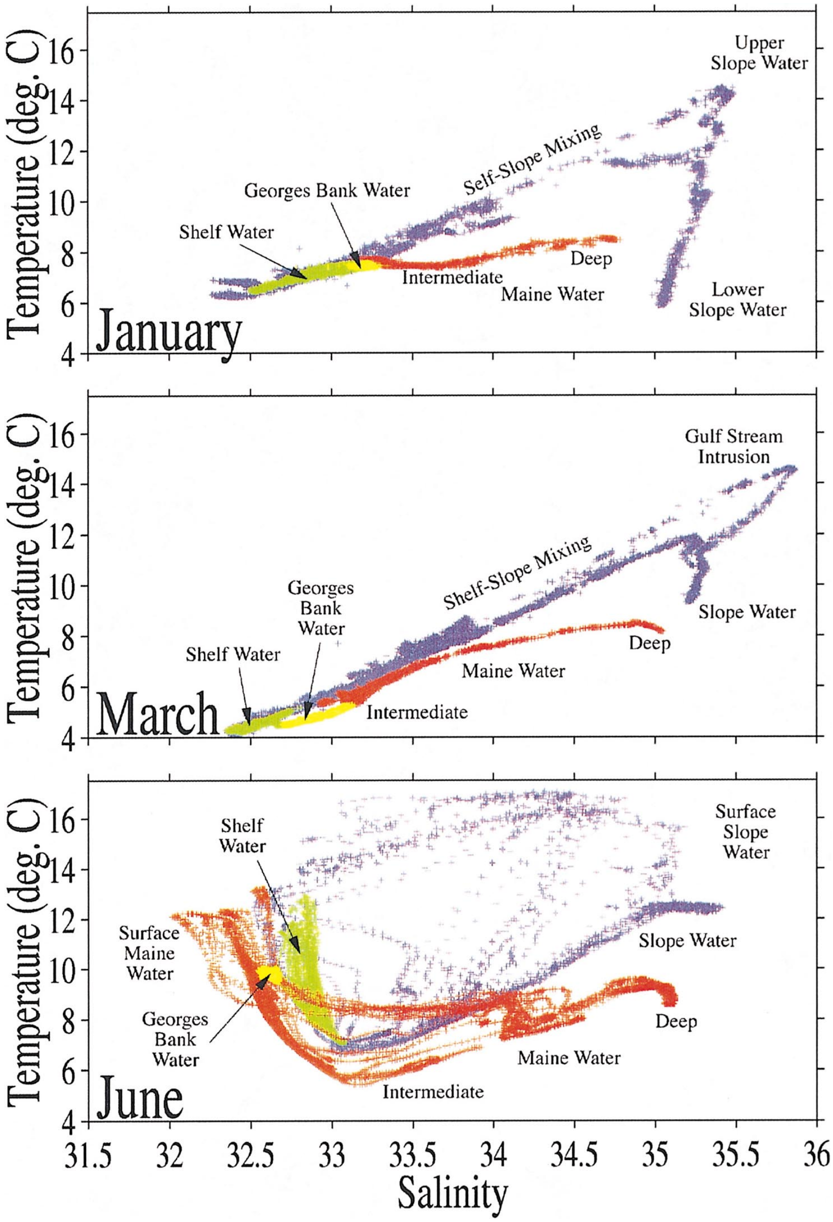

Fig. 3. Temperature/salinity diagrams for all three transects. Data collected in different geographic regions of the bank are plotted with the different colors (blue: south of the bank/Slope, green: southern flank, yellow; bank crest; red: north of the bank/Gulf of Maine). The cross-transect distances demarking the four regions differed slightly for each cruise (Slope: $\leqslant$ 30, 40, 30 km; Southern Flank: $>$ 30, 40, 30 and $\leqslant$ 100, 100, 80 km; Crest: $>$ 100, 100, 80 and $\leqslant$ 170, 150, 155 km; north/Gulf of Maine: $>$ 170, 150, 155 km for January 1995, March 1995, and June 1994, respectively). The characteristic water masses are identified on the diagrams.

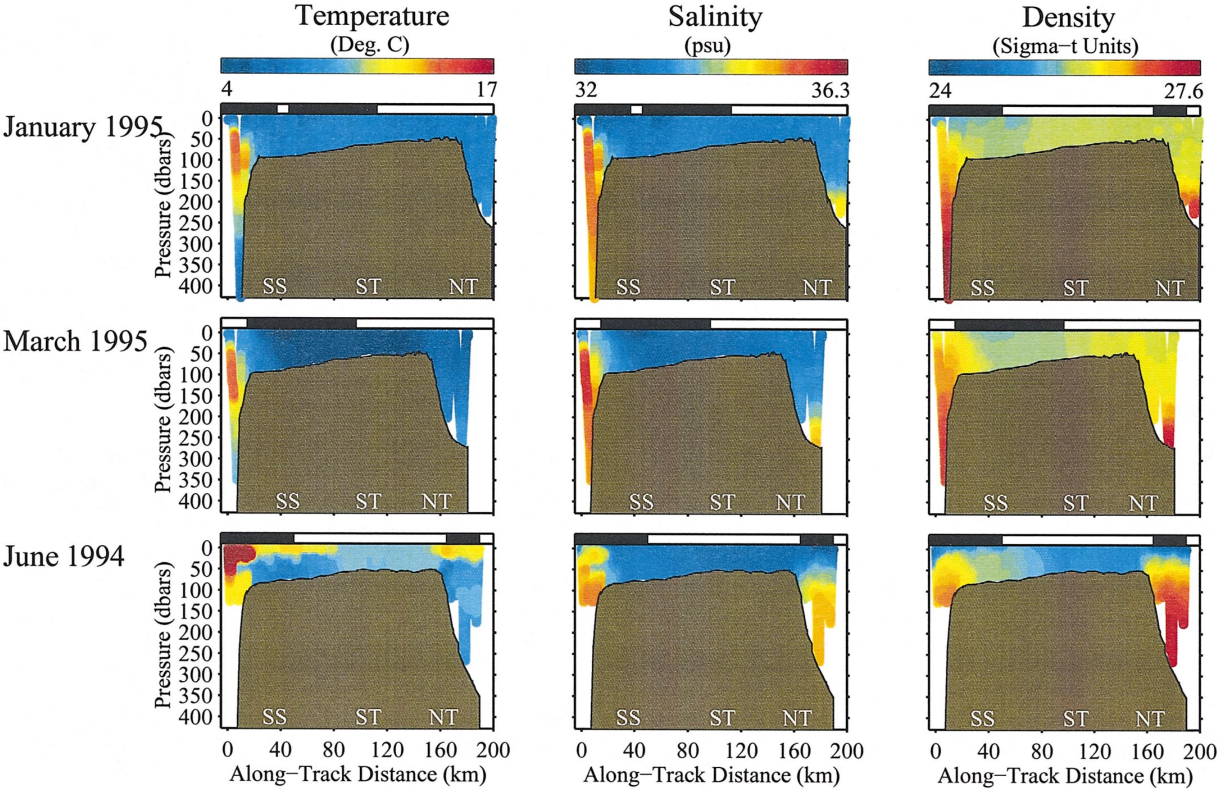

Fig. 4. Temperature (°C), salinity, and density (sigma-*t*) sections across the bank for all three transects. The distance–depth location of each observation is plotted as a dot, with the color of the symbol representing the magnitude each variable for that location. Note that transects do not start at a common geographic location. The approximate cross-transect locations of the Shelf–Slope (SS), southern tidal (ST), and northern tidal (NT) fronts are indicated. Periods of night (black) and day (white) indicated across the top of each graph. ($n = 39{,}377$, January 1995; $n = 42{,}658$, March 1995; 23,553, June 1994).

Surface Water (12°C, 32.5), Shelf Stratified Water (12.5°C, 33), and Surface Slope Water (14–16°C, 32.5–35.5).

The cross-bank distributions of temperature, salinity, and density (Fig. 4) demonstrated patterns and hydrographic features typical of Georges Bank for each season. In January 1995, both temperature and salinity were fairly uniform across the bank and into upper water column of the Gulf of Maine, with warmer and saltier water observed both in the deeper Gulf of Maine and in the deeper Slope Water. The northern flank tidal front was located at ~170 km along-transect distance and a water depth of ~50 m. To the south, the Shelf–Slope front was distinct at 30 km along-transect distance, with isoclines extending almost horizontally off of the bank over the Slope Water. As a result, Shelf Water from the southern flank extended off of the bank over the Slope Water. The southern flank tidal mixing front was located at ~100 km and a water depth of 50 m (see fluorescence and light attenuation); this feature was not obvious in the temperature and salinity

Table 1
Correlation coefficients between the hydrographic variables, fluorescence, attenuation, and concentration of *Calanus finmarchicus* for the three transects

	Temperature	Salinity	Sigma-*t*	Fluorescence	Attenuation	*C. finmarchicus*
January 1995 (n = 39,377)						
Temperature	1.00	0.73	0.45	− 0.34	− 0.38	− 0.30
Salinity		1.00	0.94	− 0.46	− 0.42	− 0.03
Sigma-*t*			1.00	− 0.43	− 0.36	0.06
Fluorescence				1.00	0.83	− 0.07
Attenuation					1.00	− 0.05
C. finmarchicus						1.00
March 1995 (n = 42,658)						
Temperature	1.00	0.97	0.87	− 0.25	− 0.20	− 0.08
Salinity		1.00	0.97	− 0.30	− 0.21	− 0.06
Sigma-*t*			1.00	− 0.30	− 0.18	− 0.05
Fluorescence				1.00	0.86	− 0.01
Attenuation					1.00	0.00
C. finmarchicus						1.00
June 1994 (n = 23,553)						
Temperature	1.00	0.14	− 0.36	0.03	0.09	0.02
Salinity		1.00	0.87	− 0.34	− 0.65	− 0.06
Sigma-*t*			1.00	− 0.33	− 0.65	− 0.07
Fluorescence				1.00	0.62	− 0.09
Attenuation					1.00	− 0.02
C. finmarchicus						1.00

distributions. Density was closely correlated to salinity (corr. coef. = 0.94) but less so to temperature (corr. coef. 0.73) (Table 1).

By March 1995, water over Georges Bank had cooled and freshened relative to temperatures in January 1995. The northern tidal front was located at ~ 150 km along-track distance, where the water depth was ~ 55 m. The location of the southern tidal front was difficult to identify in the temperature and salinity distributions but should be located at ~ 100 km distance and ~ 50 m water depth. Note also that the southern tidal mixing front was crossed during the transition from night to day. The Shelf–Slope front was distinct at ~ 40 km along track distance. In contrast to January 1995, the Shelf–Slope front was more vertical, hence Shelf Water was confined to the shallow bank (< 100 m). Because the Shelf-Slope front did not extend off of the bank, the upper 50 m at the southern end of the transect comprised a mixture both of Shelf Water and Slope Water. Inshore of the front, Scotian Shelf Water influx was present as a shallow (25 m deep), pool of cold, fresh water extended from 20–50 km along track distance. Similar features were observed in the distribution of density, which was correlated both with salinity and temperature (corr. coef. 0.97 and 0.87); temperature and salinity likewise were correlated highly (corr. coef. 0.97) (Table 1).

The hydrography of Georges Bank in late spring/summer, here demonstrated by the June 1994 physical distributions, was quite different from winter conditions. With increased insolation, stratification developed on the flanks of the bank and in the Gulf of Maine. The central bank remained well-mixed, with temperatures elevated relative to January 1995 and March 1995. The Shelf-Slope Front was located at ~ 30 km along track distance with a sharp boundary in both salinity and temperature. The southern tidal mixing front was located at ~ 80 km along track distance and was distinct especially in the temperature and density sections. Thermal stratification had developed in the Shelf Water to the south of the southern tidal mixing front. The northern tidal mixing front again was located at ~ 50 m water depth and at ~ 155 km along track distance; this front was crossed just prior to the transition from day to night. The "cold pool" in the lower half of the water column on the southern flank (~ 40 km along track distance) was a distinctive feature of the June transect. Cold bottom water also was observed on the northern edge of the bank. Density was well correlated with salinity (corr. coef. 0.87) but not correlated with temperature (− 0.36), indicating that density at this time was dependent primarily on salinity. The low correlation between temperature and salinity was evidence of thermal modification of the water masses that resulted from the increased insolation.

3.2. Fluorescence and light attenuation

Fluorescence (Fig. 5) was low during January 1995, with lowest values in the Gulf of Maine and Slope Water and slightly greater over the crest of the bank in Georges Bank Water. By March 1995, fluorescence had increased both on the crest of the bank (Georges Bank Water) and in and to the north of the Shelf–Slope Front, with greatest fluorescence at the southern end of the transect in the Shelf–Slope Front. The units in which fluorescence was measured during the June 1994 transect differed from those of the 1995 transects, so that only the relative distributions but not the absolute magnitudes of fluorescence between the three transects may be compared. Fluorescence in June 1994 was concentrated in and to the south of the northern tidal mixing front in Georges Bank Water and in stratified Shelf Water to the north of the Shelf–Slope front. Low levels of fluorescence were observed in and to the south of the southern tidal mixing front, both in well-mixed Georges Bank Water and in stratified Shelf Water. Little correlation between fluorescence and hydrographic characteristics (T, S) was observed (Table 1).

The distribution of particulate matter, represented here by light attenuation, exhibited many features similar to those of fluorescence in both January 1995 and March 1995, with lowest values in January 1995 and increased light attenuation in March 1995 (Fig. 5). Peaks in the concentration of particulate matter were seen during March 1995 at the Shelf–Slope Front and in Georges Bank Water to the south of the northern tidal mixing front. Elevated light attenuation also was observed in Maine Bottom Water, probably because of material resuspended off the bottom. Light attenuation was highly correlated with fluorescence for both January 1995 and March 1995 (0.83 and 0.86, respectively; Table 1). The distribution of light attenuation differed from that of fluorescence in June 1994, although some features were similar between the two. High light attenuation was observed in the well-mixed zone over Georges Bank, perhaps as a result of the resuspension of particulate matter at that location. This region of high particulate load extended to the south into the Shelf Water and through the upper layers of the Shelf–Slope Front. Some correlation between fluorescence and light attenuation was observed (0.616) during June 1994 (Table 1). Interestingly, light attenuation exhibited also some correlation with salinity/density during June 1994.

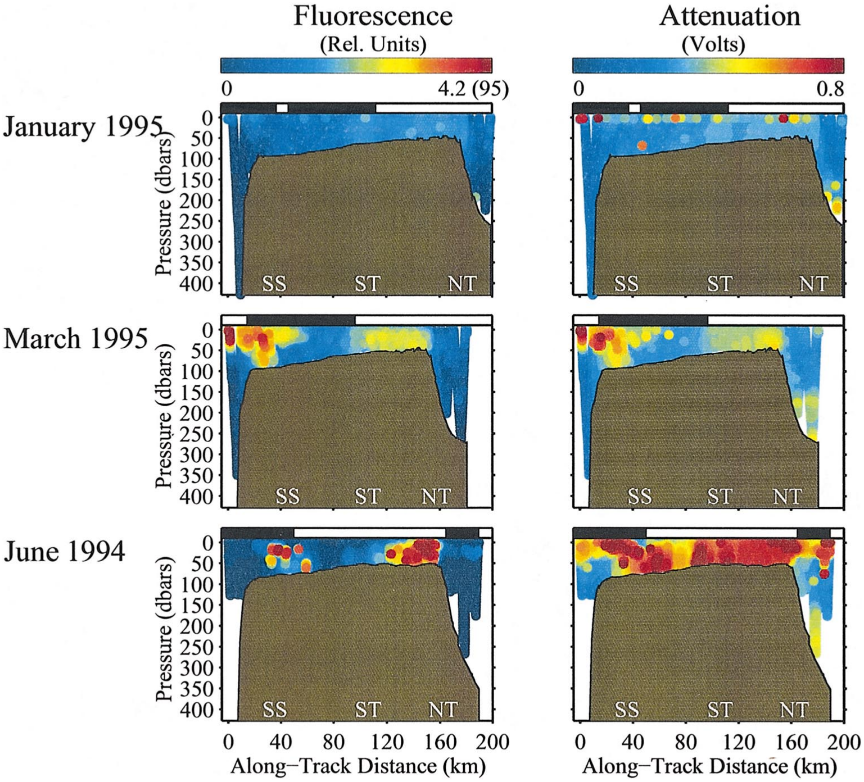

Fig. 5. Fluorescence (relative units) and light attenuation (V) sections across the bank for all three transects. The distance–depth location of each observation is plotted as a dot, with the color of the symbol representing the magnitude each variable for that location. Fluorescence ranged from 0–4.2 relative units for the January 1995 and March 1995 cruises and from 0–95 relative units for the June 1994 cruise. Note that transects do not start at a common geographic location. The approximate cross-transect locations of the Shelf–Slope (SS), southern tidal (ST), and northern tidal (NT) fronts are indicated. Periods of night (black) and day (white) indicated across the top of each graph.

3.3. Distributions of abundant plankton and particles

3.3.1. Calanus finmarchicus

Calanus finmarchicus, one of the GLOBEC Georges Bank target species, was numerous over the bank (Fig. 6), with marked changes in distribution at the different sampling times. Because of its abundance on Georges Bank and because of the relatively low diversity of copepod species on Georges Bank, it was possible to identify *C. finmarchicus* to species but not to stage within the species. Hence, references to "*Calanus*" throughout refer to individuals identified as being *Calanus finmarchicus* with no identification of life stage, although based on the magnification of the camera utilized we expect that most were late-stage copepodites. *Calanus* were significantly larger during March 1995 (1.10 ± 0.27 mm) and June 1994 (1.1 ±0.21 mm) than during January 1995 (0.98 ± 0.2 mm), based on body width measurements (mean ± standard deviation; ANOVA, $p < 0.001$; Student–Newman–Keuls post-hoc test, $p < 0.001$; Zar, 1984); this may be because of

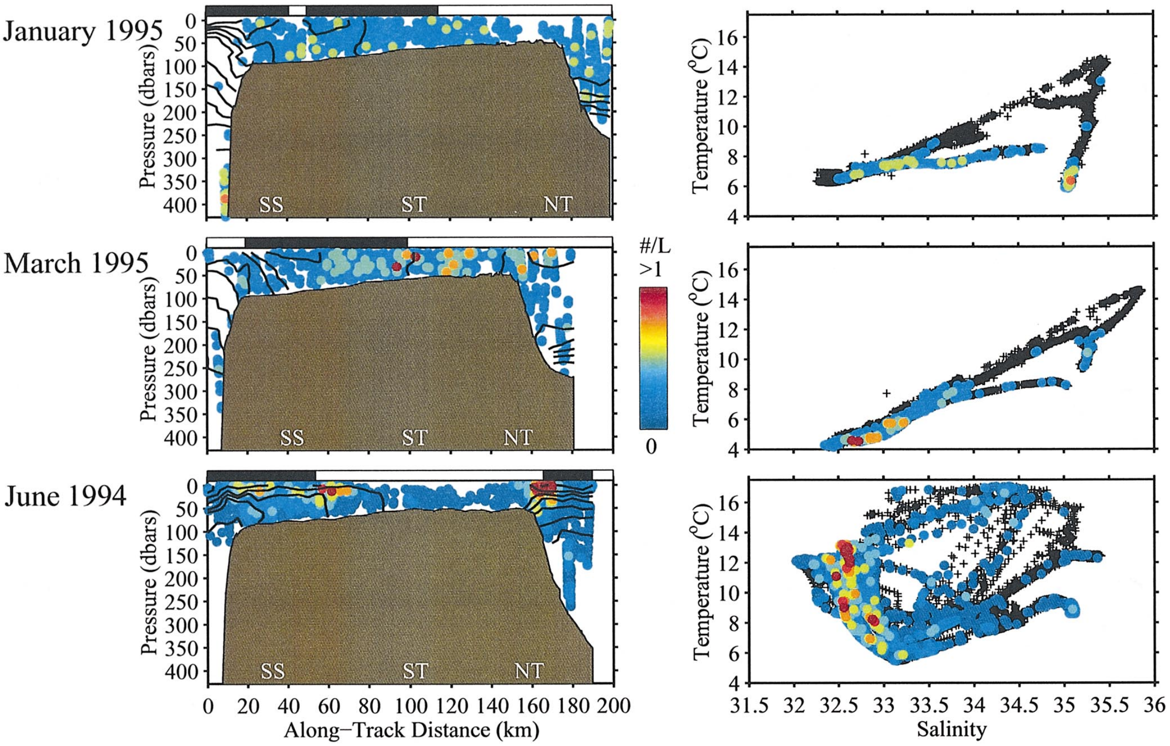

Fig. 6. Distribution of the copepod *Calanus finmarchicus* across the three transects (left) and as a function of temperature and salinity (right). The distance–depth or temperature–salinity location of each observation is plotted as a dot, with the color of the symbol representing the concentration (#/L) for that location. For the cross-transect distributions, note that transects do not start at a common geographic location. The approximate cross-transect locations of the Shelf–Slope (SS), southern tidal (ST), and northern tidal (NT) fronts are indicated. Periods of night (black) and day (white) indicated across the top of each transect graph. Contours of density also are shown (black lines). For the temperature–salinity–plankton diagrams, all *t–s* pairs are plotted as black crosses in addition to the *t–s* locations where *Calanus* were observed.

greater food availability (phytoplankton, microzooplankton) during late spring and summer, which increased the size of the animals. The association of *Calanus* with specific water types was demonstrated clearly through plots of *Calanus* abundance as a function of salinity and temperature (TSP Plots; e.g., Gallager et al., 1996) (Fig. 6). During January 1995, *Calanus* was present in low abundances in all water types except for Upper Slope Water. Greatest abundance was seen in the Lower Slope Water to the south of the bank (6°C, 35). By March 1995, abundances were elevated relative to January 1995, especially on the crest of the bank between the two tidal mixing fronts and in the upper Gulf of Maine water to the north of the northern tidal mixing front. The absence of *Calanus* from the very warm, salty Gulf Stream–Slope Water mix ($>12°C$, >35.5) found at 50–100 m at the southern end of the transect was conspicuous. *Calanus* also were not particularly abundant in the Scotian Shelf Water influx, although high abundances were seen in very cold and fresh water at other locations. *Calanus* were most abundant in June 1994. However, abundances over the crest of the bank were much diminished relative to those observed in both January 1995 and March 1995. Greatest abundances were observed in the stratified water both of the southern flank and of the Gulf of Maine located just to the north of the northern tidal mixing front. Despite the obvious association of *Calanus* with particular water mass types observed in the TSP plots, no correlations between *Calanus* abundance and any physical variable, fluorescence, attenuation, or marine snow were observed (Table 1). Vertically, *Calanus* were most abundant in the thermocline between the warm surface water and the cooler deep water, as seen both in the vertical distribution and by the high abundances of *Calanus* found in the vertical mixing portion of the shelf water and Gulf of Maine water in the T/S plot. For all three months, there was no noticeable diel change in vertical distribution at any of the seven day–night transitions based on visual inspection of the distributions (and see below), despite the coincidence or proximity of the day–night transition with the time of crossing at two of the fronts (March 1995, June 1994).

The vertical distributions of both *Calanus* and fluorescence across the transects were further examined through consideration of the weighted mean depth of the vertical distributions and the normalized weighted mean depth (e.g., Roe et al., 1984; Durbin et al., 1997). For these calculations, data were averaged into 5 km along-transect distance × 5 m depth bins. The mean depth for each along-track distance was calculated as

$$\sum_{i=1}^{49} n_i z_i \,\mathrm{d}z \Big/ \sum_{i=1}^{49} n_i \,\mathrm{d}z,$$

where z_i is the mid-depth of each 5 m ith depth bin, n_i is the concentration of *Calanus* or the fluorescence at that ith depth, and dz the depth interval between bins (5 m). Visual comparison of the weighted mean depths (Fig. 7) with the vertical sections of *Calanus* abundance (Fig. 6) demonstrated that the weighted mean depth was an accurate representation of the vertical distribution of the species, although the weighted mean depth usually was found below the abundance maximum at a particular location. For most cross-transect locations, *Calanus* were distributed homogeneously throughout the water column or concentrated in a single portion of the water column (Fig. 6), with few if any locations demonstrating a bimodal distribution. Hence, the weighted mean depth represents the central tendency of the depth distribution. The weighted mean depths were normalized to the maximum depth sampled at each 5 km along-track distance bin by dividing the mean depth by the maximum depth, obtaining values ranging from 0–1.0, which indicated the mean depth of *Calanus* relative to the total water column at that location (normalized weighted mean depth; Fig. 7). The normalized weighted mean depths indicate whether the animals or fluorescence (1) were distributed homogeneously throughout the water column or concentrated at the mid-depth (0.5) or (2) were concentrated in the upper (< 0.5) or lower (> 0.5) portions of the water column. A t-test was employed to ascertain whether the normalized weighted mean depths within a region were significantly different from 0.5 (Zar, 1984).

Calanus were found at greatest depths in the Slope Water to the south of the bank and in the Gulf of Maine to the north (Fig. 7, left panels; note that Lower Slope Water was not sampled in June 1994). Little variation in weighted mean depth was seen across the southern flank and Crest of the bank along any of the transects. The weighted mean depths of fluorescence were similar to those of *Calanus* across the southern flank and Crest of the bank during January 1995 but deeper in the water column during March 1995 on the Crest and during June 1994 on the southern flank ($p < 0.05$; Wilcoxon Signed Rank Test). Fluorescence had a shoaler distribution than *Calanus* in

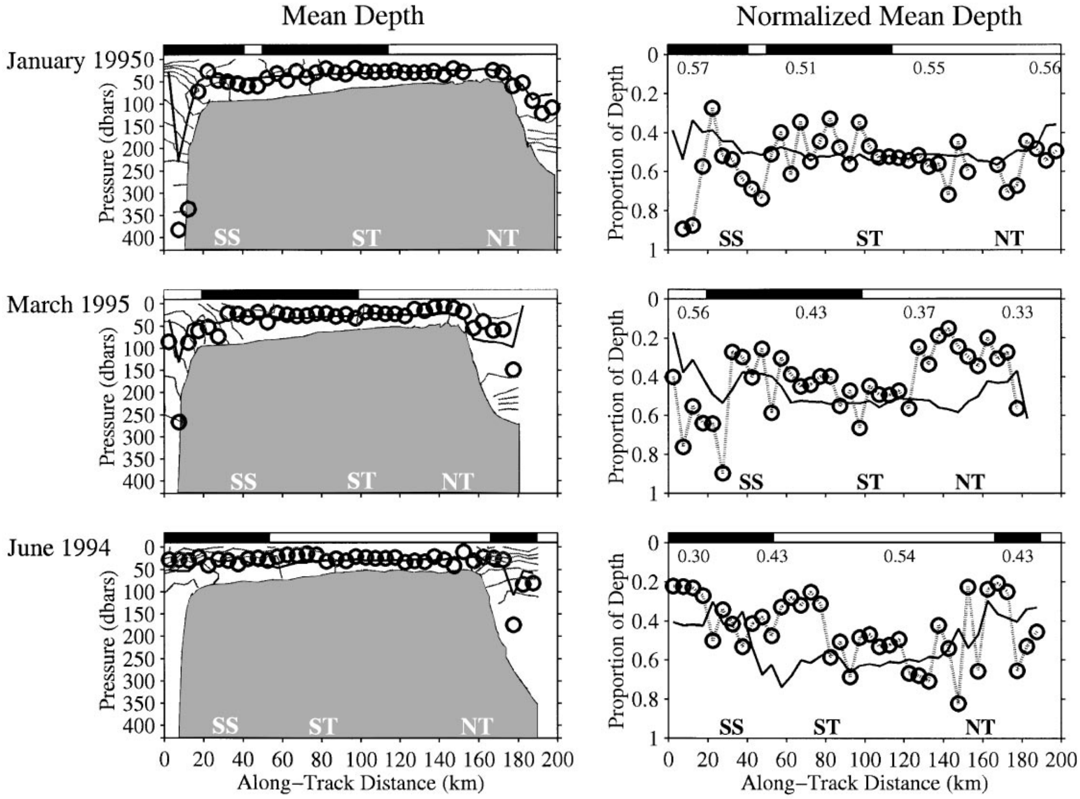

Fig. 7. Mean depth (left panels) and weighted mean depth (right panels) for the copepod *Calanus finmarchicus* (circles and dotted lines) and fluorescence (solid heavy line) across the three transects. Mean depth and weighted mean depth were calculated for all observations of these variables within 5 km along-transect distance intervals. The plot formats are as for Fig. 6, with periods of day and night, approximate cross-transect locations of frontal features, and distribution of isopycnals indicated with the thinner contour lines. The average weighted mean depth of *C. finmarchicus* was calculated within each of the cross-bank regions demarcated by fronts (seaward of Shelf–Slope Front, between Shelf–Slope and southern tidal mixing fronts, bank crest, and north of the northern tidal mixing front) and are indicated by the numbers on the right set of panels.

the Slope Water and Gulf of Maine during all three months; however, because of the low number of observations in these regions ($n = 6$–7), a significant difference between the two at the $p < 0.05$ level could not be achieved (Zar, 1984). Although *Calanus* is not considered strictly to be an herbivore (e.g., Landry, 1981; Barthel, 1988; Gifford, 1991; Kleppel, 1993; Ohman and Runge, 1994), phytoplankton (represented here by fluorescence) is one of the food sources for the animal. During January 1995, the mean depths of fluorescence and *Calanus* were positively correlated for all regions except the crest but showed weak positive or negative correlation for most regions during both March 1995 and June 1994 (Table 2), suggesting that the factors determining the depths of these two characteristics were different. Changes in the weighted mean depth of *Calanus* were not associated with the transitions between day and night, both for all data from each transect and for data within each region (Slope Water, southern flank, Crest, Gulf of Maine) for each month

Table 2
Correlation across the three transects and within each region between *Calanus finmarchicus* and fluorescence depth distribution, as expressed by the weighted mean depth (WMD) and normalized weighted mean depth statistics

Month	Region	*N*	Correlation coefficient	
			WMD	Normalized WMD
January 1995	Entire Transect	40	0.95[a]	− 0.01
	Slope Water	6	0.94[a]	0.26
	Southern Flank	14	0.86[a]	− 0.01
	Bank Crest	14	0.01	0.03
	Gulf of maine	6	0.88[a]	0.42
March 1995	Entire Transect	37	0.81[a]	− 0.09
	Slope Water	8	− 0.27	0.31
	Southern Flank	12	− 0.27	0.31
	Bank Crest	10	0.22	− 0.60
	Gulf of Maine	7	0.67	− 0.43
June 1994	Entire Transect	38	0.79[a]	0.36
	Slope Water	6	− 0.22	− 0.19
	Southern Flank	10	− 0.41	− 0.65[a]
	Bank Crest	15	− 0.22	− 0.19
	Gulf of Maine	7	− 0.33	− 0.91[a]

[a] Indicate coefficients which are significantly different from zero at $p < 0.05$ or better.

(Mann–Whitney *U*-Test, $p < 0.05$, Zar, 1984), supporting the observation that no diel vertical migration was occurring during these periods.

Greater variation was observed in the along-transect distribution of the normalized weighted mean depth for both *Calanus* and fluorescence (Fig. 7, right panels). Mean normalized weighted mean depths were calculated for each of the four geographic regions across the bank (south of the Shelf/Slope Front, southern flank, Crest, and north of the northern tidal mixing front) (Table 3). The normalized weighted mean depth may be utilized as an indicator of whether a vertical distribution is stratified, since values of the normalized WMD close to 0.5 may indicate a homogenous distribution. For January 1995, no significant differences in the normalized weighted mean depths of *Calanus* between the four regions were observed (Kruskal–Wallis test). A homogeneous distribution throughout the water column was observed in January 1995 in all regions except the bank crest where peak abundances were in the lower portion of the water column ($p < 0.03$); this apparent exception may be an artifact of the very low abundances observed in that region. For both March 1995 and June 1994, significant variations in the normalized weighted mean depth of *Calanus* between regions were observed (Kruskal–Wallis, $p < 0.03$ and $p < 0.083$ for March 1995 and June 1994, respectively). The NWMD of *Calanus* were shoaler on the Crest of the bank (0.37) and in the Gulf of Maine (0.33) than along the southern Flank (0.43) or Slope Water (0.56) during March 1995 (non-parametric post-hoc comparison of means, $p < 0.05$; Zar, 1984). Examination of the vertical distribution of *Calanus* (Fig. 6) revealed that in these two regions (southern Flank, Slope Water) *Calanus* was distributed homogeneously throughout the

Table 3
Average normalized weighted mean depths (NWMD) for *Calanus finmarchicus* and fluorescence for each of the four regions across each transect[a]

Month	Region	Average NWMD	
		C. finmarchicus	Fluorescence
January 1995	Slope Water	0.63A	0.42A,B
	Southern Flank	0.51 A	0.51B,C (0.03)
	Bank Crest	0.55 A (0.03)	0.53C (0.0002)
	Gulf of Maine	0.56 A	0.45A
March 1995	Slope Water	0.56A	0.39A (0.032)
	Southern Flank	0.43A, B	0.49A,B
	Bank Crest	0.37B,C (0.018)	0.54B (0.001)
	Gulf of Maine	0.33C (0.02)	0.47B
June 1994	Slope Water	0.30 A (0.006)	0.40A (0.0034)
	Southern Flank	0.43B,C (0.0014)	0.53B
	Bank Crest	0.54B	0.59B (0.00001)
	Gulf of Maine	0.43C	0.37A (0.001)

[a] For each month, the letters indicate regions for which the average normalized mean depths were not significantly different from each other ($p < 0.05$); the normalized mean depths for some regions were not significantly different from more than one other region and this is indicated with two letters. For example, the mean NWMD for January, 1995 was the same in all four regions (A). In March 1995, however, the mean NMWD for the southern flank was not different from that observed both in the Slope Water (A) and the crest (B). The numbers (in parenthesis) indicate the probability that the mean normalized depth is significantly different from 0.5 (*t*-test).

water column (also NWMD was not significantly different from 0.5). In contrast, in June 1994 *Calanus* were found shoaler in the Slope Water (0.3) than in the other three regions and deeper on the Crest of the bank (0.54) than in the Gulf of Maine (0.43) or on the southern Flank (0.43) (post-hoc comparison of means, $p < 0.05$). For both the Crest and Gulf of Maine, the normalized weighted mean depth was not significantly different from 0.5. Examination of the vertical distribution of *Calanus* (Figs. 6 and 7) confirmed this for the Crest while in the Gulf of Maine animals were found either in the upper water column near the northern tidal mixing front or at depth further to the north.

Regional differences were observed in the normalized weighted mean depths of fluorescence for all three months (Table 3). Fluorescence was relatively deeper in the water column over the southern flank and crest of the bank than in the Slope Water or in the Gulf of Maine. Stratification (normalized mean depth significantly different from 0.5) generally was observed in regions with elevated fluorescence across each of the transects.

3.3.2. Hydroid colonies

The asexual hydroid phase of cnidarians, when detached from their typical benthic habitat, potentially are important predators of young *Calanus* and larval fish on Georges Bank (e.g., Bigelow, 1926; Davis, 1987; Gallager et al., 1996; Madin et al., 1996). Hydroid colonies were conspicuous in the Video Plankton Recorder images, especially during March 1995 and June 1994

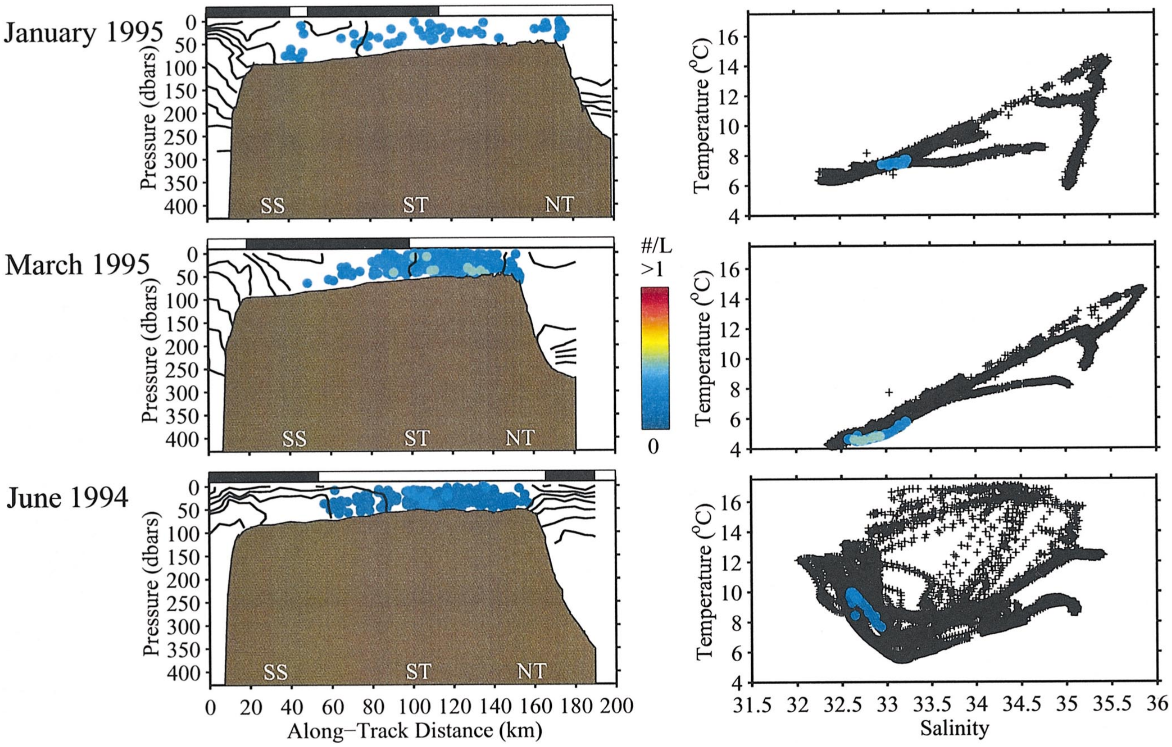

Fig. 8. Distribution of hydroid colonies across the three transects (left) and as a function of temperature and salinity (right). Plot format as for Fig. 6.

(Fig. 8). Lowest abundances of hydroid colonies were observed during January 1995, with progressively greater abundances during March 1995 and June 1994. Hydroids generally were confined to the crest of the bank in Georges Bank Water. Some colonies also were found in the Shelf Water to the south of the southern tidal mixing front during June 1994, but none were found in the Slope Water or in the Gulf of Maine. On the crest, hydroids were distributed homogeneously throughout the water column (note from Fig. 2 that the VPR did not survey to the surface during June 1994). Comparison of the distributions of *Calanus finmarchicus* and hydroid colonies from the three transects reveals that the distribution of hydroids during March 1995 corresponded to the region of greatest *Calanus* abundance while the distribution during June 1994 was associated with the region of lowest *Calanus* abundance.

3.3.3. Phaeocystis spp. protocolonies

One of the more intriguing taxa observed with the Video Plankton Recorder was the protocolonies of the colonial phytoplankton *Phaeocystis* spp. These smooth, ellipsoid objects were observed in great abundance during March 1995 and lower abundances during January 1995 (Fig. 9). Prior data on the distributional patterns of these delicate organisms was lacking owing to their very delicate nature and the lack of non-destructive sampling methods for quantifying their abundance. The distribution of *Phaeocystis* protocolonies was restricted mostly to the crest of the bank and

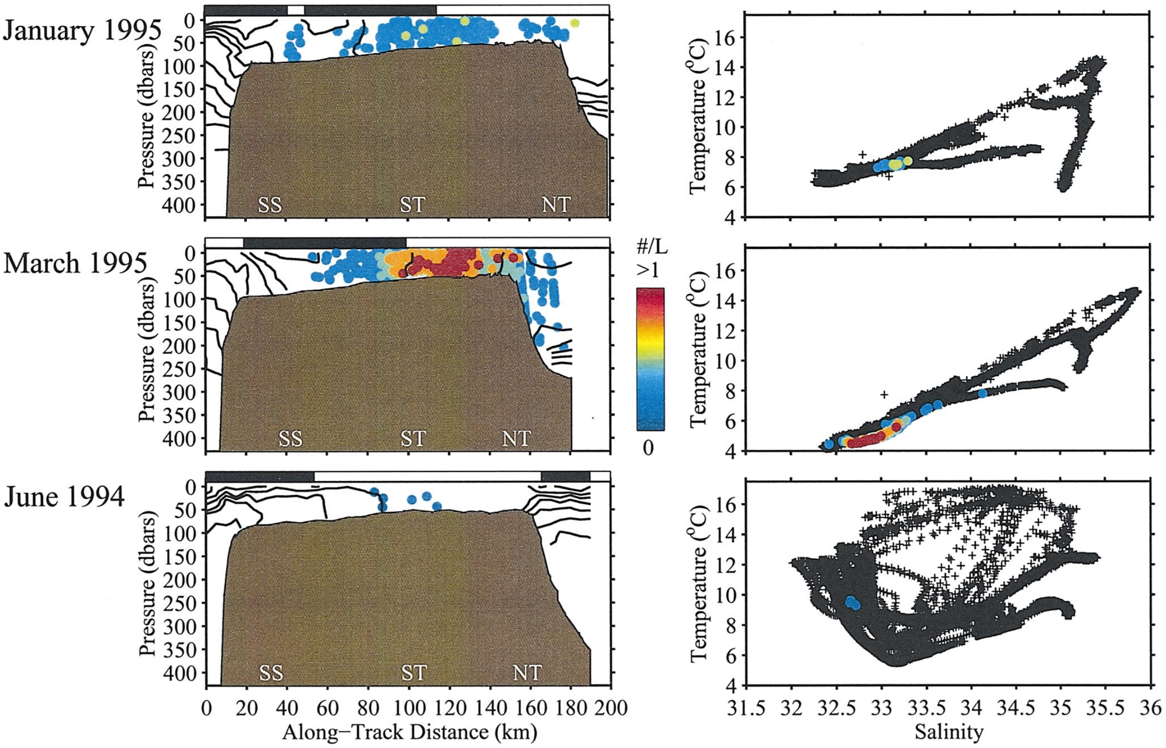

Fig. 9. Distribution of *Phaeocystis* spp. protocolonies across the three transects (left) and as a function of temperature and salinity (right). Plot format as for Fig. 6.

Georges Bank Water (between the tidal mixing fronts), although some colonies were observed both on the southern flank and in the Gulf of Maine. Very few protocolonies, or mature colonies, of *Phaeocystis* were seen in June 1994. The observed bloom of *Phaeocystis* may be an episodic event that does not occur annually.

3.3.4. Pteropods

Pteropods (likely *Limacina retroversa*; Redfield, 1939; Davis, 1987; Gallager et al., 1996) were present across Georges Bank during all three months; however, abundances and occurrence were dramatically reduced during June 1994 relative to both January 1995 and March 1995 (Fig. 10). Distribution was uniform and vertical homogeneous across the crest and southern flank of the bank during both January 1995 and March 1995, in the well-mixed Shelf Water and Georges Bank Water. Individuals were observed sporadically in the Gulf of Maine and Slope Water. During June 1994, few individuals were observed on the crest of bank and only a scant number were observed on the southern flank. The difference in seasonal abundance is likely due to life history characteristics of this cold-water species. Redfield (1939) described the counter-clockwise drift and population development of *L. retroversa* in the Gulf of Maine during spring and found a close association between population size structure and circulation.

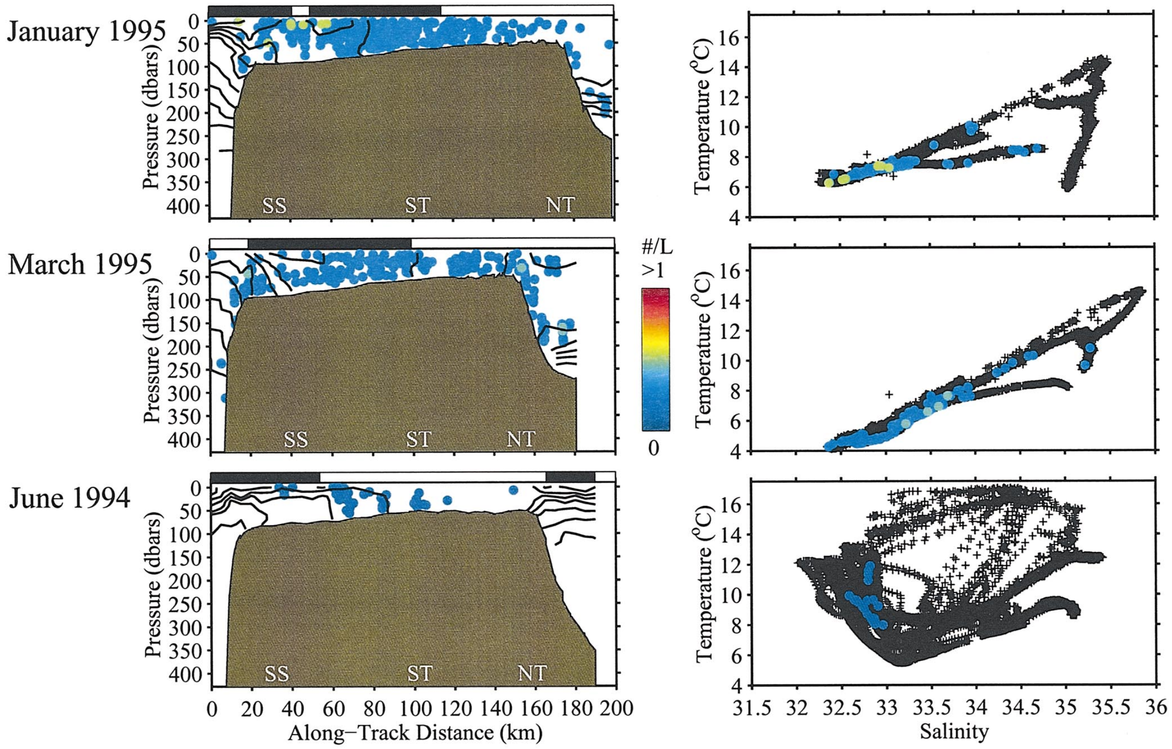

Fig. 10. Distribution of pteropods across the three transects (left) and as a function of temperature and salinity (right). Plot format as for Fig. 6.

3.3.5. Marine Snow

Marine snow was the most abundant category of plankton or particle identified (72.8, 61.2, and 80.3% of all images for January 1995, March 1995, and June 1994, respectively). Low concentrations were observed over most of the bank during January 1995 except in the Shelf Water between the Shelf–Slope and southern tidal mixing fronts (Fig. 11), where elevated concentrations were observed in at mid- and near-bottom depths. Concentrations across the bank were similar in March 1995, with nodes of elevated concentrations found on the southern flank and on the crest of the bank, in Shelf Water and Georges Bank Water. Greatest concentrations were found during June 1994 offshore of the southern tidal mixing front between the Shelf Water and Georges Bank Water. Few similarities between the distributions of marine snow and physical variables, fluorescence, light attenuation, and *Calanus* were observed (Table 1). Only on the bank crest in March 1995 was coincidence in the distribution of light attenuation and marine snow concentration observed. The mean diameter of marine snow varied significantly between months, with largest particles observed in March 1995 (2.1 ± 1.0 mm, $n = 29{,}641$), and smaller particles in January 1995 (1.9 ± 1.8 mm, $n = 10{,}497$) and June 1994 (1.8 ± 0.85 mm, $n = 23{,}679$) (mean ± SD; ANOVA, $p < 0.05$; Student–Newman–Keuls post-hoc test, $p < 0.05$; Zar, 1984). The larger size of marine

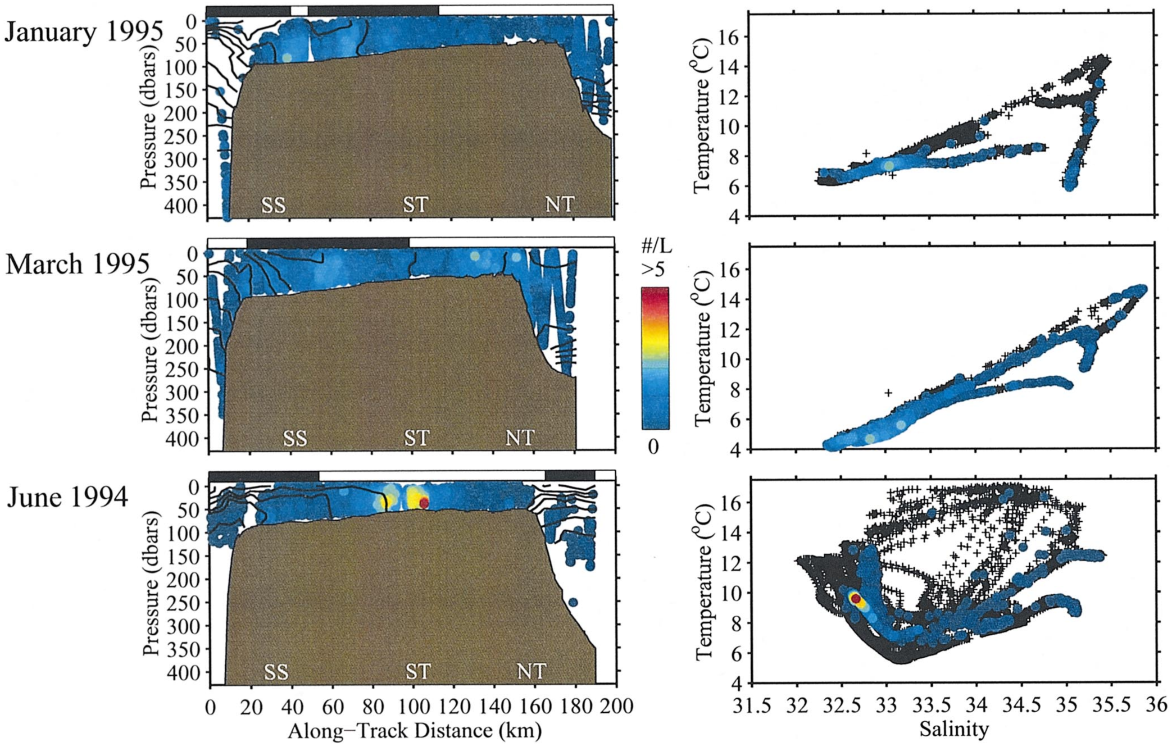

Fig. 11. Distribution of marine snow across the three transects (left) and as a function of temperature and salinity (right). Plot format as for Fig. 6.

snow particles in March 1995 may have resulted from the high abundance of material produced during primary production (e.g., decomposing phytoplankton, algal mats).

3.3.6. Algal mats

High abundances of algal mats, a type of marine snow composed of chains of diatoms were observed during March 1995 in the Shelf–Slope Front and Slope Water to the south of the bank (Fig. 12). The morphology of these large particles was similar to that described by Alldredge and Silver (1988) and likely resulted from elevated concentrations of chain diatoms produced during the spring bloom along the southern flank and in the Shelf–Slope front.

3.4. Principal component analysis

The first three modes of the principal component analyses explained up to 83% (for March 1995) of the total variability in the seven variables utilized and identified associations that were not robust in the correlation analysis; the fourth mode encompassed another ~ 13% of the total variability (Table 3). The normalized coefficients of each of the eigenvectors indicated the potential contribution of each variable to the principal component for that mode, with similar coefficients indicating similar weightings and opposing signs indicating a negative association. The spatial

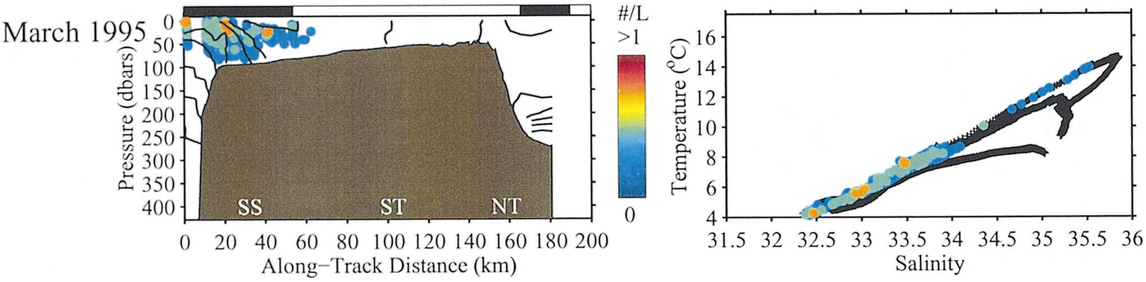

Fig. 12. Distribution of algal mats across the transect (left) and as a function of temperature and salinity (right) in March 1995. No algal mats were observed in January 1995 or June 1994. Plot format as for Fig. 6.

distribution of the principal components of each mode reflected the distributions of the variables with high coefficients for that mode. No association between *Calanus finmarchicus* and hydrographic (temperature, salinity, density) characteristics were observed, indicating that the distribution of *Calanus* was decoupled from that of the hydrography. For January 1995, hydrography, fluorescence, and light attenuation were strongly associated in the first mode; a negative association between marine snow concentration (1.00) and fluorescence (− 0.788) and attenuation (− 0.837) was seen in the second mode. Together the first two modes explained over ~ 62% of the total variance. The spatial distributions of the first modes (Fig. 13) was similar in many respects to the mesoscale distribution of water mass types across the bank, while that of the second mode was strongly influenced by elevated concentrations of marine snow on the southern flank and in the upper Gulf of Maine, which were associated with (a) near-constant hydrographic characteristics and (b) decreasing values of fluorescence and light attenuation. This suggests that the marine snow was composed of detrital rather than fluorescing material. The third mode was almost exclusively influenced by *Calanus finmarchicus*, explaining ~ 14% of the variance. The spatial distribution of this mode (not shown) resembled the distribution of *Calanus* across the bank. The fourth mode embodied variation primarily in the concentration of marine snow. For March 1995, hydrographic (temperature, salinity, density) characteristics again were strongly associated and their variability was expressed by Mode 1 (~ 46% of the total variance). Fluorescence and light attenuation were not as strongly associated with hydrography as observed in January 1995 and were the dominant variables in Mode 2 (23% of the total variance). *Calanus* was the dominant variable in Mode 3. No association was seen between fluorescence and light attenuation and *Calanus* or marine snow. The fourth mode was dominated by marine snow (~ 13%). Again, the spatial distribution of the first principal component strongly resembled that of the hydrographic features. The potential presence of a Scotian Shelf Water intrusion is seen in the across-transect distribution of the first principal component as the low value located at 20–40 km along-track distance and between 0 and 50 m (Fig. 13). The distribution of the second principal component was similar to those of fluorescence and light attenuation. Associations between variables differed in June 1994. Temperature was not associated with salinity and density, indicating that salinity may have been the primary determinant of density at this time (but see cross-transect distributions of temperature and density) and perhaps reflecting the modification of temperature from insolation and the onset of stratification. Light attenuation, and to a lesser extent fluorescence, was associated negatively with salinity and

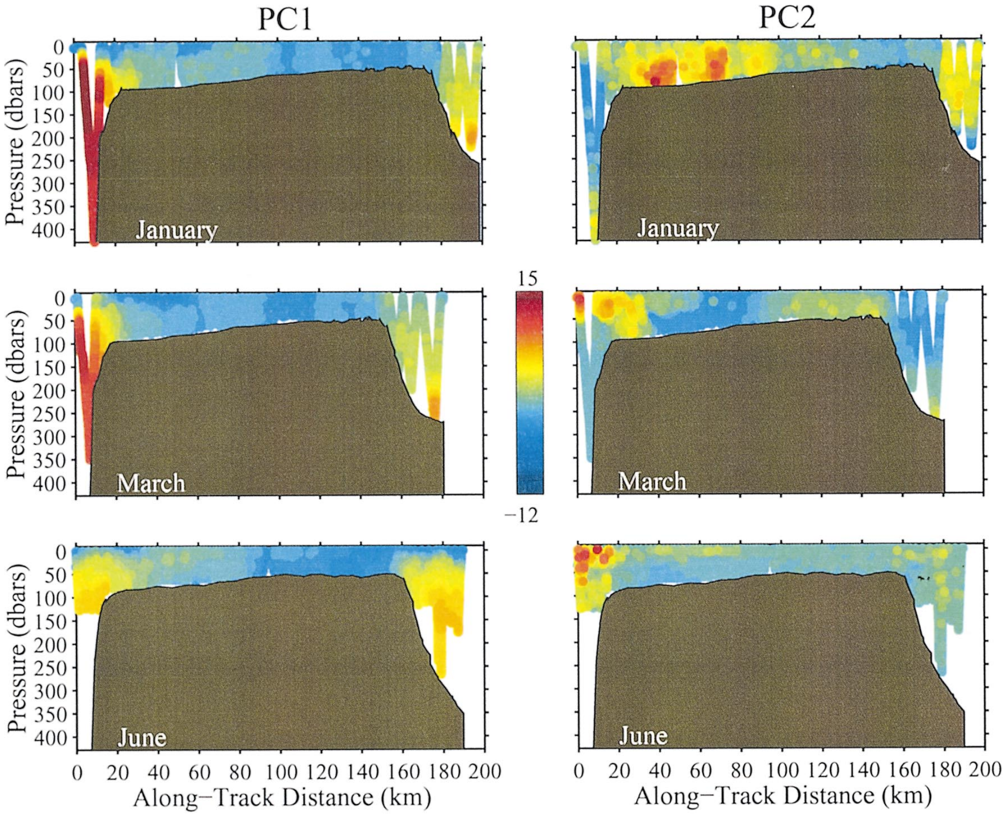

Fig. 13. First and second principal components plotted as a function of distance and pressure for the three transects. The distance–depth location of each data point is plotted as a dot, with the color of the symbol representing the magnitude each principal component for that location. The values of principal component 2 for June 1994 were multiplied by 10 prior to plotting in order to better show variations in magnitude.

density in the first mode which explained ~ 48% of the total variance. The spatial distribution of the first principal component was similar to those of salinity, density, light attenuation, and, to some degree, fluorescence. This mode, then, described the association between water mass types and the relative concentrations of particulates measured by light attenuation and fluorescence. The second mode was influenced strongly by temperature with some association seen between fluorescence (negative) and *Calanus* (positive); this mode explained ~ 16% of the total variance. The distribution of this mode resembled that of temperature. The third mode (15.7%) was influenced by marine snow, with some negative association seen between marine snow and fluorescence and temperature. Not until the fourth mode (14.9% of the total variance) is the abundance of *Calanus* important, with only some negative association between *Calanus* and temperature present. Note that little association between *Calanus* and hydrographic characteristics, biological variables, or marine snow also was seen in correlation coefficients (Table 1). The association between fluorescence and light attenuation was not as strong during June 1994 as for the other two months, which was not surprising considering the distribution of these variables (Fig. 5). Principal component analysis, then, was used to identify statistically mesoscale distributions, associations, and patterns observed visually in the data and identified the proportion of the total variance in the data set that was accounted for by each type of distribution.

3.5. Flux of *Calanus*

Velocities averaged over selected depth ranges of the upper water column demonstrated the classic Georges Bank circulation, with strong easterly advection concentrated in a jet along the northern edge and more diffuse westerly circulation across the southern flank of the bank (Fig. 14). Velocities in the Gulf of Maine (north of the 200 m isobath) were oriented in a northeasterly direction. Slope Water velocities (between 200 and 2000 m isobaths) were generally southeasterly, although surface depths demonstrated a more southerly direction. Northerly velocities in the on bank direction were observed at depth (176–208 m) in the Slope Water.

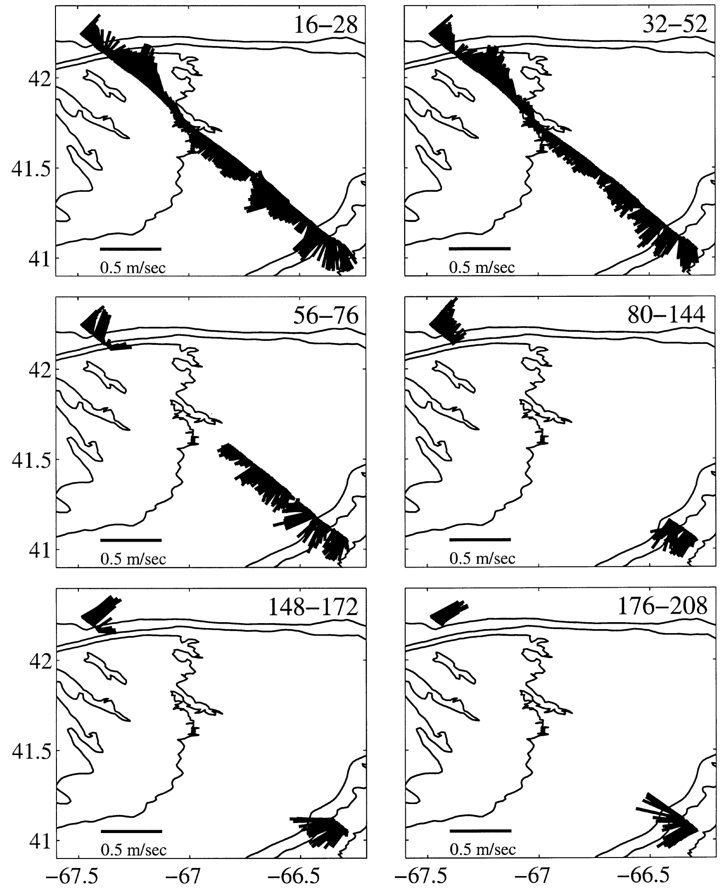

Fig. 14. Acoustic Doppler current profiler velocities, averaged over selected depth intervals, across the transect for January, 1995. Depths over which velocities were averaged were selected by examination of the velocities at all depths to identify depths for which the magnitude and direction of velocities were similar. Bottom contours of 40, 60, 100, 200, and 100 m are shown.

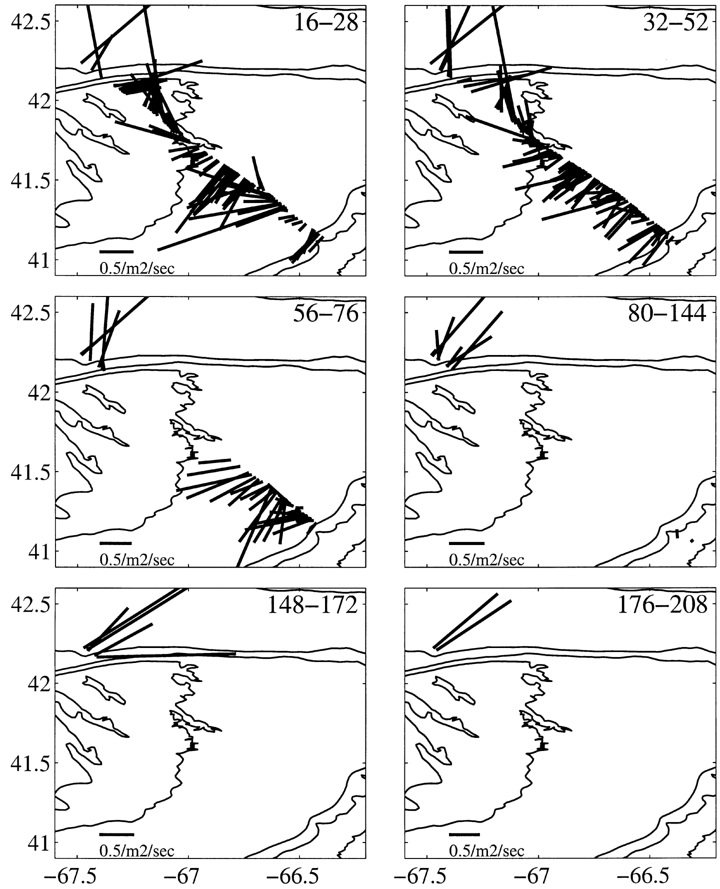

Fig. 15. Flux of the copepod *Calanus finmarchicus* across the transect in January, 1995. Flux estimates were derived by multiplying the depth-averaged velocity vectors (Fig. 15) by the abundance of *C. finmarchicus* in that depth-cross-stream location data bin. No flux estimates were derived for locations where no *C. finmarchicus* were observed. Bottom contours of 40, 60, 100, 200, and 100 m are shown.

The flux of *Calanus* on the bank itself followed the anticyclonic circulation around the bank, with little evidence of either off- or on-bank transport (Fig. 15). The jet along the northern edge of the bank appeared to concentrate *Calanus* into the center of the current in the upper water column (16–52 m). Flux of *Calanus* in the Gulf of Maine (north of 100 m isobath) was oriented away from the bank for all depths, indicating that little input *Calanus* onto the bank from the Gulf of Maine was occurring.

3.6. Spectral analysis

Much of the larger-scale variability in the spectra can be attributed to the vertical structure of the water column (Fig. 16). Because the data were collected along a towyo path, temporal changes in the spectra are relatively equivalent to spatial changes. For pressure and the hydrographic

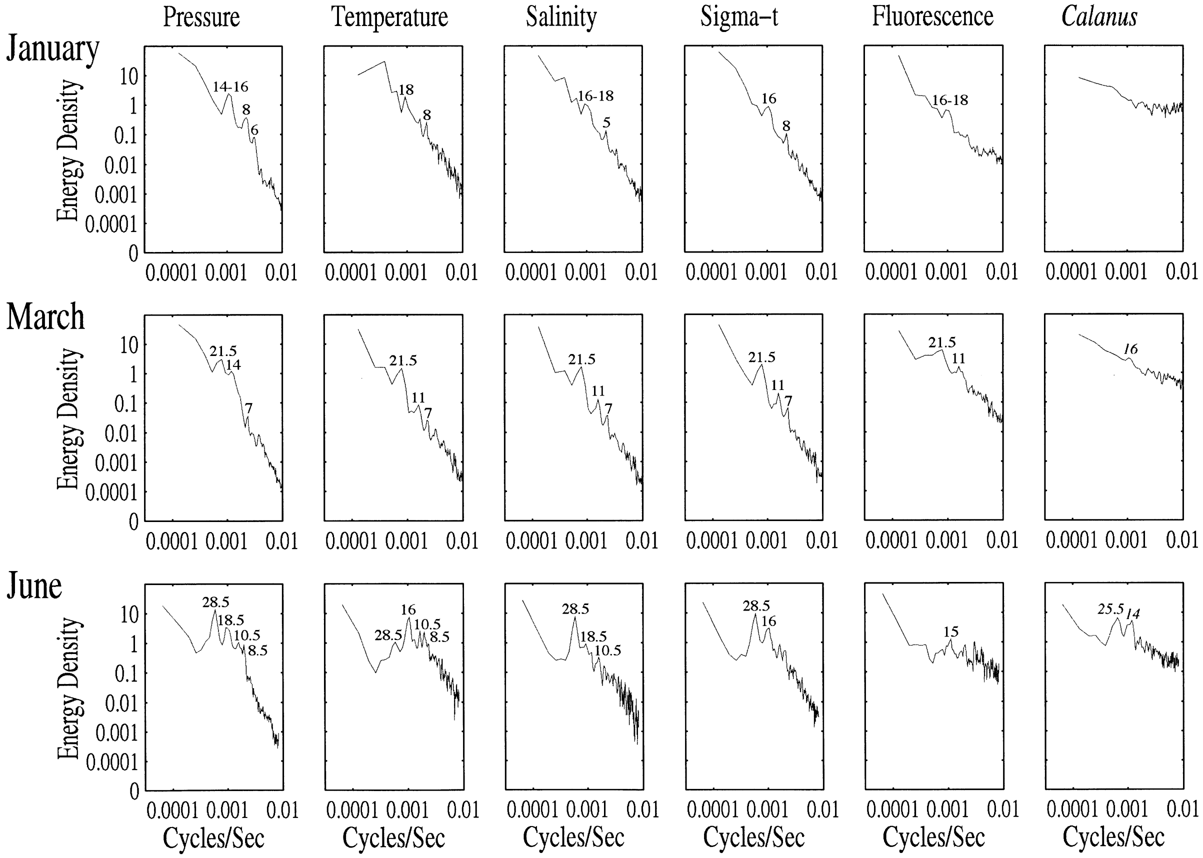

Fig. 16. Spectral analyses for pressure, temperature, salinity, sigma-*t*, fluorescence, and *Calanus finmarchicus* abundances for the three transects. Period in minutes of dominant peaks are noted on each panel; those not associated with the towyo period and vertical structure of the water column are indicated in italics.

variables, several pronounced peaks in each spectra were associated with the time interval of the towyo; the periods of the towyos varied with water depth, and hence location across the transect, and from cruise to cruise. The spectra of the reference variable, pressure, demonstrate the period of the towyos for each cruise. Vertical structure in hydrographic features was much more pronounced during June 1994 than the winter/spring months (Fig. 3). Consequently, towyo effect peaks resulting from the vertical structure of the water column and period of the towyos at the different across bank locations were observed at multiple periods for both the reference and hydrographic variables during that month.

Overall, greater energy was present in the spectra of the biological variables (fluorescence and *Calanus*), especially at longer time periods. Small-scale variability (higher energy) was greater for plankton (fluorescence and *Calanus*) than for hydrographic variables (temperature, salinity, density). The effect of vertical structure was much reduced in the spectra of the biological variables (fluorescence and *Calanus*) (Fig. 16) and was more prominent in the spectra of fluorescence than

Table 4
Eigenvectors of the first four modes from the principal component analyses for the three transects[a]

	Mode 1	Mode 2	Mode 3	Mode 4
January, 1995				
Temperature	0.799	– 0.413	– 0.114	0.217
Salinity	1.000	– 0.528	0.025	0.287
Sigma-*t*	0.902	– 0.489	0.091	0.273
Fluorescence	– 0.830	– 0.788	0.037	0.400
Attenuation	– 0.801	– 0.837	0.078	0.422
C. finmarchicus	0.068	0.303	1.000	0.143
Marine snow	– 0.046	1.000	– 0.198	1.000
% Total variance	45.2	17.5	14.3	12.600
Cumulative %	45.2	62.7	77.0	89.600
March, 1995				
Temperature	0.966	0.345	– 0.022	0.078
Salinity	1.000	0.325	– 0.008	0.137
Sigma-*t*	0.963	0.316	– 0.013	0.181
Fluorescence	– 0.576	0.939	0.005	0.066
Attenuation	– 0.491	1.000	0.024	0.083
C. finmarchicus	– 0.081	– 0.119	1.000	0.439
Marine snow	– 0.272	– 0.221	– 0.437	1.000
% Total variance	45.7	23.0	14.3	13.3
Cumulative %	45.7	68.7	83.0	96.3
June, 1994				
Temperature	– 0.187	1.000	– 0.532	– 0.445
Salinity	0.972	0.121	– 0.289	– 0.260
Sigma-*t*	1.000	– 0.386	– 0.006	– 0.033
Fluorescence	– 0.683	– 0.548	– 0.516	– 0.159
Attenuation	– 0.973	– 0.183	– 0.092	– 0.056
C. finmarchicus	– 0.024	0.448	– 0.156	1.000
Marine snow	– 0.257	0.335	1.000	– 0.243
% Total variance	40.2	16.2	15.7	14.9
Cumulative %	40.2	56.4	72.1	87.0

[a] The percentage of the total variance explained by each mode also indicated. For June 1994 only those data where the temperature was less than or equal to 13°C were employed in the analysis.

those of *Calanus*. For all three months, the towyo effect peaks associated with data collected on the southern flank were present in the fluorescence spectra, although the shorter period peak (constant variable effect) was present only in the June 1994 spectrum. For *Calanus*, no apparent effect of vertical structure was observed during January 1995, when the vertical distribution was fairly homogeneous (Figs. 6 and 7). The energy peaks in March 1995 (16 mins) and June 1994 (14, 25.5 minutes) were not associated clearly with vertical structure or the towyo period. For both March 1995 and June 1994, these energy peaks for *Calanus* were located on the spectra at times sufficiently similar to those of the pressure towyo effect peaks from locations where the animal was most abundant (the crest for March 1995 with a towyo effect peak of 11–14 min and the southern flank/northern edge for June 1994 with a towyo effect peak of 16 min) that the *Calanus* spectral peaks may have resulted from variability in the abundance maximum at adjacent towyos or from patchiness in the upper water column.

4. Discussion

High-resolution descriptions of water mass, plankton, and particle distributions across Georges Bank were obtained in the present study. The coincidence of biological and physical measurements permitted a closer and higher resolution examination of the association between these variables than is usually possible using conventional biological sampling methods. Only a few previous studies of the plankton distributions across on Georges Bank have achieved such high vertical (1 m) and horizontal (1 km) resolution (e.g., Benfield et al., 1996; Gallager et al., 1996; Norrbin et al., 1996), since most taxon specific biological sampling has been conducted at horizontal separations of kilometers and with vertical resolution of multiple meters (e.g., Durbin et al., 1997) or total water column (e.g., Davis, 1987; Meise and O'Reilly, 1996). Such high-resolution data now permits biologists to examine variability with tools such as principal component analysis and spectral analysis which previously have been utilized primarily in the analysis of physical data (e.g., Preisendorfer, 1988) or to identify associations between different taxa from net or bottle sampling (e.g., Denman and Platt, 1978).

The distributions of plankton and particles clearly were associated with the different water masses. For most taxa, these distributions, did not vary during the different months sampled, although abundances changed markedly (e.g., *Phaeocystis* protocolonies, hydroids, pteropods). For *Calanus finmarchicus*, seasonal changes in its association with a particular water mass type also was demonstrated. Although taxon–water mass associations were observed on a regional or mesoscale, biological and physical characteristics were decoupled on smaller scales so that little correlation between physical properties (e.g., temperature) and plankton abundance (e.g., *Calanus*) was observed.

The structure of the physical environment (density, temperature/salinity, advection) on Georges Bank during the three transects was representative of typical conditions and exhibited frontal features and regional water mass characteristics described previously (e.g., Hopkins and Garfield, 1981; Flagg, 1987; Butman et al., 1987). Deviations from the mean characteristics were observed in association with advective or dynamic events. For example, the Shelf–Slope Front was distinct across all three transects; however, the width of the feature and the inclination of the isopycnals varied according to the influence of dynamic features (e.g., rings or eddies) offshore of the bank. Such mesoscale features also produced the high temperatures and salinities observed during the June 1994 transect, as water of Gulf Stream origin mixed with upper Slope Water along the southern edge of the bank. The presence of Scotian Shelf Water on the southern flank in March 1995 occurred during episodic advective injection of Scotian Shelf Water across the Northeast Channel onto the bank (e.g., Bisagni et al., 1996; Smith et al., 2001).

Principal component analysis and correlations between physical and biological variables revealed differences between the winter–early spring (January 1995, March 1995) and early summer (June 1994). For example, salinity appeared to be important in determining density during June

1994 while both salinity and temperature were important in January 1995 and March 1995. Close association between fluorescence and light attenuation during January 1995 and March 1995 indicated that most particles measured by light attenuation may have contained viable chlorophyll, indicative of recent primary production. By contrast, little association was seen between fluorescence and light attenuation in June 1994, suggesting that the particles during that period may have been detrital. Furthermore, no association was seen between light attenuation and marine snow. Note also that only in June 1994 was a negative association (PCA; Table 4) between *Calanus* and fluorescence observed, suggesting either that differing mechanisms are determining the abundance of the two or, potentially, that grazing by *Calanus* on fluorescing particles had occurred. Principal component analysis also demonstrated that much of the overall variability in the data sets was derived from the across-bank presence of different water mass types and regimes, since the spatial distribution of the first mode (representing half of the total variability) resembled strongly the across bank distribution of water masses. These observations suggest that very different physical and biological regimes existed in early winter/late spring vs. early summer.

Despite the obvious coincidence of particular taxa and water mass characteristics, as observed both in the cross-transect distributions and temperature–salinity–plankton plots (Figs. 6–12), no statistical relationships (e.g., correlation, principal component analysis) could be identified between the distributions of *Calanus* and marine snow and fluorescence, light attenuation, or hydrographic characteristics. This may be a consequence in part because of the disparate nature of plankton abundance (discrete) vs. hydrographic (continuous) data. Additionally, a particular hydrographic condition (e.g., temperature range) may exist simultaneously in multiple water masses but a particular taxon is confined to a single water mass; hence, correlation coefficients would not show a relationship between that temperature range and the taxon's abundance since variation in the magnitude of the two variables would not co-vary over all the observations. This likely accounts for the lack of correlation (correlation coefficient) between *Calanus* and fluorescence during June even though principal component analysis indicated that there was association between the two. Hence, the distribution of taxa observed on Georges Bank resulted either from advection of plankton onto the bank in particular water masses or, more likely, from establishment of populations on the bank in specific regions, rather than resulting from a behavioral response by the taxon to locate preferred temperature or salinity characteristics.

Spectral analysis of the biological and hydrographic data revealed that, although some variability in the distribution of plankton and physical variables occurred on similar spatial/temporal scales, variability in the distribution of plankton at the small scale was greater than that observed either for hydrographic variables or for the reference variable of pressure. These results suggest that water mass characteristics probably were not the dominant influence on the distribution of plankton at small scales and that biologically induced patchiness may have accounted for the small-scale variability, as has been demonstrated in previous VPR studies (e.g., Davis et al., 1992b; Gallager et al., 1996).

Calanus finmarchicus was the dominant zooplankton taxon present in the size range imaged by this configuration of the Video Plankton Recorder. Distributions of *Calanus* were consistent with those observed in previous and ongoing investigations of the Georges Bank ecosystem (e.g., Davis, 1987; Meise and O'Reilly, 1996; Durbin et al., 1997). The distribution and associations of *Calanus* with particular water masses and regions on the bank are believed to result from the interaction of life history characteristics (e.g., vertical distribution, timing of reproduction) and advection which transports populations of the copepod onto Georges Bank (e.g., Davis, 1987; Meise and O'Reilly, 1996; Durbin et al., 1997; Lynch et al., 1998). Despite the inability of the VPR to distinguish between the different life stages of *Calanus finmarchicus*, the results of the present study still can be interpreted in the context of our understanding of these processes and interactions. During winter and spring, C. *finmarchicus* was found across the bank in both the Georges Bank and Shelf Water masses, as well as in the Gulf of Maine and in Lower Slope Water. By summer, however, populations of C. *finmarchicus* in Georges Bank Water (well mixed, crest of the bank) had diminished considerably while populations in the Shelf Water to the south and the northern tidal front (Surface and Intermediate Maine Water) were enhanced.

Off bank populations are thought to be the sources for repopulation of *Calanus* on Georges Bank during winter and early spring. *Calanus* spends the summer and fall at depth in the Basins of the Gulf of Maine or Scotian Shelf, migrating to surface waters in early winter to initiate reproduction (e.g., Davis, 1987; Durbin et al., 1997). Following ontogenetic migration of *Calanus* to the upper water column in the Gulf of Maine, populations on the bank should be renewed annually by several mechanisms including episodic advection of Gulf of Maine Water onto the bank along the northern edge during storms, non-storm-related advection of Gulf of Maine water onto the bank, or input from the Great South Channel region in the northeasterly flowing gyral circulation at the northern edge of the bank (e.g., Perry et al., 1993; Lewis et al., 1994; Limeburner and Beardsley, 1996; Durbin et al., 1997; Hannah et al., 1998; Lynch et al., 1998). Significant input of *Calanus* occurs in the Northeast Peak Region (e.g., Durbin et al., 1997; Lynch et al., 1998). The distributions of *Calanus* observed in the present study during January 1995 and March 1995 are consistent with these hypothesized repopulation mechanisms. Low abundances of *Calanus* were present on the bank during winter (January 1995) with greater abundances observed in the Lower Slope Water to the south and in the Maine Bottom Water to the north of the bank. Flux of *Calanus* (Fig. 15) indicated that transport of *Calanus* in upper portion of the water column from the west in the gyral circulation was occurring, with little input from the Gulf of Maine at this time. The apparent inconsistency between the flux of *Calanus* observed in this study and the mean circulation and mean flux of *Calanus* described in modeling efforts (e.g., Hannah et al., 1998; Lynch et al., 1998) may simply have resulted from variability in the circulation with low levels of Ekman flow occurring during this period. The relative importance of such wind-driven transport relative to that occurring in the easterly jet of the anticyclonic gyre cannot be assessed in the present study. By March 1995, *Calanus* was observed across Georges Bank and in the Gulf of Maine, with greatest abundances in the Georges Bank Water on the crest of the bank and in the surface waters of the Gulf of Maine and little or no *Calanus* in the Upper Slope Water to the south of the bank. The presence of *Calanus* on the crest of the bank implies that advection of Gulf of Maine and northern flank water across the northern tidal mixing front and easterly jet must have occurred in order to establish a seed population for subsequent reproduction, although this input was not obvious in the velocity or flux vectors observed during January 1995 (Figs. 14 and 15). During June 1994, greatest abundances of Calanus were found in the upper portion of the water column both on the southern flank and along the northern edge of the bank; the anticyclonic gyral circulation is strongest in these regions and at these depths and hence these populations of *Calanus* likely were transported to the NE (northern edge) or to the SW and potentially off the bank (southern flank) (e.g., Limeburner and Beardsley, 1996).

Input of *Calanus* to Georges Bank also may occur during episodic influx of Scotian Shelf Water to the bank (e.g., Bisagni et al., 1996; Durbin et al., 1997; Lynch et al., 1998). However, abundances of *Calanus* in the Scotian Shelf Water observed across the March 1995 transect were reduced relative to abundances at depth and inshore of the feature, indicating that this particular event did not input significant quantities of *Calanus* to the bank at this time.

Similarities in the temperature–salinity characteristics of Lower Slope Water and Maine Bottom Water, and the presence of a physical input mechanism of Lower Slope Water to the deep Gulf of Maine via the Northeast Channel (e.g., Ramp, 1986; Smith et al., 2001) suggest that the populations of *Calanus* observed during the present study in these water masses may have originated from a common, up-stream source along the Scotian Shelf. The acoustic Doppler current profiler velocity vectors from January 1995 demonstrated that little input of Lower Slope Water onto Georges Bank occurred along the southern flank during the sampling period. Temperature–salinity characteristics of the water surveyed on the southern flank also showed that no Lower Slope Water was found on Georges Bank. Therefore it is possible that the mechanism for input of Slope Water populations of *Calanus* to Georges Bank was influx of Lower Slope Water into the deep Gulf of Maine, rather than direct advection from the Slope Water along the southern flank of the bank.

Alternatively, the association of the *Calanus* with Maine Bottom Water and Lower Slope Water could have been due simply to downward seasonal vertical migration by animals produced in the upper waters of the shelf. The seasonal cycle of the vertical distribution of *Calanus* in the Slope Water (Miller et al., 1991) shows that the population is present in the surface waters of the slope during May and resides at a depth of $\sim$ 300–500 m during the rest of the year. It is well known that spring *Calanus* populations in the open ocean are produced in surface waters and then migrate to great depth ($\sim$ 500 m) for the rest of the year to over summer or overwinter (depending on latitude) (e.g. Fulton, 1973; Williams, 1985; Miller et al., 1991). In shelf regions, animals transported off the shelf by advection would migrate to their desired depth of $\sim$ 500 m, but animals remaining over the shelf may become trapped in basins such as in the Gulf of Maine (Bigelow, 1926; Davis, 1987; Lynch et al., 1998) and Santa Barbara Basin (Osgood and Checkley, 1997). This scenario readily explains the association of *Calanus* with the T–S properties seen in the VPR data, i.e. the *Calanus* in the deeper waters of the Gulf of Maine and Slope Water in January 1995 resulted from seasonal downward migration the previous year. Further data and biological/physical modeling of the Northeast Channel and Shelf/Slope region is needed to determine whether the deep Slope Water population is a significant source of *Calanus* to the Gulf of Maine or whether it is just a spill-over from the productive shelf region.

Distributions of *Calanus* during June 1994 were typical of summer and fall (e.g., Davis, 1987; Meise and O'Reilly, 1996; Durbin et al., unpublished data). Greatest abundances were seen in stratified waters over the southern flank and in the Gulf of Maine, with a prominent "hole" in the distribution over the crest of the bank, which has been previously described (Davis, 1987; Miese and O'Reilly, 1996). The elevated abundances resulted both from advection and in situ reproduction. Mature individuals on the southern flank would have to be introduced onto Georges Bank at the Northeast Peak as younger stages approximately 30 days earlier, according to mean circulation velocities (e.g., Limeburner and Beardsley, 1996; unpublished data) or considerably earlier if the individuals originated on the bank from the Great South Channel. For animals introduced via the latter mechanism, sufficient time would have elapsed between the introduction of actively reproducing adults at the Great South Channel in winter (January 1995) and June 1994 for animals produced by the new populations to have matured to copepodites or adults (e.g., Durbin et al., unpublished data; Campbell et al., in press). The elevated abundances of *Calanus* coincided with high fluorescence in the Shelf–Slope Front. These stratified regions, therefore, are favorable locations for large secondary producers such as *Calanus*.

The low abundance of *Calanus* in Georges Bank water at the crest of the bank in June 1994 may have resulted from a combination of high predation pressure and semi-isolation, and hence reduced immigration of plankton, of that region by the strong anti-cyclonic circulation and well-established tidal mixing fronts. High abundances of hydroid colonies, a potential predator of early and mid-life stage copepodites of *Calanus*, were observed in the Georges Bank water during June 1994 (Madin et al., 1996; Bollens et al., 2001). The distribution and temporal patterns in abundance of planktonic hydroids seen in the present data are consistent with those reported from other investigations (e.g., Bigelow, 1926; Gallager et al., 1996; Madin et al., 1996; Concelman et al., 2001). Planktonic occurrence of these primarily benthic forms occurs through mechanical dislodgment of the organisms from the bottom by storms, tidal mixing, or bottom fishing (Bigelow, 1926; Madin et al., 1996; Concelman et al., 2001). Historically, highest abundances of planktonic hydroids have been observed on the Crest of Georges Bank in late spring and early summer (Bigelow, 1926; Concelman et al., 2001), probably because the circulation retains water on the Crest at this time (e.g., Limeburner and Beardsley, 1996). In addition to hydroids, other zooplankton taxa including chaetognaths, amphipods, and euphausiids also may exert considerable predation pressure on copepod populations on Georges Bank, in particular over the crest of the bank where high abundances of these predators have been observed (e.g., Whiteley, 1948; Davis, 1987; Avery et al., 1996; Sullivan and Meise, 1996). Hence, predation likely reduces populations of *Calanus* on the crest of the bank. This predation, in combination with the semi-isolation of the crest resulting from the establishment of the strong, anticyclonic circulation gyre, contributed to the low abundances of *Calanus* observed over the crest in June 1994.

The vertical distribution of *Calanus* in the different regions across the transect varied with season. In general, the animal was distributed homogeneously throughout the water column during periods when the physical and food environment was homogeneous. During January 1995, *Calanus* was distributed homogeneously throughout the water column in all regions except the Slope Water, coincident with the lack of significant vertical structure in the environment and with the uniform distribution of phytoplankton food (fluorescence). In March 1995, however, *Calanus* were found in the upper third of the water column in both the crest and in the Gulf of Maine, despite a lack of vertical structure in the environment of these regions. This vertical distribution of *Calanus* may have resulted from the ontogenetic migration from depth to the surface during the winter/early spring in the Gulf of Maine with the similarity in distribution potentially indicating that populations on the crest originated in the Gulf of Maine. During June 1994, *Calanus* was distributed homogeneously throughout the water column only on the well-mixed, and environmentally homogenous, crest of the bank. Similar results were observed for stage-specific vertical distributions from net and pump plankton samples (Durbin, pers. comm.).

No diel variation in the vertical distribution of *Calanus* was observed, in any of the regions. Diel vertical migration on the crest and southern flank of the bank generally has not been observed for *Calanus*, although it is typical for the species under certain environmental and food conditions in the deeper regions of the Gulf of Maine and Great South Channel (e.g., Durbin et al., 1995; Wishner et al., 1988, 1995; Durbin et al., 1997). The number of day-night transitions and limited temporal coverage during the present study were insufficient to identify whether diel vertical migration was occurring in the deeper Slope Water and Gulf of Maine.

Little or no vertical structure was seen in the distribution of the other relatively abundant taxa (pteropods, *Phaeocystis* protocolonies, hydroids) during any of the three months examined. Of the three, only pteropods should be capable of sufficient vertical swimming to influence vertical distribution. The pteropod *Limacina retroversa* has been observed in association with specific environmental conditions and vertical structure of the water column (e.g., Gallager et al., 1996). In the present study, pteropods were abundant primarily during periods and in regions of low stratification (e.g., January 1995; March 1995; crest of the Bank), which may account for their lack of depth preference. Both hydroids and *Phaeocystis* protocolonies are non-motile and only marginally more dense than seawater, hence their vertical distribution should be dependent on physical mechanisms such as turbulence, mixing, and stratification, which produced a well- mixed water column, and homogeneous vertical distribution, during periods when these taxa were abundant.

Previous studies on the distributions of pteropods (*L. retroversa*) in the Gulf of Maine and on Georges Bank together demonstrated that high interannual variability is typical (e.g., Bigelow, 1926; Redfield, 1939; Riley and Bumpus, 1946). It has been hypothesized that populations of pteropods (*L. retroversa*) in the Gulf of Maine are augmented during winter (December) and spring (April) by influx from the Scotian Shelf (e.g., Redfield, 1939). The cyclonic basin-wide circulation then would advect populations on the bank at some later date. However, both the present study and that of Clarke and Bumpus (1946; as cited in Davis, 1987) demonstrated elevated abundances of pteropods during January with decreasing abundances throughout the spring and early summer, suggesting either that injection of pteropod populations occurs directly from the Scotian Shelf onto the bank in winter (January) or that population abundance on the bank is governed by additional yet unidentified mechanisms. Influx of Scotian Shelf Water onto Georges Bank itself during late winter and spring has been shown highly variable between years (Bisagni et al., 1996), which also may account for the differences in pteropod abundance patterns observed between studies. Despite a demonstrated strong affinity for Slope Water (e.g., Chen and Hillman, 1970), pteropods were not particularly abundant in Slope Water to the south of the bank or in deep Gulf of Maine Water.

A strong fluorescence signal was associated with the Shelf–Slope Front during both March 1995 and June 1994 (Fig. 5). Elevated fluorescence associated with the Shelf Break is a consistent feature observed along the Middle Atlantic Bight and Georges Bank during April–June, which likely results from nutrient enhancement and increased production in the front as a consequence of offshore displacement and upwelling of Shelf Water (e.g., Ryan et al., 1999). The elevated fluorescence observed during March 1995 in the stratified water adjacent to and in the Shelf–Slope front, however, is consistent with the timing of the spring bloom in stratified Shelf Water (e.g., Malone et al., 1983). Little stratification, and low fluorescence, was observed further inshore of the Shelf–Slope front in the Shelf Water during March 1995, suggesting that our sampling preceded the spring bloom over the southern flank. The elevated fluorescence described for the well-mixed crest region of Georges Bank relative to surrounding water masses during all three months is typical of that region (e.g., O'Reilly et al., 1987). Fluorescence levels in the Shelf Water on the southern flank were reduced relative to those observed in the Shelf/Slope Front to the south or in the Georges Bank water to the north, which may result in food limitation of *Calanus* in that region (e.g., Campbell et al., 2001).

The VPR images and data present a very different view of the planktonic environment than that obtained using conventional samplers. Optical imaging is a very useful method for describing the morphology and size of marine snow particles, including algal mats, and other delicate forms such as *Phaeocystis* protocolonies as well as their abundance and distribution patterns. Marine snow was by far the most abundant particle observed across the three transects (73–80% of all images), with largest particles seen during March 1995 coincident with the production of diatom chains and ensuing algal mats. The present study also presents one of the first descriptions of the distribution of *Phaeocystis* protocolonies on Georges Bank. Nets and bottles are unable to collect marine snow and other delicate particles/organisms such as *Phaeocystis* without destroying them, thus only hard-bodied forms such as copepods are observed which are only a small fraction of the total particulates in the mesoplankton size range. Sampling of individual particles/organisms by divers yields much lower abundances and a less robust description of the distribution and size frequency (Alldredge and Silver, 1988; Sieracki et al., 1998). The VPR, then, is a useful method by which to describe the abundance and morphology of particulate matter. The high proportion of marine snow in the water column also suggests that care must be taken in the interpretation of data collected with acoustical and optical devices that do not identify objects, since marine snow particles may be mistakenly assumed to be live organisms.

The present study describes the distributions of plankton and particles across Georges Bank with higher horizontal and vertical spatial resolution than has been possible to achieve previously. The capability to sample biological and physical characteristics coincidentally affords the investigator greater opportunity to explore the associations and relationships between the biological and physical environment utilizing a suite of methods previously unavailable because of the mismatch between sampling statistics achieved utilizing traditional methods (nets, CTD, hydrocasts). The distributions of plankton across the three transects were associated with particular water masses or regions but small scale patchiness was not associated with hydrographic variability. Distributions of *Calanus*, the most abundant zooplankton taxon, were consistent with what is understood regarding the species life history and seasonal distribution in the region, including the potential for predation by hydroids on the crest of Georges Bank. The strong affinity of *Calanus* for particular water mass types, and the lack of correlative associations between *Calanus* distributions and specific environmental conditions, supports our understanding that *Calanus* populations on Georges Bank are established annually by physical advection of water parcels and *Calanus* populations onto Georges Bank.

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