Abundance and condition of larval cod (*Gadus morhua*) at a convergent front on Western Bank, Scotian Shelf

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Abstract: In November and December 1992, Atlantic cod (*Gadus morhua*) larvae were most abundant at a convergent front located at the periphery of a well-mixed gyrelike water mass rotating near the crest of Western Bank (outer Scotian Shelf). Zooplankton wet biomass and plankton abundance (272 and 529 μm size-classes) were also higher in the frontal region relative to the adjacent water masses. We used the frontal feature to test the hypothesis that larvae in frontal regions are in better condition than larvae elsewhere. No significant differences in triacylglycerol content (an index of nutritional condition), Fulton's *K* condition index, nor in the daylight feeding ratio were found between larvae in the frontal region and those in the adjacent waters. The convergent front acted as a larval collector, but exchange with other water masses eliminated measurable differences in larval condition. Our observations indicate that physically driven retention, not differential mortality (approximated by condition), was responsible for high abundances of cod larvae at this front.

Résumé : En novembre et décembre 1992, les larves de morue (*Gadus morhua*) étaient les plus abondantes dans un front convergent situé à la périphérie d'une masse d'eau bien brassée en rotation, semblable à un tourbillon, près de la crête du banc Western (plate-forme Scotian extérieure). La biomasse humide de zooplancton et l'abondance du plancton (classes de taille de 272 et 529 μm) étaient également plus élevées dans la région frontale par rapport aux masses d'eau adjacentes. Nous avons utilisé la caractéristique frontale pour vérifier l'hypothèse que les larves dans les régions frontales sont en meilleur état physique que les larves vivant ailleurs. Aucune différence statistiquement significative dans la teneur en triacylglycérol (un indice de l'état nutritionnel) dans l'indice *K* de l'état physique de Fulton ni dans le rapport d'alimentation à la lumière naturelle n'a été observée entre les larves vivant dans la région frontale et celles qui vivent dans les eaux adjacentes. Le front convergent a agi comme collecteur de larves, mais l'échange avec d'autres masses d'eau a éliminé les différences mesurables touchant l'état des larves. Nos observations ont indiqué que la rétention à motivation physique, et non la mortalité différentielle (telle qu'établie de manière approximative par l'état), était responsable de l'abondance élevée de morues dans ce front.
[Traduit par la Rédaction]

Introduction

Strong positive correlations between larval fish abundance and the abundance of their prey are frequently observed at hydrographic fronts (e.g., Richardson et al. 1986; Govoni et al. 1989; Sabates and Maso 1990). One explanation for high abundances of ichthyo- and zoo-plankton at fronts is higher survival due to better growth in enhanced feeding environments (Taggart et al. 1989; Brandt 1993). Buckley and Lough (1987) noted that prey levels were higher and haddock larvae exhibited better growth in stratified water masses near the shelf slope front than in well-mixed water masses inside the 60-m isobath on Georges Bank. An alternative explanation for the higher levels of plankton at fronts is that passive transport and convergence accumulate larvae and their prey in frontal regions (Govoni et al. 1989).

Several hypotheses attempt to explain recruitment variability through interactions between the early life history of marine fish and their local feeding environment (Hjort 1914; Cushing 1972; Lasker 1975). These hypotheses predict that strong year-classes may result from positive temporal or spatial correlations between larval fish and their prey. However, correlations between the abundance of fish larvae and their food could be associated with large year-classes through several mechanisms. Enhanced feeding in a high food environment may lead to improved nutritional condition and increased survival. Alternatively, physical processes responsible for the retention of zoo- and ichthyo-plankton in a particular geographic region could lead to strong year-classes in, or from, that region regardless of whether condition and survival are enhanced through increased predator–prey interactions. However, examining these predator–prey interactions in the field, where physical process can have an enormous influence, has

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scale-related problems that require careful consideration (Taggart and Frank 1990).

Hydrographic fronts and their surrounding waters masses can be viewed as "natural laboratories" where the influence of enhanced prey abundance on larval abundance, condition, and (or) survival can be studied at small time and space scales that match the scale of the governing physical and biological processes. However, to draw conclusions about growth, survival, and recruitment in relation to frontal features and to provide for improvements in our predictive capabilities, it is necessary to determine not only the reasons for high abundances but also what benefits, if any, larvae derive from frontal residence. Of course the nutritional benefit of occupying an enhanced food environment such as an oceanographic front may be reduced if the front is ephemeral or larval residence in the frontal region is brief. Thus, fronts offer the opportunity to quantify the relative importance of physical and biological processes leading to observations of high larval abundance and to quantify the links between the feeding environment, nutritional condition, and survival under naturally occurring conditions.

The Ocean Production Enhancement Network (OPEN) research programme was designed, in part, to quantify directly in the field the variability in several characteristics of cod larvae in time and space and the physical processes that are thought to directly influence that variability (Anonymous 1995). During one of OPEN's ichthyoplankton surveys on the eastern Scotian Shelf we observed a maximum in the abundance of Atlantic cod (*Gadus morhua*) larvae in a frontal region near the crest of Western Bank and took the unique opportunity to ask whether cod larvae in the frontal region were in better condition than those larvae residing in the surrounding water masses. This analysis is part of a larger collaborative study designed to determine the characteristics of cod larvae that survive the larval period by tracking a water mass and continuously re-sampling a group of larvae resident therein.

In this paper our assessments of feeding and nutritional condition are based on gut content, gravimetric or morphometric, and lipid biochemistry measures.We present the relevant hydrographic data describing the water mass structure near the crest of Western Bank and describe its relationship to various biological measures. Finally, we provide a conceptual model of the frontal processes that is consistent with the biological and physical observations.

Materials and methods

Field

Physical and biological data were collected during the Petrel V Cruise No. 92-31 on Western Bank (Fig. 1*a*) during the period 22 November – 16 December 1992 (Griffin and Lochmann 1993). A complete description of the technical aspects of the cruise are presented elsewhere (Bowen et al. 1995; Taggart et al. 1996; Griffin and Thompson 1996). Here we provide a description of the aspects that are relevant to this frontal study, and we do so in a generally chronological order so that the reader can appreciate the real-time evolution of the study.

We began with an initial mesoscale survey comprised of three sampling transects on Western Bank during 23–25 November (Fig. 1*b*) to map the temperature, salinity, and density fields and the abundance distribution of larval cod. On each transect temperature and salinity profiles were collected at ~7 km intervals with a Seabird™-25 conductivity–temperature–depth sensor (CTD), and plankton samples were collected at ~7- to ~21-km intervals with a 60 cm diameter bongo net sampler (Posgay and Marak 1980) fitted with 333 μm mesh nets. Bongo nets were towed at a nominal ship speed of 1 $m \cdot s^{-1}$ in a continuous double oblique manner (~1 $m \cdot s^{-1}$ wire speed) to depths of between 5 and 10 m above the bottom. Depth was determined by the length of tow wire deployed and its incident angle. The average volume filtered per net, for each deployment, was 150 m^3 and was monitored using General Oceanics™ flow meters. Cod larvae from plankton samples collected during the initial survey were immediately sorted after net recovery, enumerated, and preserved in 95% ethanol.

The initial survey revealed several water masses in the region (see Results below and Taggart et al. 1996; Griffin and Thompson 1996), one of which was termed crest water (CW) located near the crest of the bank. This water mass was well mixed and of intermediate temperature and salinity relative to the surrounding water masses, and because it contained high abundances of larval cod, it was targeted for water mass tracking.

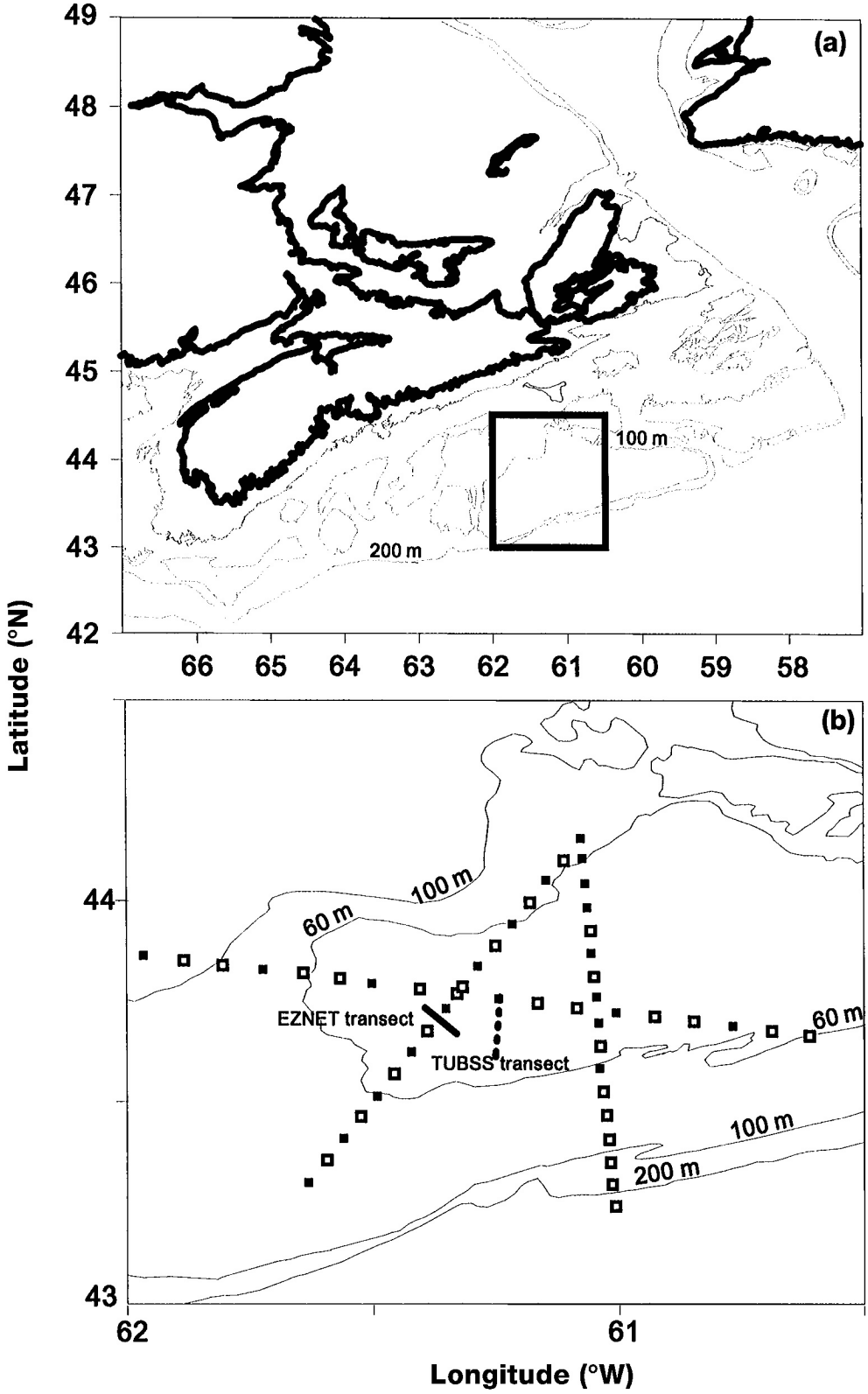
Tracking was achieved by using the Ocean Probe real-time oceanographic monitoring system (see Bowen et al. 1995 for complete details) which included shipboard and moored telemetering instrumentation as well as telemetering Loran-C drifters (Sanderson 1995). The Ocean Probe system delivered oceanographic data in real-time to a data-assimilative hydrodynamic model (Griffin and Thompson 1996) which produced time-dependent flow fields within a 60×60 km model domain of the study area. By employing this model (updated at least twice daily) in a Lagrangian frame of reference the flow fields could be used to assess the present and predict the future positions of previous sampling locations as they were advected around and across the bank within the moving water mass. Thus, we were able to track the aggregation of larval cod found within the crest water.

One radio-telemetering Loran-C surface drifter with a 2×10 m window-blind panel drogued at a depth of 20 m was deployed near the crest of the Bank on 25 November where the local larval cod abundance maximum was found. Thirteen similarly configured drifters were subsequently deployed in an evenly spaced pattern around the central drifter within the ~20 km diameter CW containing the larval cod (Sanderson 1995).

Subsequent to the initial survey 25 oblique bongo samples and 27 vertical profiles of zooplankton were collected during the 25 November – 3 December period. Vertical profiles were conducted using a 1-m^2 EZNET™ (Open Seas Instruments, Musquodoboit Harbour, N.S.), the marketed version of the Bedford Institute of Oceanography Net and Environmental Sampling System (BIONESS; Sameoto et al. 1980). The EZNET was fitted with ten 333-μm mesh nets, General Oceanics digital flow meters (internal and external), pitch and roll sensors, a Seabird-19 CTD, and an Optical Plankton Counter™ (OPC; Focal Technologies Inc., Dartmouth, N.S.). The EZNET was used to sample discrete depths in a stepped oblique manner at 5- or 10-m intervals (depending on bottom depth) to within 10 m of the bottom. Towing speed averaged 1 $m \cdot s^{-1}$ and each net was deployed for ~5 min and the filtered volume averaged 250 m^3 per net. Plankton samples other than those collected during the initial bongo survey were processed as follows. After recovery the nets were rinsed to the codends and samples were immediately sorted for cod larvae. Ten larvae (when available) from a single bongo net, or from each EZNET net, were videotaped through a dissecting microscope for morphometric analysis (Miller et al. 1995) and individually preserved in liquid nitrogen for biochemical analyses. The remaining larvae were preserved in ethanol in bulk, and the plankton samples were preserved in 4% $MgCO_3$ buffered formalin in seawater.

A severe storm interrupted the study from 3 to 6 December. Although tracking and sampling continued between 7 and 16 December,

Fig. 1. (*a*) Bathymetric chart of the Scotian Shelf showing the 100- and 200-m isobaths with the Western Bank sampling area outlined. (*b*) Enlargement of sampling area showing the 60-, 100-, and 200-m isobaths, the locations of CTD (open symbols) and CTD–bongo (solid symbols) stations from the initial survey, the EZNET frontal transect (solid line), and the TUBSS frontal transect (broken line).



we focus here on data collected between 23 November and 3 December when the frontal feature was studied.

A fine-scale sampling transect, across and normal to the front, was conducted on 29 November using the EZNET (Fig. 1*b*). Sampling was accomplished by sequentially towing each of the 10 EZNET nets at a fixed depth of 12.5 m, for 5 min, over a distance of ~330 m, at a towing speed of 1 $m{\cdot}s^{-1}$, beginning in the tracked CW. The fixed sampling depth was chosen because it was the depth of maximum larval cod abundance according to our previous sampling efforts (see also Fig. 8). We subsequently conducted a 12 km frontal transect on 29 November using the undulating Towed Underwater Biological Sampling System (TUBSS). TUBSS included an OPC, an Ocean Sensors™ CTD, and a Variosens™ fluorometer (see Sprules et al. 1992). The TUBSS frontal transect (Fig. 1*b*) was also normal to the front and was located approximately 10 km east of the location of the EZNET frontal transect.

Laboratory

Abundance and biomass estimates

Plankton collections were examined again in the laboratory and any remaining cod larvae were removed, enumerated, and preserved in 95% ethanol. The remainder of each sample was then washed and concentrated on a 200 μm mesh preweighed sieve, towel-dried to remove excess water, and weighed to the nearest gram to obtain wet biomass estimates. In all EZNET deployments, except the fine-scale frontal transect, the towing profile was stepped oblique. For a direct comparison between the depth-integrated bongo samples and the discrete-depth EZNET samples, zooplankton wet biomass and larval abundance estimates from the latter were depth averaged, though weighted by the volume filtered. Larval abundance was standardized to larvae per 100 m^{-3} and zooplankton wet biomass was standardized to grams per cubic metre.

Gut content and feeding ratio

Cod larvae initially preserved in liquid nitrogen were thawed and their stomachs removed for gut content analysis. This procedure also avoided contamination of stored lipid measures in larvae by lipids found in the undigested prey in the gut (Lochmann et al. 1996). Micro-zooplankton in the gut were enumerated and identified to the lowest possible taxonomic level (McLaren and Avendano 1995). As the functional response of cod larvae to their prey field varies with prey abundance, an index of gut fullness is not a sufficiently direct measure of feeding rate (Munk 1995). Nonetheless, we did calculate the feeding ratio (average number of prey per larva) among sample groups. This was done not to directly assess differences in feeding rates among samples but to use as an index of recent feeding activity (Powell et al. 1990). The index can also provide evidence of a link between the prey field and larval nutritional condition (Canino et al. 1991).

Biochemical condition

To quantify lipid-class composition and the defatted dry weight (DDW) of the thawed larvae, each was placed into 1 mL of dichloromethane–methanol solvent (2:1 v/v, HPLC grade) and extracted for approximately 24 h. Five micrograms of nonadecane (internal standard) were added to each extraction tube to estimate recovery efficiency. Samples were kept on ice prior to evaporation under purified nitrogen gas and reconstituted twice in 10 μL of extraction solvent. The remaining larval carcass was dried to a uniform weight and weighed to the nearest 0.1 μg using a Cahn Gram Electrobalance (Model G, Ventron Corp., Paramount, Calif).

Lipid class measurements were made using TLC–FID (thin-layer chromatography – flame ionization detection) with a Chromarod- Iatroscan™ Mark V (Iatron Laboratories Inc., Tokyo, Japan; Ackman et al. 1990). We used a RSS/ANCAL A/D card and T DATASCAN software(version 2; RRS, Inc., 3176 Pullman Street, Suite 110, Costa Mesa, CA 92626, U.S.A.) for data acquisition and analyses.

We examined quantities of sterol esters, triacylglycerol (TAG), free fatty acids, diacylglycerol, sterols, and phospholipids in each cod larva. For each larva, 5–10 μL of extract was spotted on an S-III Chromarod (Iatron Laboratories Inc., Tokyo, Japan) using a microsyringe. Chromarods were first developed in hexane – diethyl ether – formic acid (67.9:2.1:0.04, v/v/v) for 33 min and then dried for 2 min at 60°C and partially scanned to detect the internal standard and sterol esters. Chromarods were then developed in hexane – diethyl ether – formic acid (47.9:21.2:0.06, v/v/v) for 33 min and after drying were partially scanned for neutral lipid classes (diacylglycerol and TAG, free fatty acids, and sterols). Finally, Chromarods were developed in dichloromethane–methanol–water (42.2:25.3:2.5, v/v/v) for a further 33 min and after drying the entire rod was scanned for phospholipids. Rods were cleaned using the blank and origin scan procedures outlined in the Iatroscan instruction manual and stored in a dessicator when not in use.

Lipid compounds in individual larvae were identified by the position and the shape of the detector response curve (chromatograph) relative to known standards developed under identical conditions. Integration of the area under the chromatograph for each lipid class was used to estimate quantities (μg) of the classes present in a larva, and these estimates were corrected for recovery efficiency. Peak integration is somewhat subjective due to user-adjustable parameters in the T DATASCAN software. Two parameters that strongly affect peak integration are the maximum noise level and the tangent triggering percentage.

The maximum noise level is a percentage of the maximum signal amplitude. If the point to point change in amplitude is less than the designated percentage (in our case 0.2%) the signal is considered to be noise and is used to define the baseline. In most cases, this noise level provided an adequate fit. When the noise level did not provide an adequate fit the baseline was manually fit. This led to more accurate peak integrations.

The tangent triggering percentage determines which peaks are automatically detected and integrated. We set the tangent triggering percent at 0.2%, which was appropriate for automatic detection under most circumstances. Occasionally, dust particles on the chromarods resulted in narrow, spike-like peaks, which were not integrated despite their being identified as peaks by the T DATASCAN software.

We considered 0.03 μg as our limit of detection based on our calibrations, Lochmann et al. (1995), and Sebedio and Juaneda (1991). The calibration curves for tripalmitin (the synthetic standard for TAG) were linear to 0.05 μg. The minor extrapolation beyond this value maximized the information obtained from each larva without significantly exceeding the error around the lowest calibration value.

We corrected for larval size by dividing the square root of the lipid class measures by the DDW estimate of the larva. The square root transformation resulted in a higher coefficient of determination than any other transformation when transformed lipid concentration was regressed against DDW. The amount of TAG (the energy storage lipid) was used as the index of nutritional condition (Lochmann et al. 1995).

Morphometric condition

Total dry weight (TDW) was calculated by adding the absolute total of all measured lipids to the DDW. Standard lengths (SL) of videotaped larvae were measured to the nearest 0.1 mm using the OPTIMUS™ image analysis system (Bioscan, Seattle, Wash.; Miller et al. 1995). As regression analysis of the logarithmically transformed TDW and SL data showed evidence of allometric growth, we employed a Fulton-type index as another measure of condition (Fulton's $K = (TDW/SL^3) \times 100$). This condition index has proved useful to an number of investigators working with larval fish (Blaxter 1971; May 1971; Frank and McRuer 1989). However, as some marine fish larvae

undergo a reduction in length and weight during periods of limited feeding (Ehrlich 1974), this index is best used in conjunction with other measures of condition.

Statistical analysis

Larvae collected from different locations were compared using analyses of variance. Trends in larval characteristics along the EZNET frontal transect were examined using linear regression analyses. Characteristics and indices of larval condition among samples were assessed using analyses of variance.

Results

Water mass physical structure

The three initial transects across the crest of Western Bank during the period 23–26 November revealed two distinctly different water masses and a third intermediate water mass (Fig. 2). Depth averaged measures showed relatively cool (<8.5°C), relatively fresh (<31.6 percent salinity units (psu)), low density (σ_t < 24.5) stratified water to the east of the bank crest that we refer to as the cold, fresh, water mass (CFW; Fig. 2). South of ~43°30′N there was warmer (>9.5°C), more saline (>32.2 psu), more dense (σ_t>24.8), and stratified slope water we refer to as the warm, salty water mass (WSW; Fig. 2). Water in the vicinity of the crest of Western Bank (~61°20′W, ~43°45′N) was intermediate in temperature (8.5–9.5°C), salinity (31.6–31.8 psu), and density (σ_t = 24.5–24.6), was well mixed, and we refer to it as the CW (Fig. 2). The temperature and salinity sections of the third transect (Fig. 3) show the tongue of stratified CFW (stations 5–9 and 14–17; Fig. 3) immediately southwest and northeast of the well-mixed CW (stations 10–13; Fig. 3) as it enveloped the CW from the east (Fig. 2). The stratified WSW (stations 1–4; Fig. 3) was located to the extreme southwest of the CFW along the 100-m isobath of the Scotian Shelf continental slope. The temperature difference between the CFW and the CW nearly compensated for the density difference between the water masses that would result from salinity differences alone, and thus, the density gradient between the two water masses was not strong (Fig. 3*b*).

The tongue of CFW intruding from the east at the beginning of the study continued to do so over the following week. Griffin and Thompson (1996) describe how the assimilation model was used to reconstruct a series of synoptic views (Fig. 4) of sea surface temperature (SST) observations by computing the trajectories of the thermally sampled waters. The reconstruction shows the CW as an anticyclonic gyre rotating around the crest of Western Bank during the period 25 November – 3 December. The reconstruction is perfectly consistent with Sanderson's (1995)[2] analyses of the drifter cluster that show the CW as a strongly anticyclonic eddy with baroclinic structure at its fringes. It is at the edges of the eddy, between the CW and the CFW, where the thermohaline front was formed as the tongue of CFW wrapped clockwise around the CW from the east. The frontal region was located at approximately 43°40′N, 61°15′W during the 27–28 November period (Fig. 4). Errors associated with computing the positions of the SST samples (Fig. 4; observations from several days) and the large averaging interval (~30 min) for the SST data reduce the

[2] Sanderson (1995; p. 6762) erroneously reports his analyses as over the period 5–11 November 1992 when his analyses actually cover the period 25 November to 1 December 1992.

Fig. 2. Bathymetric charts (60-, 100-, and 200-m isobaths) of Western Bank for the period 23–25 November 1992 showing 10–40 m depth-averaged (*a*) temperature (°C), (*b*) salinity (psu), and (*c*) density (σ_t) isopleths, each showing the approximate locations of well-mixed crest water (CW), the stratified cold, fresh water (CFW), and the stratified warm salty water (WSW). Data are derived from the initial CTD survey in Fig. 1.

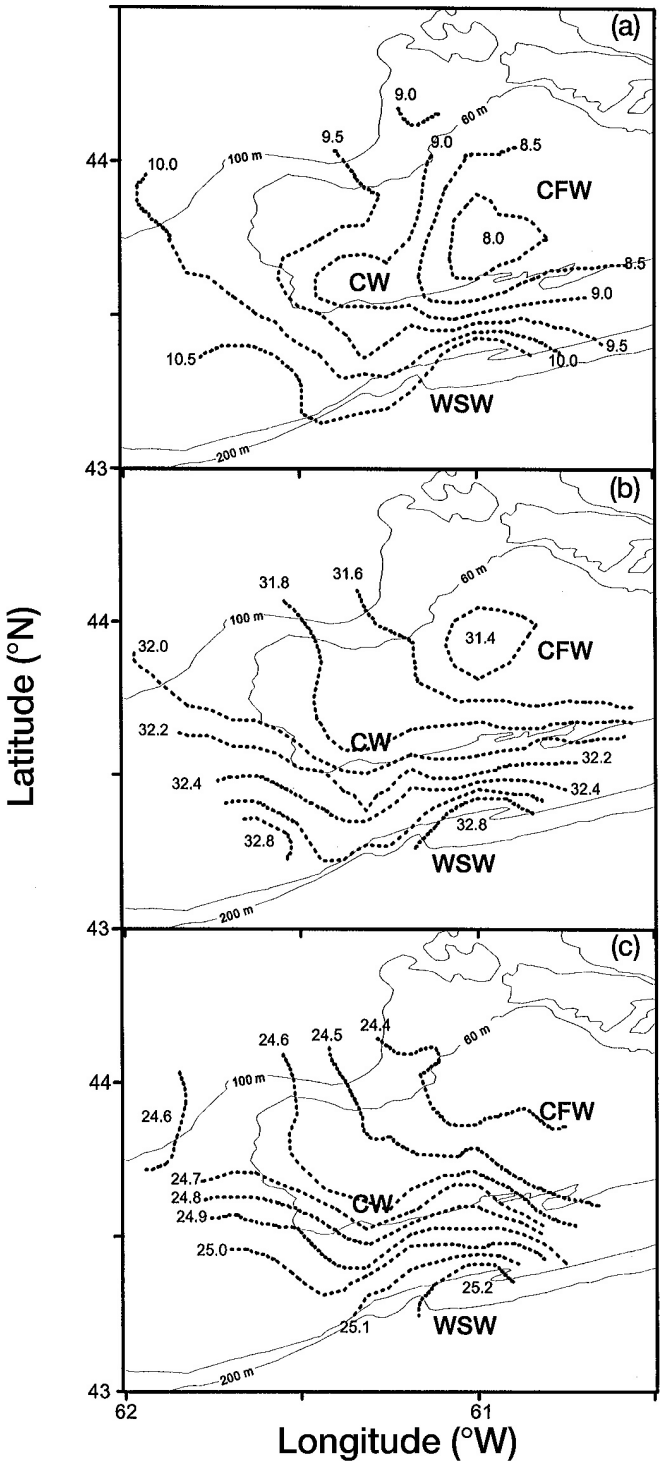


Fig. 3. (*a*) Bathymetric chart (60-, 80-, 100-, and 200 m isobaths) of Western Bank showing locations of specific CTD stations from the initial CTD survey in Fig. 1 that were used to construct (*b*) density (σ_t), (*c*) temperature (°C); and (*d*) salinity (psu) sections across the crest of the bank, each showing the approximate locations of well-mixed crest water (CW), the stratified cold, fresh water (CFW), and the stratified warm salty water (WSW).

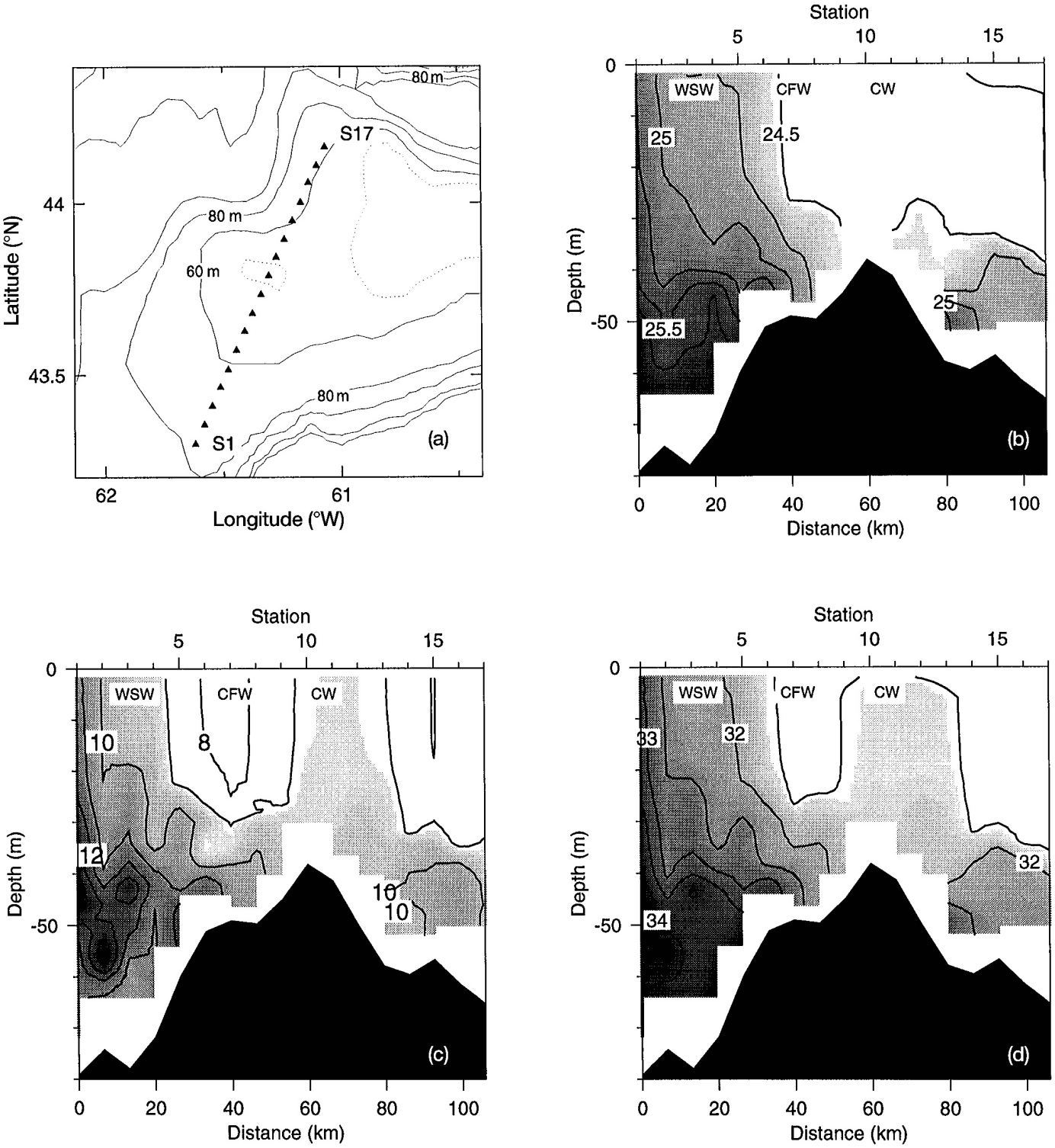
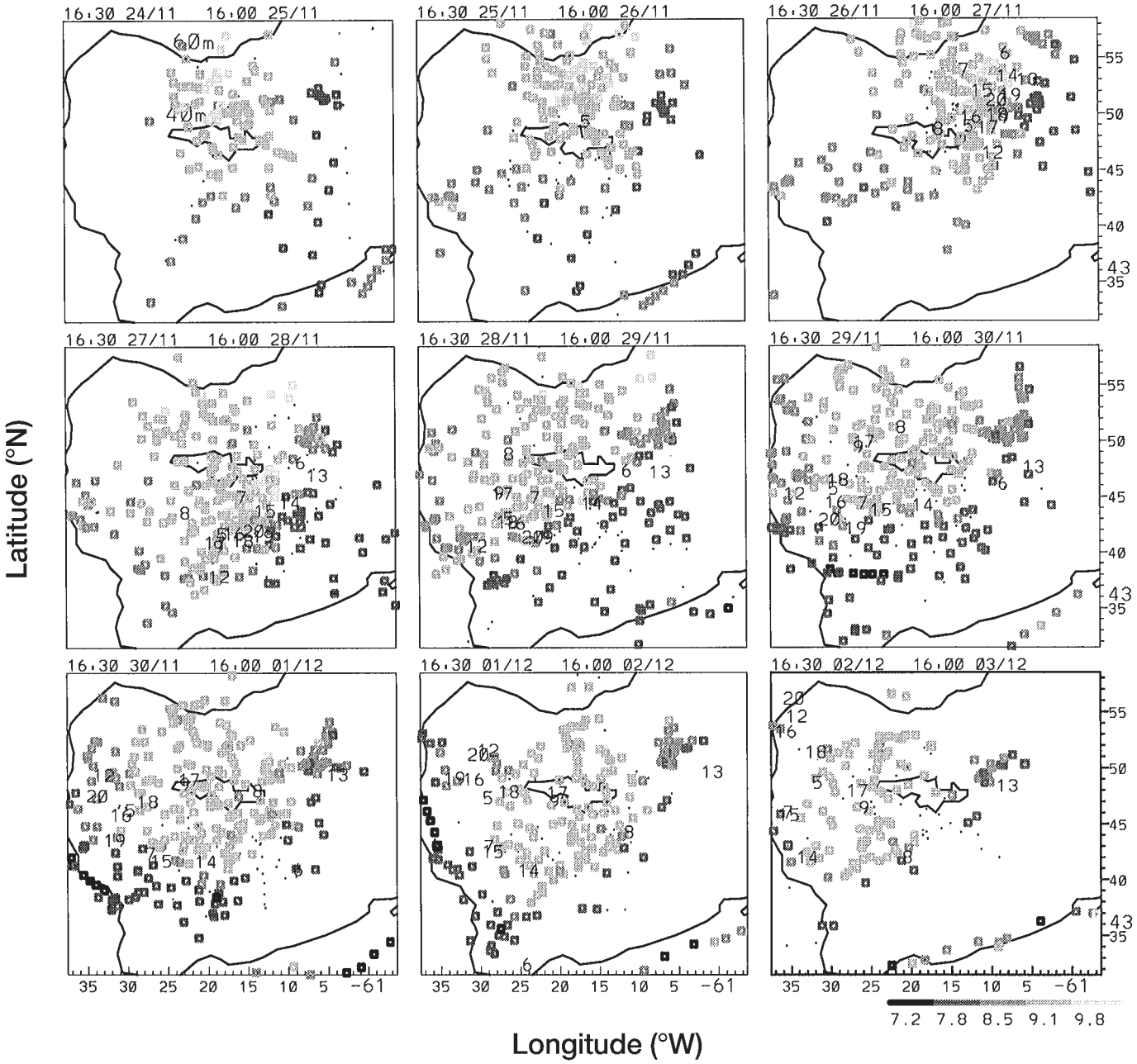


Fig. 4. Bathymetric charts (40- and 60-m isobaths) near the crest of Western Bank showing the evolution of the sea surface temperature (SST) fields computed using the flow fields provided by the data assimilative model of Griffin and Thompson (1996). Each panel shows the positions at the end of each 24-h period (UTC) noted at the top of each panel (hour:minute, day/month) of waters sampled by the ship and current meters during the preceding and succeeding 50 h. SST at the time of sampling is grey-scaled from cold (7.2°C, dark) to warm (9.8°C, light). Drifter positions at the end of each period are noted by their individual numbers as detailed in Fig. 5. Note how the drifters converge in panels 4 and 5 (27–29 November) in the frontal region between the warmer CW (light grey-scale) and the colder CFW (darker grey-scale) water masses. A more comprehensive analysis of these data are found in Plates 1 and 3 of Griffin and Thompson (1996).

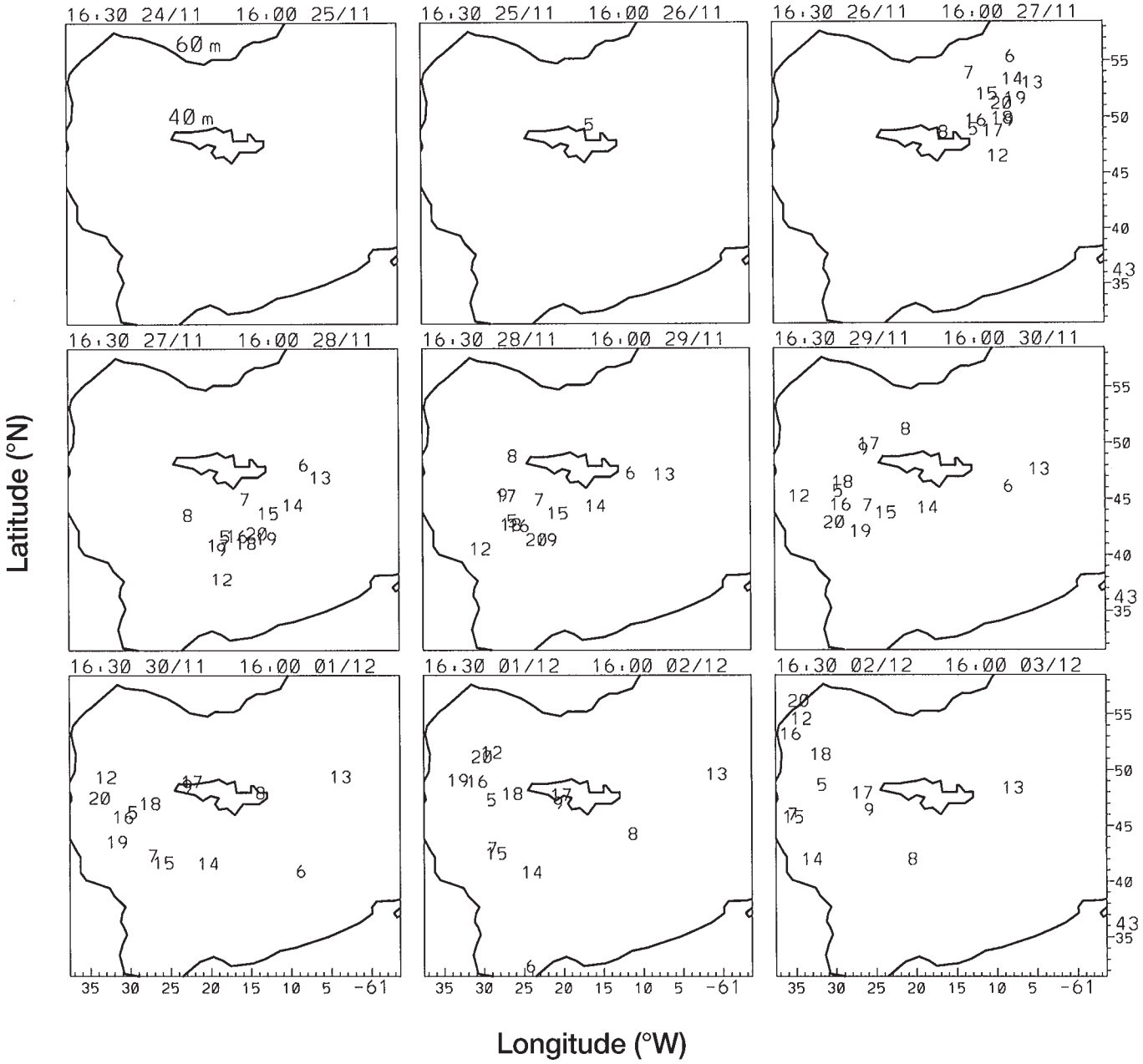


sharpness of the front in this figure. The front could actually be visually observed at the surface as the ship crossed.

Drifter trajectories

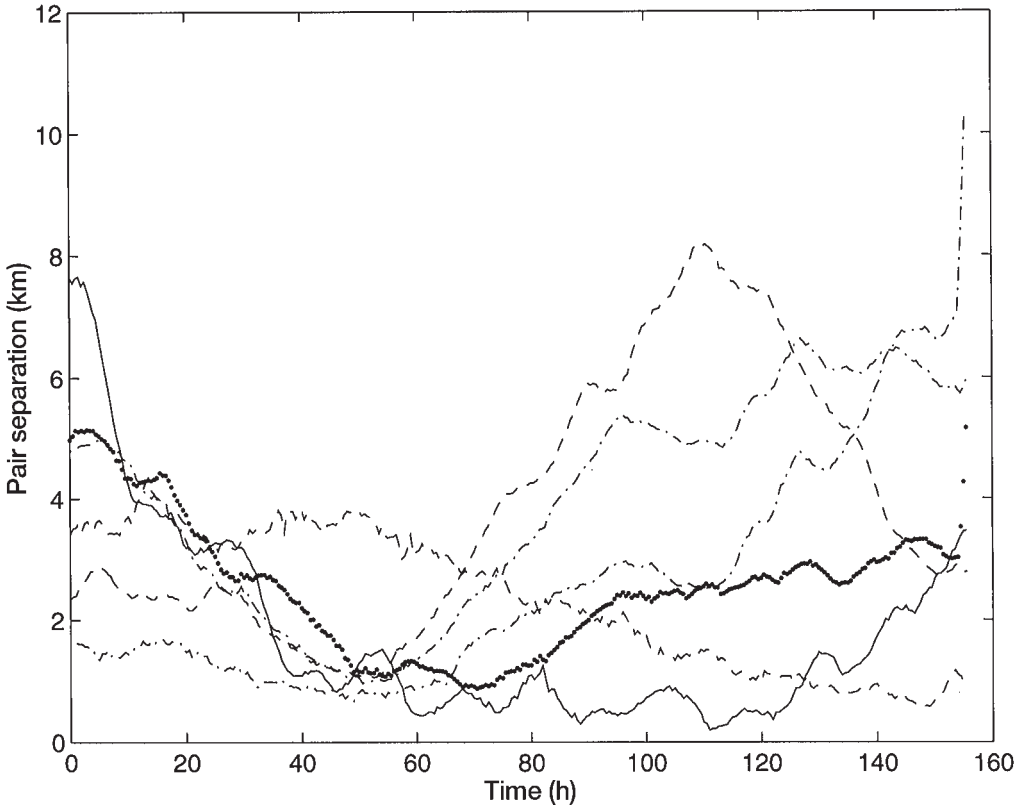
Drifter trajectories provided information regarding the persistence and nature of the frontal feature (Figs. 4 and 5) We observed the basic gyral structure of the CW rotating near the bank crest while a tongue of CFW wrapped around it from the east over an 8-day period (25 November – 3 December; Fig. 5). The drifter data indicated that the gyral structure at the crest and the frontal region became more irregular during, and subsequent to, the storm period that commenced on 3 December when the water mass became stretched and distorted (Sanderson 1995). However, drifter trajectories from 26 November to 3 December

Fig. 5. Bathymetric charts (40- and 60-m isobaths) near the crest of Western Bank showing the daily sequence of 14 drifter positions. Drifter positions at the end of the time period concerned (UTC at top right of each panel; hour:minute, day/month) are indicated by their individual numbers 5–9 and 12–20.



provide evidence not only of the gyrelike structure, but that the frontal region was convergent. Drifter 5 was deployed near the crest of the bank in the CW (Fig. 5). The other 13 drifters, also deployed in the CW, were evenly spaced around drifter 5 by 04:30, 27 November UTC. Nine of the 14 drifters converged (Figs. 5 and 6 and see Sanderson 1995, Fig. 13) with one or more other drifters. This degree of convergence is much more than could be expected from random motion but insufficient to give a clear picture of the complexities of the convergence process. Note that between 27 and 29 November the drifters converged in the frontal region between the warmer CW (light grey-scale, Fig. 4) and the cooler CFW (darker grey-scale). Sanderson (1995) shows the drifter motion to be anything but random but noted that there were local zones of convergence or divergence and shear evident in the residual flow fields derived from the drifter data. Figure 6 shows how drifter pairs converged over periods ranging from 2 to 3 days and remained together for periods of 10–30 h before beginning to diverge. The velocity shear across the front is evident from the trajectory of drifter 6, which spent several days in the CW (Fig. 5; 27–30 November) before crossing the front (Fig. 5; 30 November – 1 December), to be swept quickly to the southwest (Fig. 5; 1–2 December). Conversely, drifter 12, which had entered CFW (Fig. 5; 27–28 November), moved rapidly west and then

Fig. 6. Separation of those pairs of drifters shown in Fig. 5 that converged at some time between 04:30 on 27 November and 16:00 on 3 December UTC. Pairs are 17 and 9; 5 and 18; 18 and 16; 5 and 16; 20 and 19; and 7 and 15.



converged toward the front (28–30 November) to finally recross the front and return to the CW (Fig. 5; 30 November – 2 December).

Water mass biological structure

Bongo net collections during the period 23–26 November indicated that cod larvae were present almost exclusively within the CW (Fig. 7). We used the hydrographic data and results above to classify the bongo and EZNET samples with respect to water mass. Samples collected in well-mixed, generally isothermal (to 25 m or more) water, with SST > 8.8°C were classified as CW samples. Those collected in stratified water with SST < 8.8°C were classified as frontal region samples. Samples collected in water that was isothermal to ~20 m, with SST < 8.0°C were classified as CFW samples. Samples were rarely collected in WSW and are not considered in these analyses.

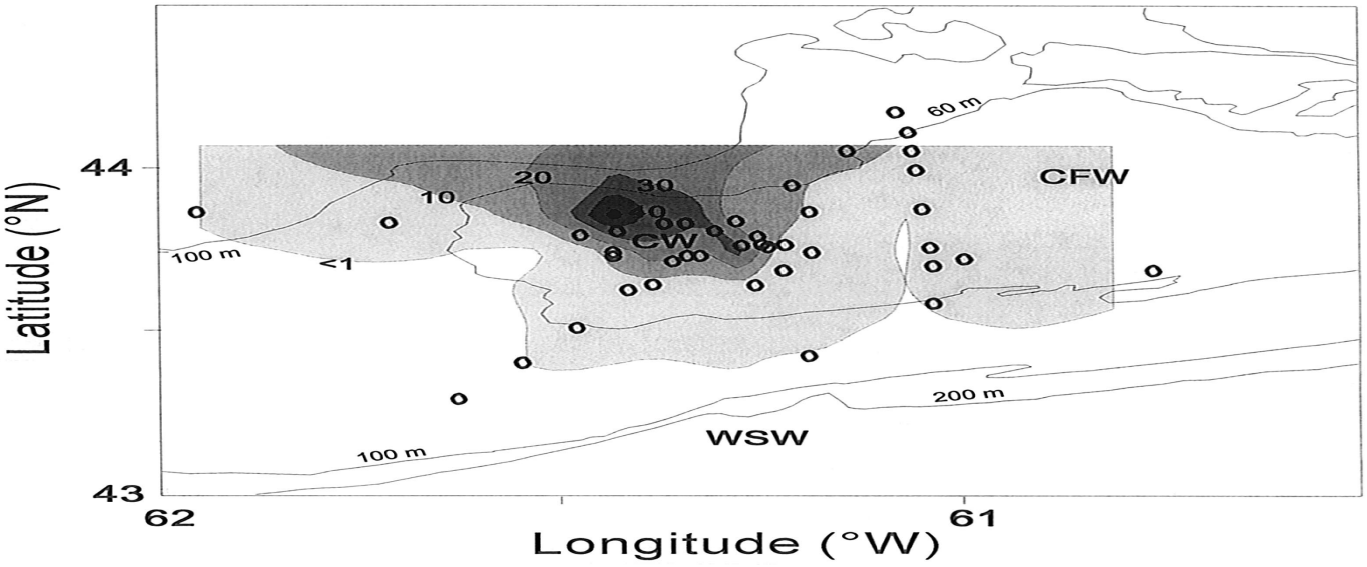
The frontal region and adjacent water masses

Examples of EZNET deployments in the well-mixed CW and in the stratified frontal region show how the larval abundances were typically higher in the frontal region than in the CW, though similarly distributed through the water column and centred between 10 and 15 m (Fig. 8). The abundance of larval cod in the CW between 25 November and 3 December averaged 52 ± 33 larvae·100 m^{-3} (mean ± SD) while the abundance in the frontal region during the same period averaged 174 ± 40 larvae·100 m^{-3} (Table 1). Abundance estimates in both water masses were significantly higher (5- to 20-fold; Table 1) than those in the CFW (9 ± 12 larvae·100 m^{-3}). Co-incidentally, zooplankton wet biomass was also significantly higher in the CW and in the frontal region than in the CFW (Table 1). Cod larvae from the CW and from the frontal region were marginally longer but not significantly heavier than larvae collected in the CFW (Table 1). As larval abundances in the CFW were systematically low (only nine larvae from CFW were available for morphometric and lipid analyses; see also Fig. 7) the significance of differences in length between the larvae collected there and in the other locations must be interpreted cautiously.

The TUBSS transect showed that the frontal region was several kilometres wide (Fig. 9). Relative to the CW, the CFW was cooler by ~1.5°C and fresher by about ~0.6 psu (Figs. 9*a* and 9*b*). Density differences were small over the same distance (Fig. 9*c*), consistent with the earlier mapping of the density field (Fig. 3*b*). Relative to the CW, the chlorophyll concentration was slightly lower in the frontal region and decreased further from ~7.0 mg·L^{-1} in the CW to <6.5 mg·L^{-1} in the CFW (Fig. 9*d*). Plankton abundances in the 231–314 μm equivalent spherical diameter (ESD) size range were also elevated to ~16–18·L^{-1} in the frontal region relative to ~8–12·L^{-1} in the CW (Fig. 9*e*).

Temperature and salinity observations from the EZNET frontal transect showed that, at the time and sampling location, the frontal region was approximately 1–1.5 km wide (Fig. 10). Temperature and salinity at 12.5-m depth decreased by ~1°C and ~0.35 psu respectively over a horizontal distance of 1.5 km from the well-mixed CW to the more stratified frontal

Fig. 7. Bathymetric chart (60-, 100-, and 200-m isobaths) of Western Bank showing grey-scaled depth-averaged abundance isopleths (larvae·100 m^{-3}) of cod larvae derived from bongo-net collections during the period of 23–26 November 1992 (open symbols). Grey-scale contours are in 10 larvae·100 m^{-3} intervals from <0 larvae·100 m^{-3} (open) to >50 larvae·100 m^{-3} (solid) and are associated with approximate locations of well-mixed crest water (CW), the stratified cold, fresh water (CFW), and the stratified warm salty water (WSW).

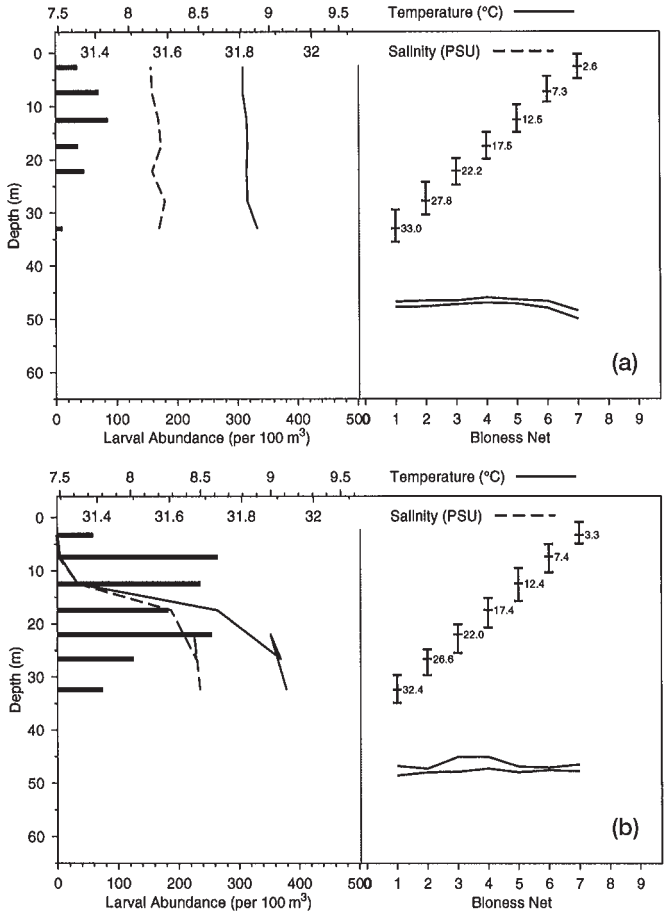


region. Near the frontal region but still within the CW (nets 1–5; Fig. 10*d*), larval cod abundance was at or above the upper estimates typically observed in the CW as reported above (Table 1). However, larval abundance estimates virtually doubled over a distance of about 1 km (nets 4 and 5 compared with nets 7 and 8; Fig. 10*d*). The decreased larval abundance estimate for net 10 (Fig. 10*d*) reflects the change in depth as the BIONESS was removed from the water. Abundance estimates of plankton in two size-classes, 231–314 μm ESD (geometric mean 272 μm ESD) and 485–571 μm ESD (geometric mean 529 μm ESD) approximately doubled from the CW into the frontal region (Fig. 10*e*) while light attenuation decreased (Fig. 10*f*). Light attenuation, as measured by the OPC, is an indication of water colour (e.g., chlorophyll) and (or) the abundance of plankton below the resolution of the OPC (<231 μm ESD). We interpret the decrease in attenuation as an indication that phytoplankton (chlorophyll) abundance decreased in the frontal region, an observation that is consistent with fluorometer measurements collected during the TUBSS frontal transect (Fig. 9*d*).

Cod larvae collected in different nets during the EZNET frontal transect had similar average SL, TDW, and feeding ratio (Figs., 11*a*–11*c*, Table 2). Sample size for each net ranged from 8 to 10 larvae·net^{-1}. Average Fulton's *K* values were also similar for larvae from different nets (Fig. 11*d*, Table 2). Average TAG concentrations appeared higher in the frontal region than in the CW, but the differences among nets were not significant (Fig. 11*e*, Table 2). TAG concentrations of larvae from nets 7 to 10 in the frontal region were more variable than TAG concentrations from the other nets in the CW. The high variability of TAG concentrations in larvae in those nets was not due to the influence of one or two larvae with anomalously high TAG concentration (discussed below). Spatial trends were examined using linear regression of each larval characteristic or condition index against distance along the transect. No significant trends were found (i.e., regression slopes were not significantly different from zero at $\alpha = 0.05$). Analyses of variance showed no significant differences between the CW larvae (nets 1–5 combined) and frontal region larvae (nets 6–10 combined) for any characteristic or condition index (Table 2). It is possible that, by including larvae collected in net 6, which clearly sampled both the CW and the frontal region (Fig. 10), our analysis was unduly biased, and therefore, real differences between larvae from each water mass, particularly in the TAG index, could not be detected. However, no significant differences ($p = 0.064$) were detected when we repeated the analysis using only those samples collected in nets 1–5 (clearly in the CW) and those collected in nets 7–10 (clearly in the frontal region).

To further examine the variation in larval condition and to

Fig. 8. Vertical profiles of larval cod abundance (larvae·100 m^{-3}, horizontal histograms), temperature (7.5–9.5°C, solid line) and salinity (31.4–32 psu, broken line) in the left panels, and bottom depth (minimum and maximum, solid lines) and sampling depth interval (minimum, maximum, and average) for each net in the right panels for EZNET (BIONESS) deployments in (*a*) the well-mixed crest water (CW) and in (*b*) the stratified frontal region.



expand temporal and spatial resolution and sample size, we included all larvae available from samples in the CW and from those in the frontal region that were collected between 25 November and 3 December (>1000 larvae) in an analyses of variance (Table 3). For reference purposes, statistics for the nine larvae from the CFW were also tabulated but were not included in the analyses of variance. There was no significant difference in the TAG index, nor in the Fulton's *K* index between larvae from the CW and those from the frontal region (Table 3). However, feeding ratio was significantly higher for larvae from the CW than for larvae from the frontal region. As feeding periodicities have been noted in cod larvae (Kane 1984; McLaren and Avendano 1995), our inclusion of all cod larvae, regardless of collection time, may account for the difference in feeding ratio. Fifty-two of the 113 larvae analysed for gut contents from the CW were collected during the day, as were all of the larvae analysed for gut contents from the frontal region. When we repeated the analysis using daylight collections only, the feeding ratio showed no significant difference (Table 3).

Discussion

This study demonstrates that, relative to adjacent water masses and at scales of kilometres and less, larval cod can be as high as 20-fold more abundant in a narrow frontal region located between well-mixed CW and CFW on the Scotian Shelf. A number of processes may lead to such an observation. A simple explanation might be feeding-related differential survival of larvae among water masses (i.e., higher abundances of cod larvae are observed in the frontal region because larvae elsewhere are more food limited and are therefore dying at a faster rate). McLaren and Avendano (1995) showed that 3–6 mm cod larvae on Western Bank fed on plankton ranging from 80–480 μm ESD. Although the mesh size of the plankton nets (333 μm) used in this study and the lower limit of resolution for the OPC (231 μm) do not cover the entire feeding range, the 231-314 μm size-class was certainly well within the size range of prey consumed by larval cod in the region at the time of the study. The elevated levels of plankton in this size range in the frontal region are consistent with the resident larvae being provided with a relatively enhanced (more abundant) prey field. A logical consequence of enhanced feeding is improved condition and, thus, improved growth and survival in the frontal region.

Although the number of prey items in the gut is not an indication of feeding rate (Munk 1995), the index has been effectively used to quantify feeding success (Powell et al. 1990; Canino et al. 1991). The average number of prey items we observed in the guts of the larvae examined indicated that larvae from the CW and from the frontal region were feeding successfully but not differentially. This is consistent with the fact that neither the average of Fulton's *K* nor the average TAG concentration differed significantly between larvae from the CW and the frontal region, suggesting that condition and survival probability were similar in both water masses. We thus conclude that the elevated abundance of cod larvae in the frontal region did not stem directly from differential survival that resulted from differential condition and (or) food availability.

An alternative, and equally simple, explanation for the elevated abundance of cod larvae in the frontal region is convergence, whereby passive transport brings larvae into the frontal region. Depending upon variations in hydrography and the nutritional condition of the cod larvae (see Sclafani et al. 1993), the buoyant nature of larvae could allow them to remain at a convergent front while the water that carried them into the frontal region was subducted and advected away. The drifter trajectories shown here and those of Sanderson (1995) indicate that the front was convergent. As we have no evidence to suggest that the elevated abundance of larvae in the frontal region was due to differentials in the biological processes we considered, we conclude that the simplest explanation is that a physical process was responsible for the enhanced larval abundance in the frontal region. This is consistent with McLaren and Avendano (1995) who concluded that enhanced zooplankton abundance on the bank did not result from enhanced in situ productivity but rather from physical concentration within the gyrelike CW.

In summary, larvae in the stratified frontal region experienced an enhanced prey field, but they were not in signifi-

Fig. 9. Sections of (*a*) temperature (°C); (*b*) salinity (psu); (*c*) density (σ_t); (*d*) fluorometer (mg chlorophyll $a \cdot L^{-1}$); and (*e*) 231–314 μm ESD plankton abundance (particles$\cdot L^{-1}$) derived from the TUBSS transect at the front (~43°40′N, 61°14′W on 29 November; see Fig. 1*b* for location). The frontal region (FRONT, ~5–7 km) was located between stratified cold, fresh water (CFW, ~0–5 km) and the well-mixed crest water (CW, ~7–12 km). The TUBSS tow profile is shown in the top panel (*a*).

Table 1. Mean (±SD) characteristics of larval cod and zooplankton collections from crest water (CW), the frontal region (Front), and cold, fresh water (CFW) during the period 25 November – 3 December 1992 on the Western

	Location		
Characteristic	CW	Front	CFW
Larval cod abundance (no.·100 m^{-3})	52±33 (42)*b*	174±40 (10)*a*	9±12 (11)*c*
Zooplankton wet biomass (g·m^{-3})	0.22±0.11 (42)*a*	0.29±0.12 (10)*a*	0.12±0.13 (11)*b*
Standard larval length (mm)	4.75±0.95 (794)*a*	4.86±0.84 (294)*a*	4.01±0.56 (9)*b*
Larval total dry weight (μg)	103.2±85 (747)*a*	107.5±84.4 (284)*a*	63.4±36.1 (9)*a*

Note: Values followed by the same letter are not significantly different ($\alpha = 0.05$) according to Duncan's multiple-range test. Sample size (number of deployments or larvae) for each location and characteristic is given in parentheses.

cantly better condition than larvae from the CW. This appears contrary to the hypothesis that positive correlations between larvae and their prey result in improved condition and survival. While we observed no difference between cod larvae from stratified and well-mixed sites at small scales, Buckley and Lough (1987) showed that, at somewhat larger scales, haddock (*Melanogrammus aeglefinus*) larvae on Georges Bank in stratified water masses were in better condition (index based on RNA/DNA ratio) than larvae in well-mixed water masses.

It is possible that larvae did not reside in the frontal region long enough to be distinguished from larvae elsewhere on the basis of their condition alone. The seemingly contrary nature of our results led us to explore this possibility. We used the drifter trajectories in and around the frontal region to estimate the range of time a cod larva might reside in the enhanced food environment of the frontal region, and we examined the estimates in relation to estimates of the latency period for the condition indices we used.

To a first approximation, drifters, larvae, and prey items will all be aggregated by the evolving convergent flow field and subsequently dispersed at the same rate. Hence, one estimate of the length of time that the larvae and prey are both aggregated is simply given by the length of the period (2–3 days) that pairs of converging drifters took to converge, since this is an estimate of the lifetime of the structure drawing them together. In other words, if one drifter is approaching another, then at least one of them is in a region where elevated abundances of buoyant material are likely to be found. A more conservative estimation is to measure the time that convergent drifters remained aggregated, which ranged from 0 to 30 h. The drifter trajectories also provide an estimate of the concentration factor achieved by the convergence and subduction process. Assuming that the drifters converged to a line rather than to a point, then the ratio of the initial separation to the final separation is an estimate of the increase of the number of particles per unit area. Figure 6 shows this factor to be of the order 5. Hence, we conclude that larvae sampled in the frontal region may have experienced a prey field that was up to fivefold more concentrated than in the adjacent waters for periods as long as 3 days. Given the paucity of data, we are reluctant to estimate the uncertainty of these estimates but note that larvae and zooplankton in the frontal region were observed to be at least twice as abundant as in the CW.

Ferron and Leggett (1994, p. 252) defined the latency of a condition index as "the time required for a given change in food availability to be reflected as a significant change in the particular index of condition used." Their summary suggests that the latency period for morphological and lipid-based indices are days and hours to days, respectively (see Ferron and Leggett 1994, Table 2, p. 284). Calculations, based on optimal feeding rates, prey lipid composition, and energy content, and oxygen consumption rates suggest that it could take between 18 h and 3.3 days for a cod larvae to increase its TAG level from 0.0025 to 0.0075 $(\mu g)^{1/2} \mu g^{-1}$ DDW (see Appendix for details of the assumptions and calculations). In our laboratory experiments (Lochmann et al. 1995), starved cod larvae lost an average of 0.005 $(\mu g)^{1/2} \mu g^{-1}$ DDW over a 6-day period, and the average TAG concentration of cod larvae fed at 1000 prey$\cdot L^{-1}$ increased from 0.005 to 0.015 $(\mu g)^{1/2} \mu g^{-1}$ DDW over a 6-day period. Together, all of these estimates suggest that it could take from 18 h to 6 days for the TAG concentration of a larva to increase from the lowest average level observed in the CW during the frontal transect (0.0020 $(\mu g)^{1/2} \mu g^{-1}$ DDW; Fig. 11, net 4) to the highest average level observed in the frontal region (0.0082 $(\mu g)^{1/2} \mu g^{-1}$ DDW; Fig. 11, net 9).

The 18-h to 6-day time scale for changes in our condition measures and the estimated time that a larva might have experienced an enhanced prey environment (as high as 3 days) are of the same order. All larvae collected from the frontal region may not have resided in the region long enough to have improved in condition to a point where differences between groups from there and elsewhere became apparent. Some larvae may have benefitted from a longer residence in the frontal region, which is consistent with the high TAG concentration variances observed in nets 7–10 of the EZNET frontal transect (Fig. 10*e*). If larvae in relatively poor condition from outside the frontal region were mixed with larvae in relatively good condition within the frontal region, then sample variances in the frontal region would be expected to be higher than elsewhere, though the sample means would not necessarily be statistically different. We observed larvae in equally poor condition in the CW and in the frontal region. However, the higher variances in nets 7–10 of the EZNET frontal transect were due to several

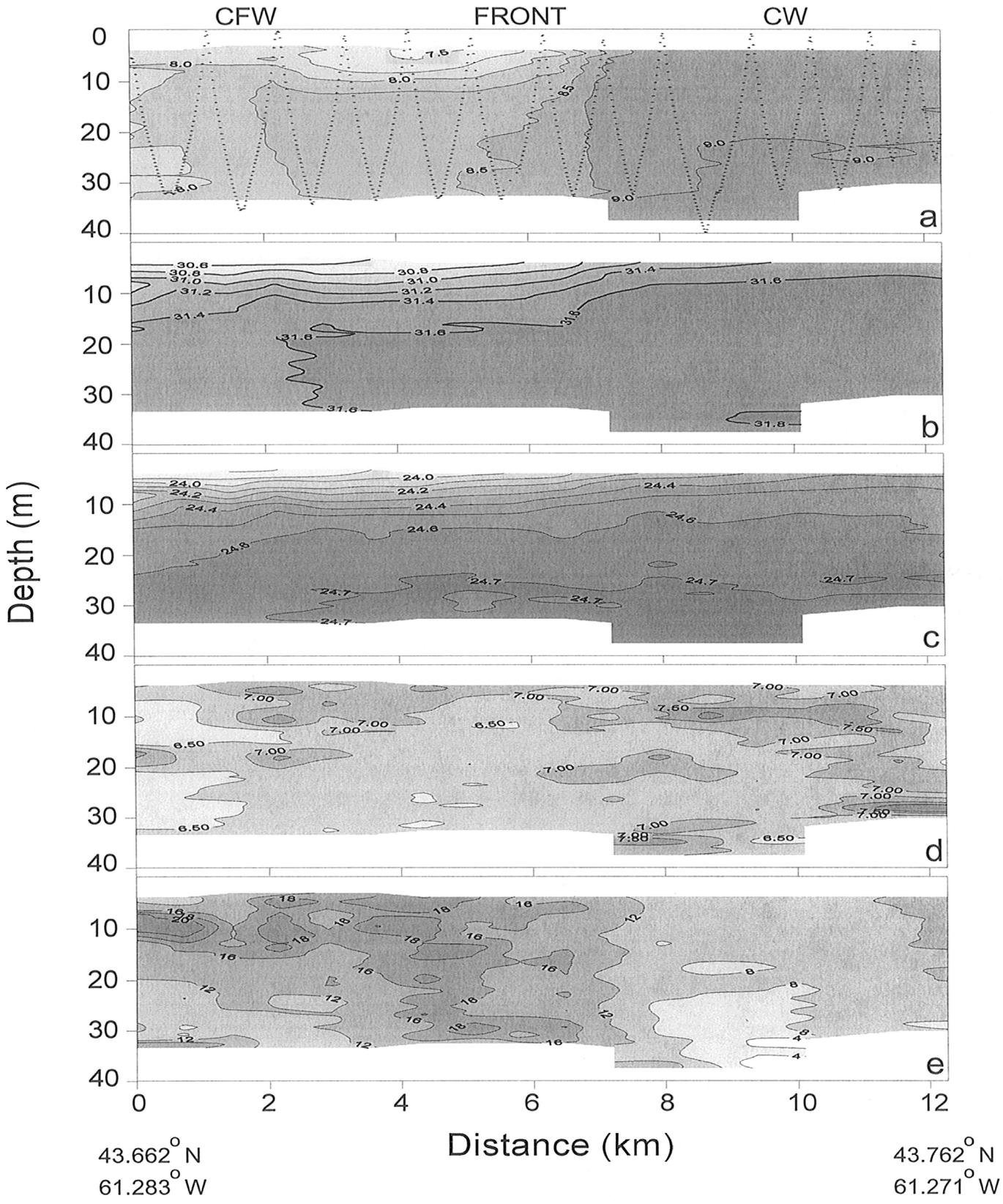


Fig. 10. (*a*) Sampling depth (m), (*b*) temperature (°C), (*c*) salinity (psu), (*d*) larval cod abundance (larvae·100 m^{-3}), (*e*) 272 and 529 μm geometric mean ESD zooplankton abundance (particles·L^{-1}), and (*f*) light attenuation (relative) derived from the frontal transect with the EZNET towed at a fixed depth (~12.5 m) normal to the front on the Western Bank (see Fig. 1*b* for chart location). Larval cod abundances are reported at the midpoint of each sequential net tow. Net numbers and locations of closures are noted by vertical lines on the depth profile in

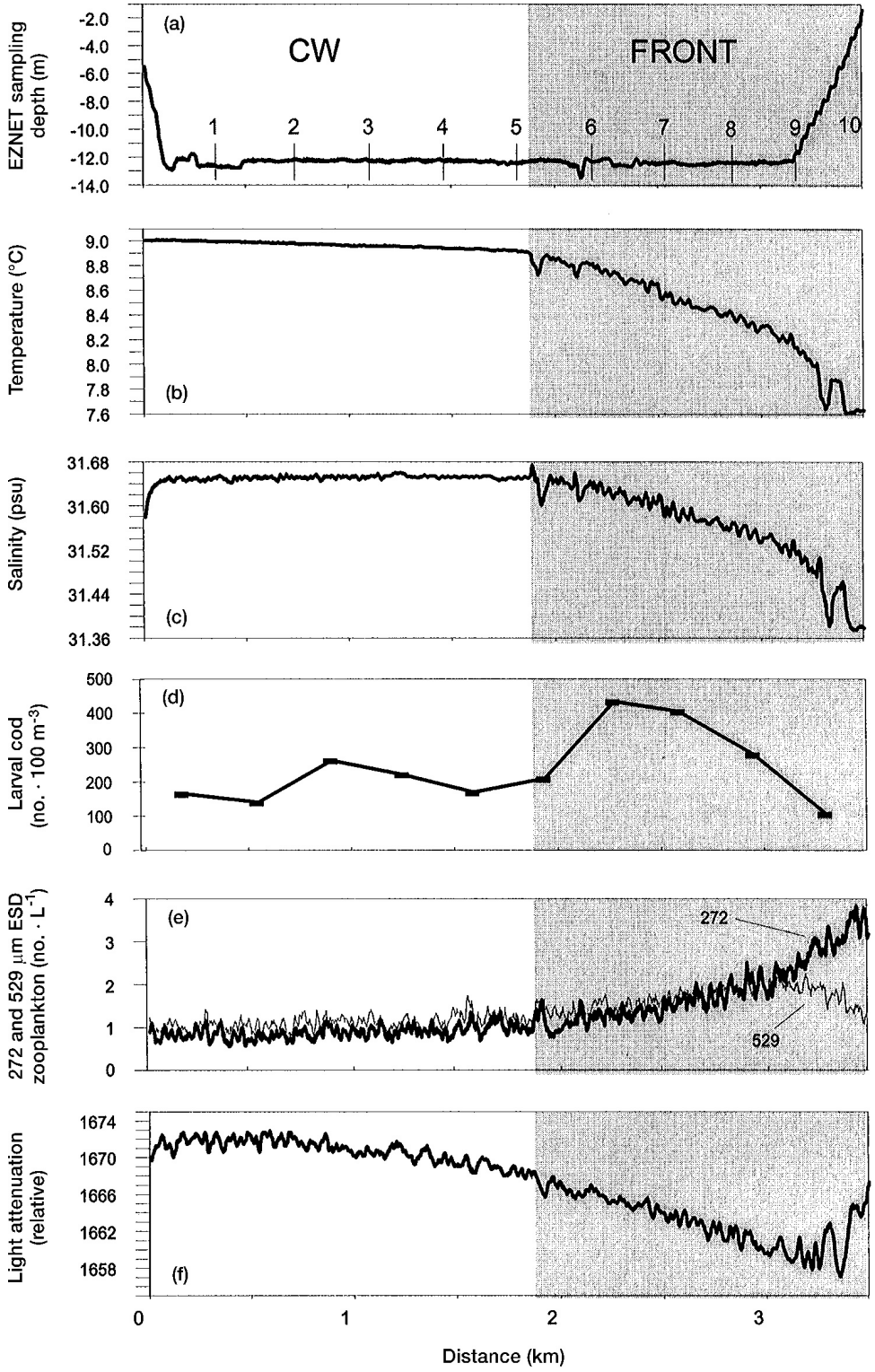


Fig. 11. Average (±2 SE) of (*a*) standard length (mm); (*b*) total dry weight (μg); (*c*) feeding ratio; (*d*) Fulton's *K*; and (*e*) triacylglycerol (TAG) concentration ($(\mu g)^{½}\mu g^{-1}$ DDW) of cod larvae collected in each of 10 different nets along the EZNET transect normal to the front shown in Fig. 10 (see Fig. 1*b* for chart location).

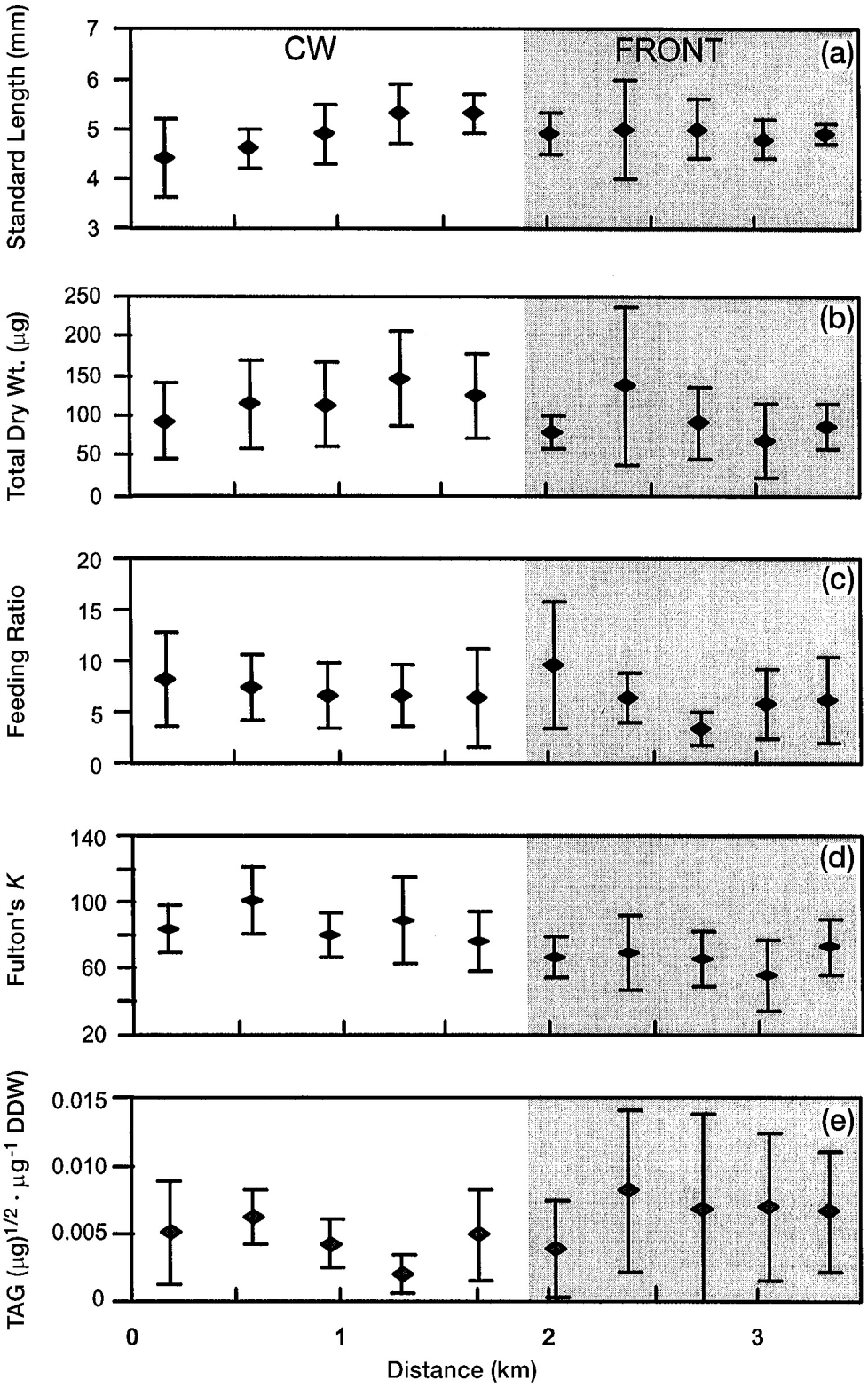


Table 2. Mean (±SD) characteristics of larvae from nets 1–5 deployed in crest water (CW) and nets 6–10 deployed in the frontal region (Front) during the EZNET frontal transect.

	Location	
Characteristic	CW	Front
Standard length (mm)	4.9±0.9 (48)	4.9±0.8 (44)
Total dry weight (μg)	118.1±79.4 (46)	92.8±75.9 (43)
Triacylglycerol ($(\mu g)^{1/2}\mu g^{-1}$ DDW)	0.005±0.004 (46)	0.006±0.007 (43)
Fulton's *K*	85.9±28.6 (46)	77.2±75.5 (43)
Feeding ratio	7.0±5.9 (50)	6.1±6.0 (50)

Note: Means were not significantly different according to Duncan's multiple-range test. Sample size for each location and characteristic is given in parentheses.

Table 3. Mean (±SD) condition of larvae from crest water (CW), the frontal region (Front), and cold, fresh water (CFW).

	Location		
Condition index	CW	Front	CFW
Triacylglycerol ($(\mu g)^{1/2}\mu g^{-1}$ DDW)	0.006±0.006 (758)*a*	0.005±0.006 (288)*a*	0.014±0.009 (9)
Fulton's *K*	86±43 (745)*a*	84±60 (284)*a*	89±23 (9)
Feeding ratio (day and night)	8.9±6.0 (113)*a*	6.5±5.9 (100)*b*	17.0±8.4 (8)
Feeding ratio (day samples only)	6.8±4.0 (52)*a*	6.5±5.9 (100)*a*	

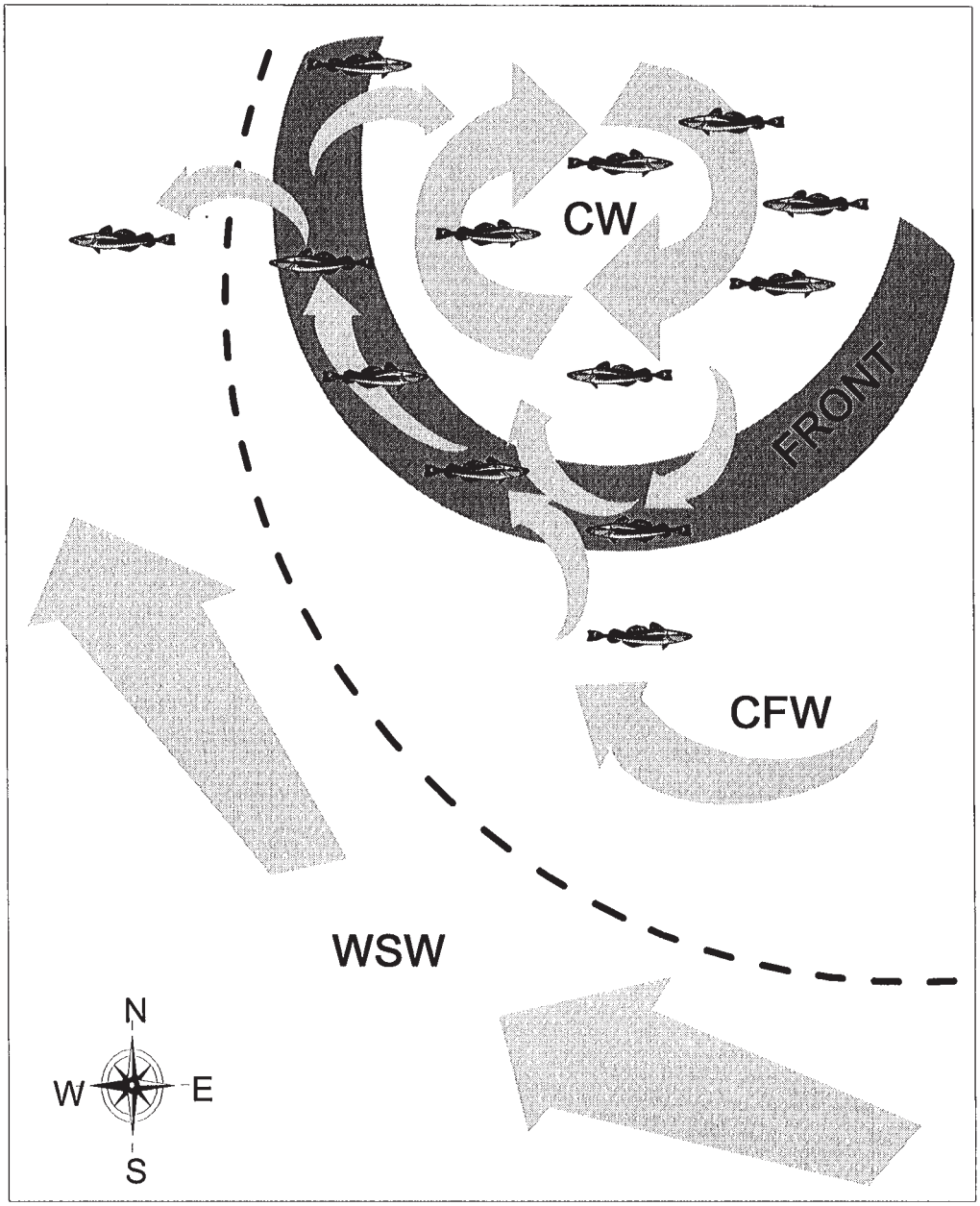
larvae from each of those nets having high TAG concentrations, and not due to just one or two outliers. The overall average TAG index for all CW and frontal larvae (Fig. 11, all nets) was 0.0054 and 33% of the larvae (15 of 46) from the CW were in better than average condition while 44% of the larvae (19 of 43) from the frontal region were in better than average condition. In retrospect, condition indices that have shorter latencies, such as RNA/DNA ratios or digestive enzyme activity, may be a more appropriate index when addressing questions at the times scales of the physical processes occurring in frontal regions.

Here we provide a conceptual model of the processes occurring in the frontal region that is consistent with the above results. Figure 12 summarizes how the CW, intermediate in temperature and salinity between the CFW and the WSW, rotated anticyclonically as a slab-like water mass near the crest of Western Bank (see also Sanderson 1995; Griffin and Thompson 1996). A tongue of CFW, impinging from the east, wrapped around the rotating CW creating a convergent frontal region at the margin between the CW and the CFW. Cod larvae from the CW (and presumably spawned there; see Frank et al. 1994; Miller et al. 1995) and larvae from CFW (which we noted were very few in number) were retained in the CW and (or) concentrated in the frontal region where they experienced an enhanced prey field. The frontal region included larvae that had spent varying amounts of time (hours to days) within the enhanced prey environment, resulting in our inability to reject the null hypothesis that larvae in the frontal region were in the same condition as larvae elsewhere. As the CW continued to rotate, larvae in the frontal region were either reintroduced to the CW inside the frontal region or dispersed outside the frontal region and advected from the region by west-south-west residual currents (Sanderson 1995, Griffin and Thompson 1996).

The global importance of gyrelike features and convergent fronts, which allow early stage fish to remain on or near banks, was first discussed by Iles and Sinclair (1982). Although simple geographic observations of persistently high larval abundance are insufficient to distinguish between physically driven retention and biologically driven differential mortality, our observations clearly suggest it is physically driven retention and not differential mortality (at least as approximated by condition indices) that is responsible for the high abundances of cod larvae within a relatively small area on the crest of Western Bank. The difference between these two mechanisms is important as they directly determine which measures are necessary for predictive purposes. However, retention in this area also seems to provide larvae with a more abundant and more appropriate prey field than elsewhere on the bank (McLaren and Avendano 1995). A high percentage of the drifters that converged in the frontal region were re-introduced into the CW, rather than being carried away from the bank crest in the CFW or the WSW. Larvae entrained into the frontal region and recirculated within this semiclosed system (the CW and the frontal region), probably benefitted from retention in a small region near the crest of the bank where the large-scale prey field is clearly enhanced relative to the entire bank.

The semiclosed system and convergent front we describe appears to have important life-history consequences for cod. We know this area is an important cod spawning region (Frank et al. 1994) and most recently an important spawning region in the October–December period (Miller et al. 1995) when the prey field for larvae is regionally enhanced (McLaren et al. 1995). Thus, we hypothesize that interannual variability in the formation and stability of the gyrelike feature and the integrity

Fig. 12. Conceptualized model of the biophysical processes at the crest of Western Bank. Crest water (CW) rotates as an anticyclonic slab. Periodically, a tongue of cold, fresh water (CFW) is wrapped around the CW forming a frontal region between the two water masses. Cod larvae from CFW (rare) and CW (abundant) are entrained (converge) at the front where the prey field is enhanced. Larvae are transported in the frontal region to the west and north where they are either mixed back into the CW or out into the CFW or the warm salty water (WSW) flowing along the bank margin. Residual currents transport larvae outside the CW and the frontal region off the bank. Larvae mixed back into the CW are retained on the bank and may be repeatedly entrained into the frontal region.



of the frontal system may account for some of the recruitment variability observed in Western Bank cod. Alternatively, retention on the bank may simply maintain a spatial overlap between cod larvae and their prey. Observations of the abundance and condition distributions at the crest of Western Bank in years when retention occurs but when prey fields are less favourable should help ascertain which of the biological, physical, or biophysical processes are most significant in explaining and predicting recruitment variation in the region.

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Appendix

We considered a range of daily consumption rates for larval cod. Tilseth and Ellertsen (1984) provide a feeding rate of 1.5 nauplii·h^{-1}. As cod larvae are visual feeders (Ellertsen et al. 1980) and need a minimum light level for feeding we assumed a 12 h feeding period on the Scotian Shelf in November, leading to an estimate of 18 nauplii·day^{-1}. This a conservative estimate as cod larvae from the study area have been observed with as many as 29 nauplii per gut (McLaren and Avendano 1995).

Solberg and Tilseth (1984) report a caloric content of 1.7×10^{-6} kcal (1 kcal = 4.186 kJ) for a 0.3-µg nauplii, which is consistent with a caloric content of 1.5×10^{-6} kcal for a 0.3-µg nauplii on the basis of a proximate composition of 60% protein, 27% lipid, 10% ash, and 3% carbohydrate (Parsons et al. 1984). Assimilation efficiencies for cod larvae are estimated at between 40 and 50% (Solberg and Tilseth 1984). Using the maximum estimates of consumption (29 nauplii·day^{-1}), caloric content (1.7×10^{-6} kcal·$nauplii^{-1}$), and assimilation efficiency (50%), a cod larva might have 2.47×10^{-5} kcal·day^{-1} available to meet energy requirements.

Estimates of oxygen consumption rates for early cod larvae range from 2.0 µL O_2·mg^{-1}·h^{-1} (Solberg and Tilseth 1984) to 2.5 µL O_2·mg^{-1}·h^{-1} (I. Hunt Von Herbing, Department of Biology, Woods Hole Oceanographic Institute, Woods Hole, Mass., personal communication). Therefore, using a metabolic conversion of 4.6×10^{-6} kcal·μL^{-1} O_2·mg^{-1} an early cod larva weighing approximately 50 µg total dry weight (Lochmann et al. 1995) would have catabolic requirements ranging from 1.10×10^{-5} to 1.35×10^{-5} kcal·day^{-1}. Growth rates for cod larvae range from 5 to 7%·day^{-1} (Solberg and Tilseth 1984) and to 10%·day^{-1} (Buckley and Lough 1987). The energy content of cod larvae has been estimated to be approximately 5.0×10^{-6} kcal·μg^{-1} ash free dry weight (Solberg and Tilseth 1984). Therefore, anabolic requirements for a 50-µg cod larva would range from approximately 1.25×10^{-5} to 2.50×10^{-5} kcal·day^{-1}. Assuming an oxygen consumption rate of 2.0 µL O_2·mg^{-1}·h^{-1} and a growth rate of 5%·day^{-1} there would be a maximum excess of 1.2×10^{-6} kcal·day^{-1}.

According to the estimates of the proximate composition of copepods, one half of the available energy comes from lipids and the other half from proteins. We assumed that one half of the excess (storage) energy is in the form of lipids. Nine kilocalories are equivalent to one gram of lipid. Estimates of the proportion of lipid in the form of TAG range from 4% for *Calanus helgolandicus* (Lee et al. 1970) to 4–12% for *C. pacificus* (Hakanson 1984). However, wax esters, another energy storage product might be converted to TAG for storage in cod larvae. Wax esters make up 30% of the lipids in *C. helgolandicus* (Lee et al. 1970) and between 12 and 65% of lipids in *C. pacificus* (Hakanson 1984). If wax esters were not converted to TAG by cod larvae, and TAG made up only 4% of the excess lipids, then TAG would accumulate at a rate of 0.0027 µg TAG·day^{-1}. If 65% of lipids were wax esters and 12% of lipids were TAG, and wax esters were converted to TAG for storage in cod larvae, then TAG would accumulate at a rate of 0.0511 µg TAG·day^{-1}. Lipids make up approximately 30% of the total dry weight of early cod larvae (Lochmann et al. 1995), so a 50-µg cod larvae would have a DDW of 35 µg. If we correct the TAG accumulation rates for body size using the index defined in the main body of the text TAG would accumulate at between 0.0015 and 0.0065 $(\mu g)^{1/2}\mu g^{-1}$ DDW·day^{-1}. As we observed differences in TAG concentration between CW (0.0025 $(\mu g)^{1/2}\mu g^{-1}$ DDW· day^{-1}) and frontal (0.0075 $(\mu g)^{1/2}\mu g^{-1}$ DDW·day^{-1}) larvae, then we can estimate that it would take between 18 h and 3.3 days for a larva to increase its TAG concentration by 0.005 $(\mu g)^{1/2}\mu g^{-1}$ DDW·day^{-1}. This estimate is not only sensitive to the range of values for the variables used above but also to the proportion of energy requirements that are met by utilizing protein as opposed to lipids.