Abundance distribution of larval cod (*Gadus morhua*) and zooplankton in a gyre-like water mass on the Scotian Shelf

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ABSTRACT: Ichthyoplankton and hydrographic surveys of Western Bank on the outer Scotian Shelf were completed in November 1992 as part of a study of the early life history of cod (*Gadus morhua*) in the Ocean Production Enhancement Programme (OPEN). We located and tracked a well-mixed, gyre-like, water mass and an associated front near the crest of Western Bank during the survey and used a data assimilation model to track the water mass and sample a cohort of larval cod resident in the water mass for a 20 day period. The highest concentrations of cod larvae (123-238 larvae 100 m^{-3}) were found along a convergent front between the crest water mass (CW), where concentrations ranged from 2 to 158 larvae 100 m^{-3}, and a surrounding cold fresh water mass (CFW) where concentrations ranged from 0 to 89 larvae 100 m^{-3}. Zooplankton wet biomass and particle concentrations were also higher in the frontal region relative to the surrounding water. However, the sizes of cod larvae collected at the front were not significantly different from larvae collected in the CW. There was a high degree of variation in the wet biomass of > 333 μm zooplankton within the CW that was tracked through time, varying between 0.15 g m^{-3} and 3.75 gm m^{-3} but there was no significant trend in biomass concentration and no significant difference in average concentrations before and after a major storm. Concentrations of the larval cod cohort in the tracked water mass showed a classic exponential decay ($z = 0.2$; $r^2 = 0.9$). To our knowledge, this is the first time that a data assimilative hydrodynamic model has been used in real-time to guide biological sampling efforts during the study of a larval fish cohort within their advective environment. The semi-closed system and convergent front we describe appears to have important life history consequences for cod. Inter-annual variability in the integrity of the frontal system and the associated gyre-like feature may account for some of the recruitment variability observed in Western Bank cod.

1 INTRODUCTION

Several hypotheses which attempt to explain recruitment variability in fish species are based on interactions between the early life stages and the local feeding environment and imply temporal-spatial correlations between the concentration of larval fish

and their prey (Hjort 1914, Cushing 1972, Lasker 1975, Taggart & Frank 1990). However, recruitment mechanisms are complex and regression-based explanatory models frequently fail with time (Frank 1991). Explanatory models will improve if the mechanisms underlying the hypotheses for explaining recruitment variability are identified and quantitatively determined. For example, a positive correlation between larval fish and their prey would indicate a potentially strong, future year-class if survival is higher in a high food environment (Ellertsen et al. 1986). However, the temporal basis for the correlation can lead to misinterpretation (Taggart & Frank 1990) as can assumptions regarding actual size of prey within the feeding environment (Frank 1988).

Marine fish species with pelagic eggs or larvae exhibit fluctuations in recruitment which are, at least partially, attributed to factors affecting early life stages (Houde 1987, Lukmanov & Mukhina 1989, Peterman et al. 1988). The successful change from endogenous to exogenous nutrition is a crucial step in early development (Hjort 1914, May 1974). Adequate nutrition during periods of rapid larval growth is also critical to survival (Ellertsen et al. 1981, Theilacker 1986, Werner & Blaxter 1981). Poorly nourished fish larvae exhibit changes in buoyancy (Tilseth & Stromme 1976) with associated effects on drift (Sclafani et al 1993), cellular structure (Theilacker & Watanabe 1989), enzyme activity (Dabrowski 1982), growth (Lasker et al. 1970), and survival (Laurence 1974). However, the relative importance of starvation mortality compared to other sources of mortality during the larval phase is a matter of debate.

Maxima in phytoplankton, zooplankton, and larval fish concentration frequently occur at fronts (e.g. Govoni et al. 1989, Richardson et al. 1986a, Sabates & Maso 1990). Explanations involve frontal convergence and passive transport (Govoni et al. 1989), elevated in situ production (Kiørboe et al. 1988, Richardson et al. 1986b), spawning behaviour (Sabates & Maso 1990,) and higher survival probability due to better growth in high food environments (Brandt 1993, Taggart et al. 1989). However, the factors controlling plankton levels at fronts are not easily deduced from distributions of concentration. To make predictions about survival and growth in relation to frontal features, it is necessary to determine the reasons for high concentrations and what benefits, if any, larvae derive from frontal residence.

We recently located and tracked a well-mixed gyre-like water mass and an associated front on the Scotian Shelf, near the crest of Western Bank, during an ichthyoplankton cruise designed to track a cohort of larval cod. In this paper we detail the water mass and associated frontal feature and examine variation in a suite of physical and biological measures which are relevant to the abundance and distribution of larval cod and zooplankton at relatively small time and space scales.

2 MATERIALS AND METHODS

2.1 *Field collections*

Data were collected during the Petrel V cruise 92-31 to Western Bank (Fig. la) during the period 22 November to 16 December, 1992. A complete description of the

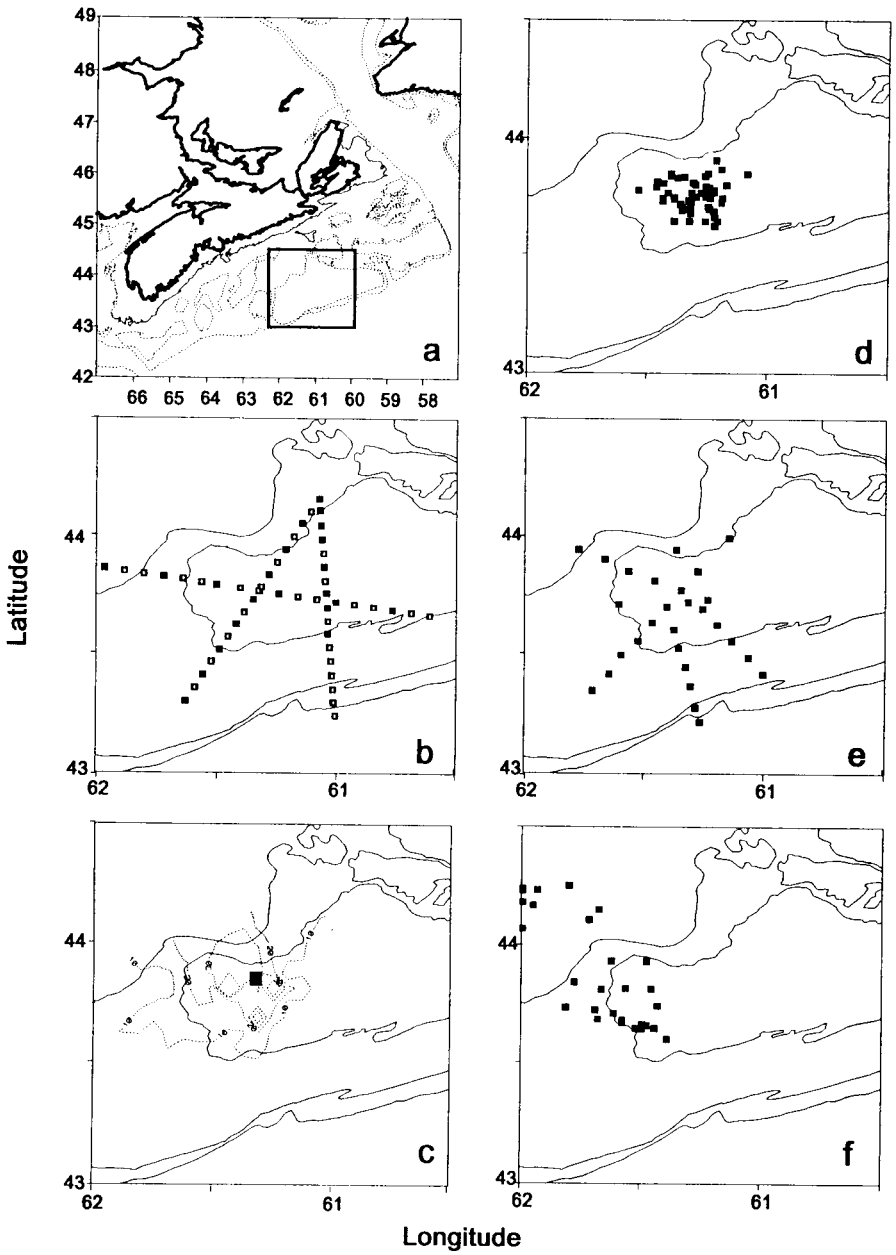

Figure 1. (a) Bathymetric chart of the Scotian Shelf showing the 100 and 200 m isobaths with the Western Bank sampling area outlined. (b) Crest area of Western Bank with the 60, 100, and 200 m isobaths showing the initial survey (23-25 November). Open boxes are locations of CTD deployments, and filled boxes are locations of CTD and BONGO deployments. (c) Crest area showing larval concentration (larvae 100 m^{-3}) isopleths, and the filled square is the position of deployment of initial drifter. (d) Crest area showing locations of zooplankton samples collected within the tracked water mass (25 November-3 December). (e) Crest area showing second CTD and BONGO survey (8-9 December). (f) Crest area showing locations of zooplankton samples collected within the tracked water mass (10-12 December).

technical aspects of the cruise are presented elsewhere (Bowen et al. 1995, Griffin & Lochmann 1993).

Three initial transects were conducted from 23 to 25 November across the crest of Western Bank (Fig. 1b) to measure temperature, salinity and ichthyoplankton concentrations. Temperature and salinity profiles were taken at 7 km intervals with a Seabird-25 conductivity, temperature, depth sensor (CTD) and plankton samples were collected every 7-21 km with a 60 cm diameter bongo net sampler fitted with 333 μm mesh nets (Posgay & Marak 1980). Bongo tows were conducted at a ship speed of 1 $m.s^{-1}$ in a continuous double oblique manner down to between 5 and 10 m above the bottom for 10-15 min. Tow depth was determined by the length of tow wire out and incident angle. Average volumes filtered were 150 m^3 and were monitored using General Oceanics flow meters. Plankton samples were sorted immediately for Atlantic cod (*Gadus morhua*) larvae which were enumerated and each larva was video taped, and preserved in 95% ethanol. The standard length (SL) of each larva was subsequently determined to the nearest .01 mm using the video image with the OPTIMUS image analysis system (Miller et al. 1995).

One radio-telemetering drifter was deployed at the crest of the Bank on 25 November where a local larval concentration maximum was found (Fig. 1c). Thirteen additional drifters were deployed in an evenly spaced pattern around the central drifter, within a 30 × 30 km water mass containing a distinct group of larval cod. The Ocean Probe system (Bowen et al. 1995) and a data assimilation hydrodynamic model run in real-time on board the ship (Griffin & Thompson 1995) were used to track the water mass and resample the resident cod larvae. Ocean Probe hardware included: i) two radio-telemetering moorings, each equipped with acoustic transponding S4 current meters located at 20 m and 40 m depth, and Aanderaa WLR6 pressure gauges mounted at the bottom; ii) two non-telemetering moorings each with one S4 current meter at 20 m; iii) fourteen radio- and satellite-telemetering Loran-C or global positioning satellite (GPS)-equipped surface drifters fitted with 2 m wide × 10 m long window-blind drogues centred at 20 m depth (Sanderson 1995); iv) a 300 kHz hull mounted RDI Acoustic Doppler Current Profiler (ADCP); v) shipboard navigation and environmental monitoring equipment, including a GPS system, gyro-compass, Loran-C, speed log, depth sounder, sea-surface temperature (SST),and meterological sensors (e.g. wind speed and direction, atmospheric pressure etc.); and vi) an ether-network of ten data acquisition PCs and seven Sun Microsystems SPARC stations and SLC workstations for data analysis, data assimilation and modelling. Additional data on water mass characteristics were collected using a vertically-profiling Seabird-25 CTD and bottle sampling rosette.

Position locations from the telemetering drifters, data from the CTD casts, and measurements from the other Ocean Probe sensors delivered information to a data assimilative hydrodynamic model (Griffin & Thompson 1995) which produced time-dependent flow fields within a 60 × 60 km model domain of the study area. The flow fields were used to predict the present and future positions of previous sampling locations. Using these predictions we tracked a water mass and continuously sampled the resident cod larvae.

Twenty five oblique bongo samples and 27 vertical profiles of zooplankton were collected between 25 November and 3 December. Vertical profiles were conducted using a 1 m^2 EZNET (Open seas Instruments, Musquodoboit Harbour, NS), the mar-

keted version of the Bedford Institute of Oceanography Net and Environmental Sampling System (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, NS). The EZNET was used to sample discrete depths at 5 m intervals to 35 m and approximately 10 m intervals to within 10 m of the bottom. Net speeds averaged 1 $m \cdot s^{-1}$, towing duration was nominally 5 $min \cdot net^{-1}$ and filtered volumes averaged 250 m^3. After recovery, the nets were rinsed to the codends and plankton samples were immediately sorted for cod larvae. Ten larvae from a single bongo net or from each EZNET net were videotaped through a dissecting microscope (Miller et al. 1995) for morphometric analysis and individually preserved in liquid nitrogen. The remaining larvae were preserved in ethanol 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. Sampling resumed on 7 December and the bank was re-surveyed by 9 December. Twenty-one bongo tows and seven EZNET deployments were completed between 10 and 16 December, when the study ended.

During the course of the study, we sampled the frontal region that bordered the tracked water mass. A frontal transect was accomplished by sequentially towing each EZNET net at a fixed depth of 12.5 m, for 5 min, over a distance of 330 m, at a net speed of 1 $m \cdot s^{-1}$, on a transect normal to the frontal region, beginning in the tracked parcel. The depth for this survey was chosen according to the depth of maximum larval cod concentration identified from previous sampling efforts. We also collected data during a 12 km transect across the frontal region 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 Spruies et al. 1992). The TUBSS frontal transect was also normal to the front, approximately 10 km from the location of the EZNET frontal transect.

2.2 *Laboratory procedures*

Plankton collections were resorted after the cruise and all remaining cod larvae were removed, enumerated and preserved in 95% ethanol. Plankton samples were then sieved on a 200 μm mesh pre-weighed sieve, towel dried to remove excess water, and weighed to the nearest g to obtain wet biomass estimates. To allow for a direct comparison between the depth integrated bongo samples and the discrete depth EZNET samples, zooplankton wet biomass and larval concentrations from the latter were depth averaged by calculating the total number of larvae (or wet biomass) collected by all nets within a deployment divided by the total volume of water sampled during the deployment. Larval concentrations were standardized to $larvae \cdot 100\ m^{-3}$ and zooplankton wet biomass measures to $g \cdot m^{-3}$.

Determination of standard length (SL) of videotaped larvae followed the protocol described in Miller et al. (1995) and lengths were reported in millimetres. An age (in days) was assigned to each larva according to an age-length relationship for cod larvae previously collected, in December, on the Scotian Shelf (M. Meekan, Department of Biology, Laval University, Quebec, Quebec, G1K 7P4, pers. comm.).

3 RESULTS

3.1 *Water mass structure and temporal evolution*

The first bongo survey indicated that cod larvae were located primarily at the crest (61°20′W, 43°45′N) of Western Bank (Fig. lc). CTD data collected across the crest

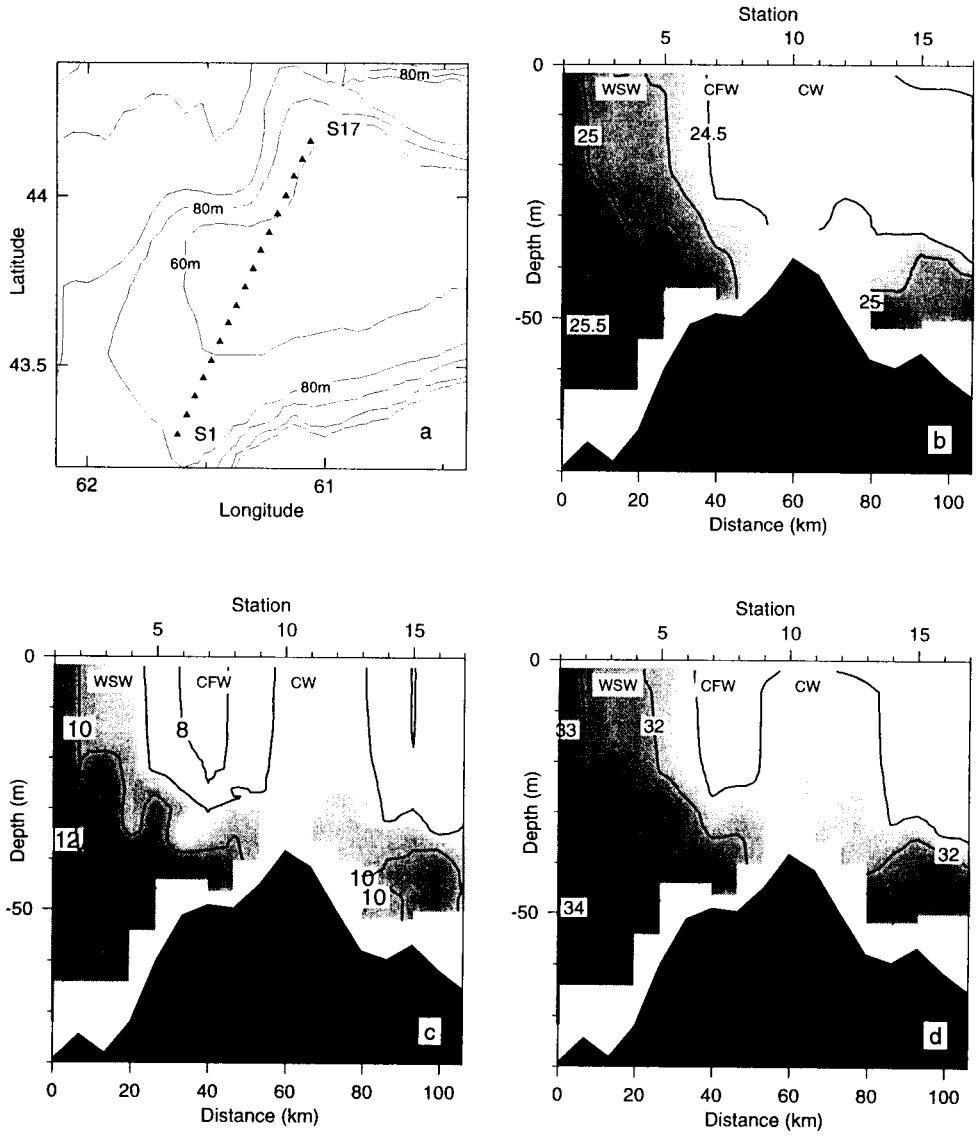

Figure 2. (a) Bathymetric chart (60, 80, 100 and 200 m isobaths) of Western Bank showing locations of specific CTD stations used for sections. (b) Temperature (°C), (c) Density (σ_t), and (d) Salinity (psu) isopleths for transect across the crest of the Bank. Sections show the approximate locations of crest water (CW), cold, fresh water (CFW), and warm salty water (WSW)

of the Bank revealed several water masses in the region (Fig. 2). Seaward of the crest of the Bank was relatively warm and salty stratified slope water (WSW). Crest water (CW), on the crest of the Bank, was relatively well mixed and of intermediate temperature (9.1°C) and salinity (31.6 psu). Surrounding the CW was a lens of relatively cold fresh water (CFW). The eastern and southeastern margin of the CW marked a front between CW and CFW (Fig. 2). Although the density differences between CW (stations 10-13) and CFW (stations 6-9) are not striking (Fig 2b), the temperature and salinity sections show a shallow tongue of CFW centered at station 7 between WSW (stations 1-4) and CW (Fig. 2c,d). The TUBSS frontal transect showed that the frontal region was several kilometres wide (Fig. 3). The CFW was cooler than the CW by 1.5°C and fresher by 0.8 psu (Fig. 3a,b). Density differences were marginal over the same distance (Fig. 3c).

To stay with the chosen water mass, we used the assimilation model in a Lagrangian frame of reference twice per day to show us where all previously sampled waters now were. New sampling positions within the water mass with respect to old sampling positions were then chosen, and the model was used to intercept them as the time for each approached. To do this, the model needed only to project currents several hours into the future, this being the time required to update the data base with new observations and re-run the model.

In addition to considering the locations of previous samples and the present state of the flow field, we also took the locations of the drifters and our under-way SST observations into account. Figure 4 shows SST samples taken during the cruise, advected forward to synoptic times spanning the entire period. The sequences of panels show how cold water swept around the nearly stationary CW (25 November to 3 December), until the storm swept all waters southwards, stretching and tearing the CW in the process (4-6 December). Figure 4 also shows how the waters resampled after the storm period had maintained a local SST maximum (7-13 December). The local larval concentration maxima and sea surface temperature maxima coincided with the location of a cluster of drifters and the model prediction of the location of the remnants of the CW (Griffin & Thompson, 1995). The remnant CW mass moved northward between 8 and 12 December, when it left the bank and was broken apart, ending the study.

Most, but not all of the plankton sampling occurred within the tracked (CW). We assigned every plankton collection from the study to one of three groups: (1) samples inside the CW, (2) samples collected at the convergent thermohaline front (FRONT) and (3) samples taken in either the cooler (CFW) or warmer (WSW) water. Assignments were based on an unweighted pair-group method of cluster analysis (Proc Cluster, SAS 1985) based on latitude, longitude, date and time of collection, and sea surface temperature, with 20 clusters. The first two clusters clearly represented samples taken within the CW before and after the sampling hiatus. However, this analysis grouped samples, which, on the basis of their vertical temperature profiles, were taken at the thermohaline front, together with samples taken inside the CW. On the basis of temperature profile, we separated frontal samples from those within the CW. Plankton samples in the CW had larval cod concentrations ranging from 2 to 158 larvae,100 m^{-3} (Average = 40; SD = 30). Samples outside (WSW or CFW) the tracked water parcel had concentrations ranging from 0 to 89 larvae-l00 m^{-3} (Average = 19;

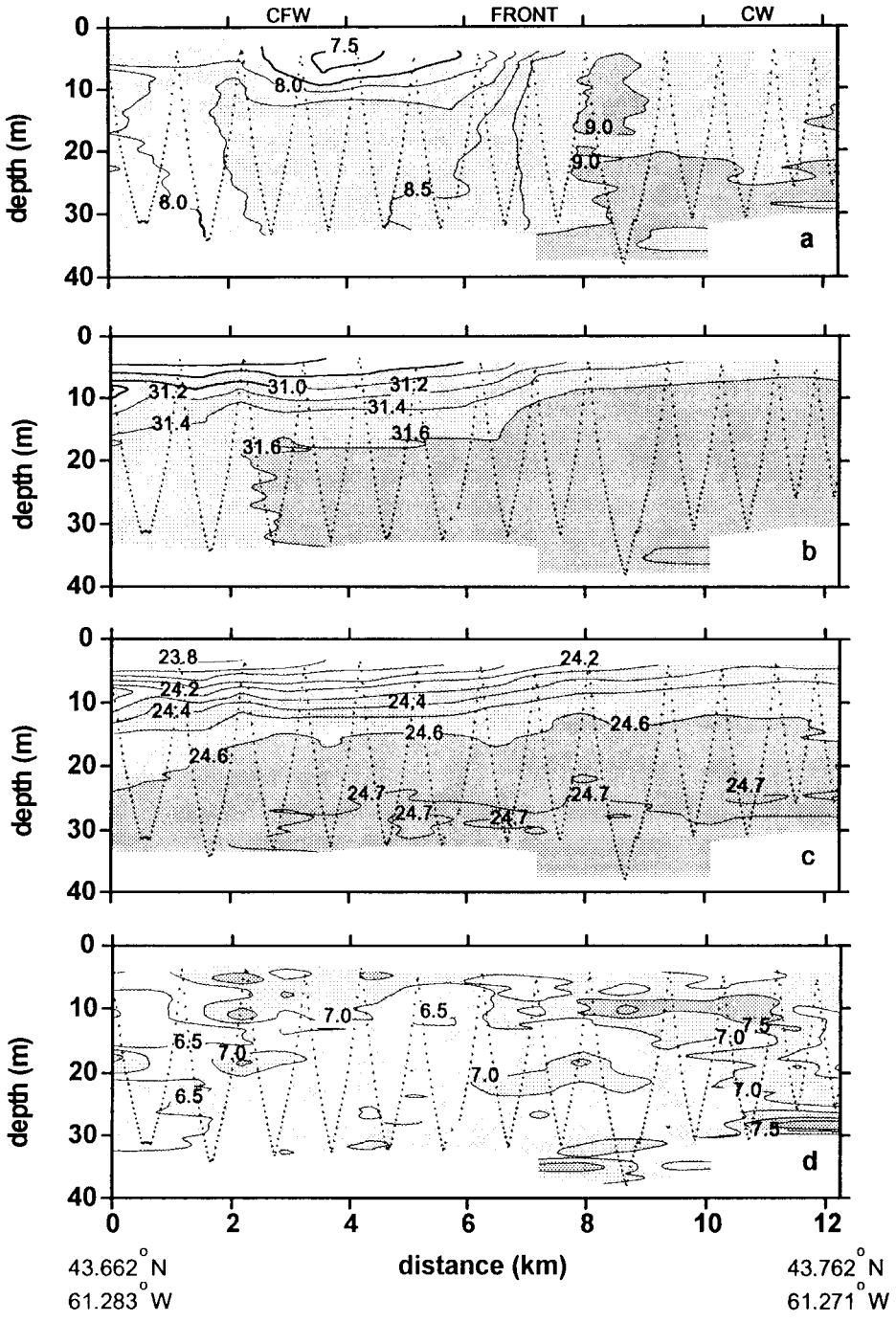

Figure 3. (a) Temperature (°C), (b) Salinity (psu), (c) Density (σ_t), and (d) Fluorometer (μg Chl-a·L^{-1}) sections derived from the TUBSS transect across the front at approximately 43°40′N, 61°14′W on 29 November. The frontal region (Front) was located between CFW (2-5 km) and CW (8-12 km).

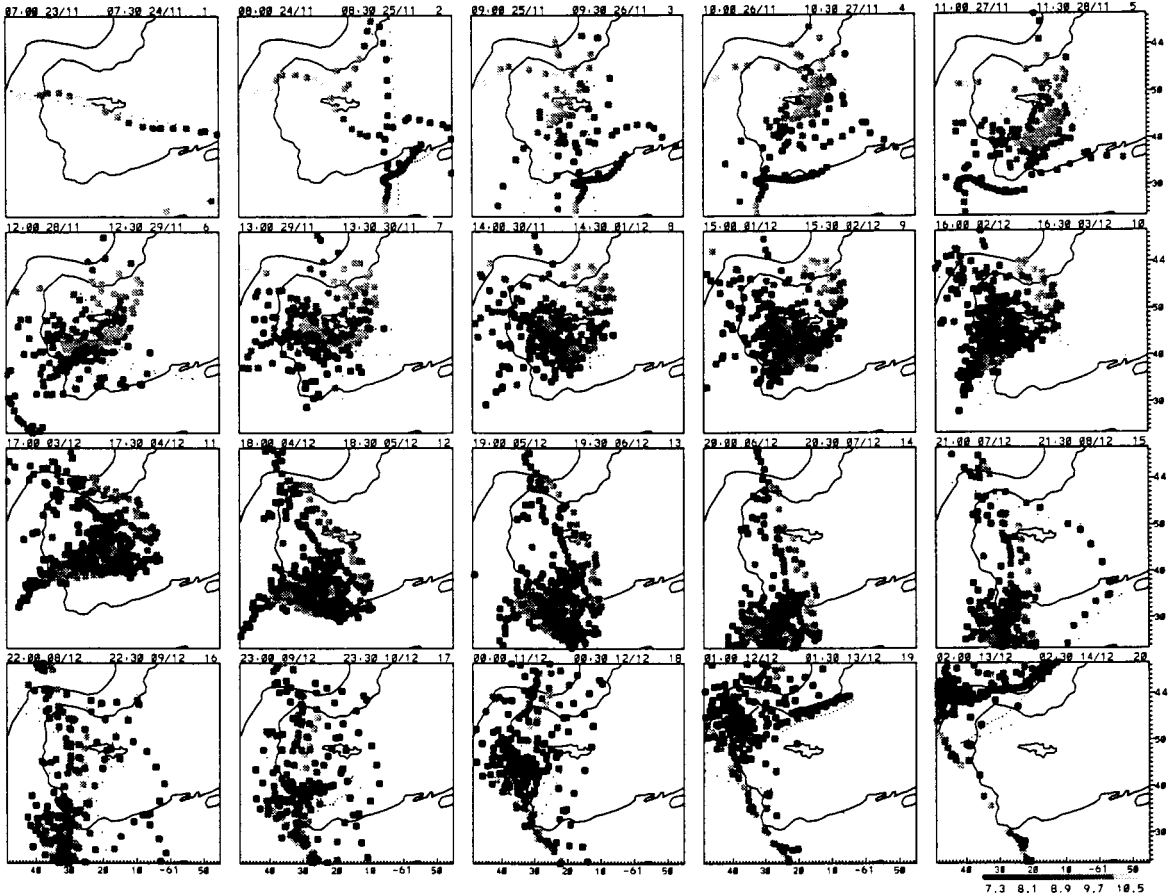

Figure 4. Bathymetric charts (40, 60 m isobaths) of Western Bank showing sea surface temperature (SST) fields as the tracked crest water (CW) was continuously measured and advected through time. Temperature is grey-scale coded (bottom right) in relative terms from cold (black) to warm (light grey). A modeled flow field was used to reconstruct the synoptic view and advance the location of SST samples forward to the end of the time period concerned (UTC at top left of each panel).

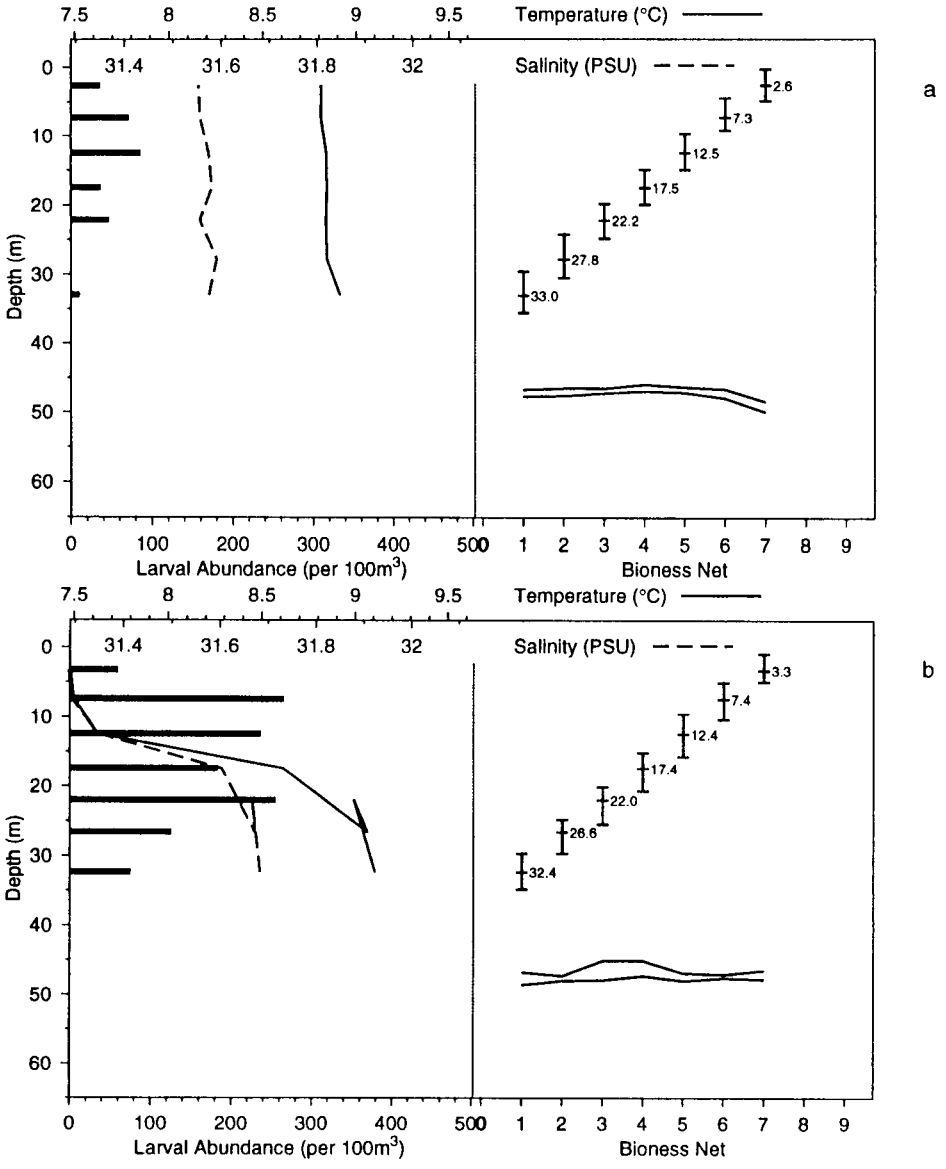

Figure 5. Typical vertical profiles of larval cod concentration (larvae ·l00 m^{-3}, histograms), temperature (°C, solid line) and salinity (psu, dashed line) in the left panels, and bottom depth (minimum and maximum, solid lines) and sampling depth interval (minimum, maximum and average) for each net in the right panels for EZNET (Bioness) deployments in (a) Crest water and (b) The frontal region.

SD = 22) and samples at the front had concentrations between 123 and 238 larvae ·100 m^{-3} (Average = 174, SD = 40).

An example of the well mixed nature of the CW relative to the more stratified water at the front is clearly evident in Figure 5 which also shows the higher concen-

trations of cod larvae at the front relative to the CW and the modal depth distribution of larvae near 12.5 m.

3.2 *Frontal feature*

The synoptic reconstruction of the SST field (Fig. 4) shows the front between CW and CFW at about 43°40' N, 61°15' W on 27 November. Errors associated with computing the positions of SST samples in the assimilation model and the large averaging interval (30 min) of the SST data reduce the sharpness of the front in this figure, although it is readily apparent in Figures 3 and 6. Temperature and salinity observations from the EZNET frontal transect showed that at the time and location of sampling, the frontal region was approximately 1-1.5 km wide (Fig. 6, see also Fig. 3). Temperature and salinity at 12.5 m depth decreased about 1°C and 0.35 psu over a horizontal distance of 1.5 km from the well-mixed CW to more stratified frontal region. Near the frontal region, but still within CW (nets 1-5 in Fig. 6), larval cod concentrations were at or above the upper end of the observed range for CW (3-157 larvae 100 m^{-3}) However, larval concentrations virtually doubled over a distance of 0.5 km into the frontal region (nets 7 and 8 in Fig. 6). Concentrations of zooplankton in two size classes (312 µm equivalent spherical diameter (ESD) and 531 µm ESD), approximately doubled from CW into the frontal region and at the same time light attenuation decreased (Fig. 6). Light attenuation, as measured by the OPC, is an indication of water colour (i.e. chlorophyll) and concentration of plankton below the resolution of the OPC (< 250 µm ESD). We interpret the drop in attenuation as an indication that phytoplankton concentration decreased at the front. This is consistent with fluorometer measurements collected at the TUBSS frontal transect (Fig. 3) which showed a decrease in chlorophyll from > 7.5 $\mu g \cdot L^{-1}$ in CW to < 6.5 $\mu g \cdot L^{-1}$ in CFW, but there was no enhanced chlorophyll level at the front per se.

One-way analyses of variance indicated that SL of larvae from different nets of the frontal transect were similar (Fig. 7). Furthermore, the SL of larvae collected at the front were not significantly different from larvae collected in the CW, even though larval concentration was significantly higher (Table 1). However, larvae in the CW and at the front were significantly larger than the larvae in CFW where concentrations were significantly lower (Table 1). The significant difference in length of the CFW larvae must be interpreted cautiously as the sample size in the CFW was low.

3.3 *Biological variation in the tracked crest water (CW)*

In all EZNET deployments except the fine-scale frontal transect, the towing profile was stepped oblique. For comparisons between waters sampled with different gear, depth-averaged concentrations were calculated for EZNET deployments as described above.

There was a high degree of variation in the wet biomass of > 333 µm zooplankton within the CW that was tracked through time (Fig. 8). Daily averaged biomass varied between 0.15 g m^{-3} and 3.75 gm^{-3}, but there was no significant trend in biomass concentration and no significant difference in average concentrations before and after the storm (Fig. 8). Although the average concentrations of zooplankton biomass were

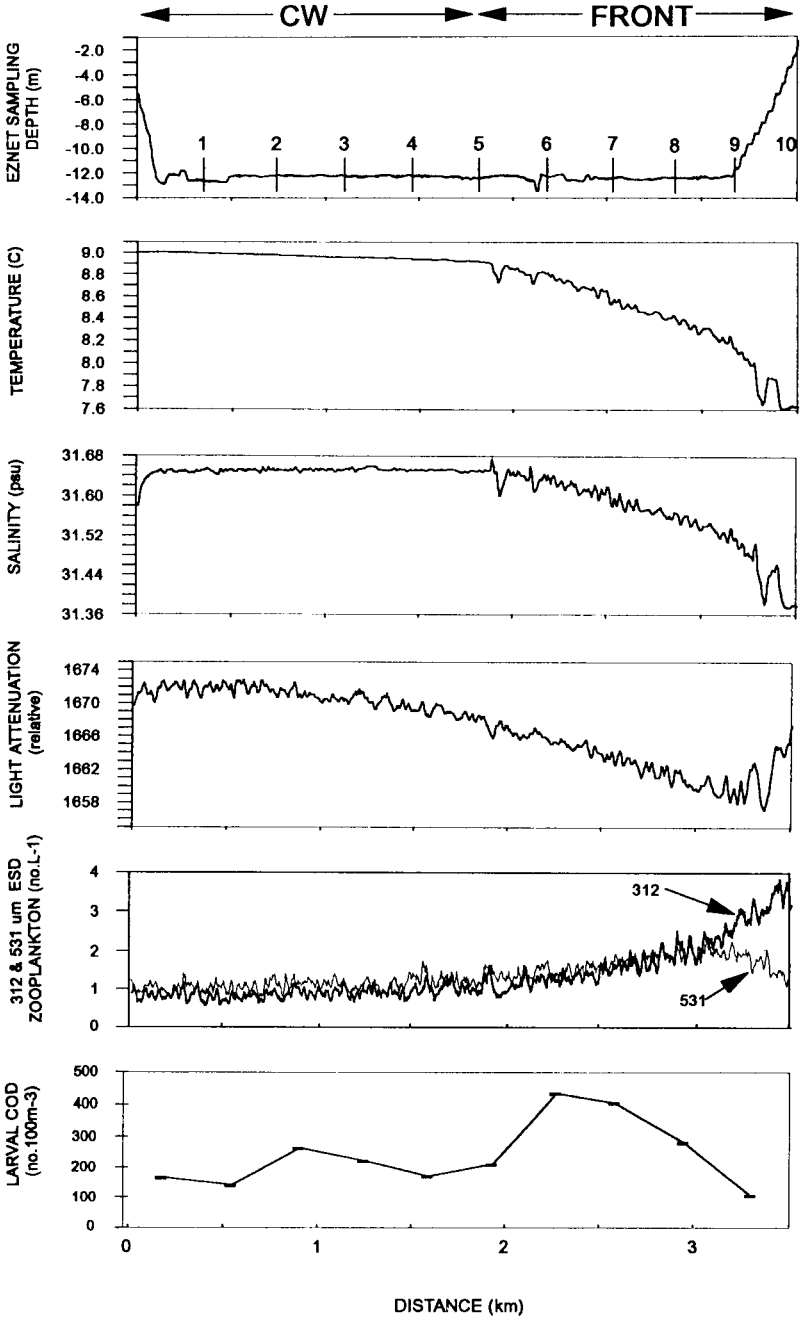

Figure 6. (a) Sampling depth (m), (b) Temperature (°C), (c) Salinity (psu), (d) OPC light attenuation (relative), (e) OPC 312 and 531 μm ESD zooplankton concentration (particies · L^{-1}), and (f) Larval cod concentration (larvae · 100 m^{-3}) derived from the EZNET frontal transect towed at a fixed depth and normal to the front on Western Bank (see Fig. lb for location). Larval cod concentrations are reported at the mid-point of each sequential net-tow. Net number and closures are noted by vertical lines on the depth profile in (a).

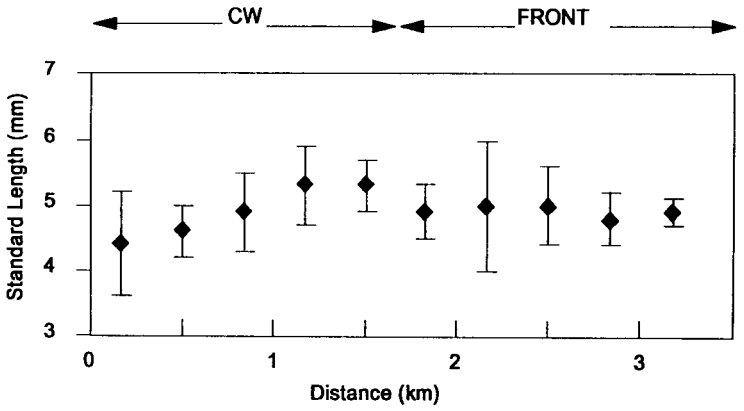

Figure 7. Average (± 2 Std errors) standard length (mm) of cod larvae collected in different nets during the EZNET frontal transect normal to the front (see Fig. 6).

Table 1. Average (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 to 3 December 1992 on Western Bank. Means underlined together are not significantly different (α = .05) according to Duncans Multiple Range test. Subscripts indicate the sample size (number of deployments or larvae) for each location and characteristic.

Characteristic	Location		
	CW	Front	CFW
Larval cod concentration (no · 100 m^{-3})	52 $(33)_{42}$	174 $(40)_{10}$	9 $(12)_{11}$
Zooplankton wet biomass (g · m^{-3})	0.22 $(0.11)_{42}$	0.29 $(0.12)_{10}$	0.12 $(0.13)_{11}$
Standard length (mm)	4.75 $(0.95)_{794}$	4.86 $(0.84)_{294}$	4.01 $(0.56)_{9}$

higher in the frontal region than in the CW, the differences were not significant (Table 1). Concentrations of smaller zooplankton particles of geometric mean size of 312 µm 420 µm 531 µm ESD (size ranges of 266-312, 371-468, and 480-513 µm ESD respectively) all revealed a temporal increase (approximate doubling) within the CW during the first 10 days of sampling the CW (Fig. 8) and approached concentrations similar to those measured in the frontal region (Fig. 6). The concentrations within, the CW were not significantly different after the storm from concentrations measured just before the storm (Fig. 8).

As the goal of the study was to monitor a unique group of larvae, only larvae and samples from the tracked CW mass were considered in further analyses.

Daily length frequency histograms indicated continuous production of cod larvae in the CW during the study. To assess the temporal evolution of a single cohort within the tracked CW, we considered only larvae hatched during a specific time period. Larvae that were, on the basis of the age-length relationship, less than 5 days old on 25 November were retained for analysis. This 'hatch window' was stepped through time, such that larvae collected on 26 November were retained if they were at least 1 day and no more than 6 days old. We used this conservative approach to minimize bias in our analysis of changes in larval concentration for the cohort through time. Preliminary analyses of ages based on otolith increments for these larvae suggest that variance of average length at a specific age increased with age. The length range for 17-23 day old larvae was approximately 1 mm wider than the

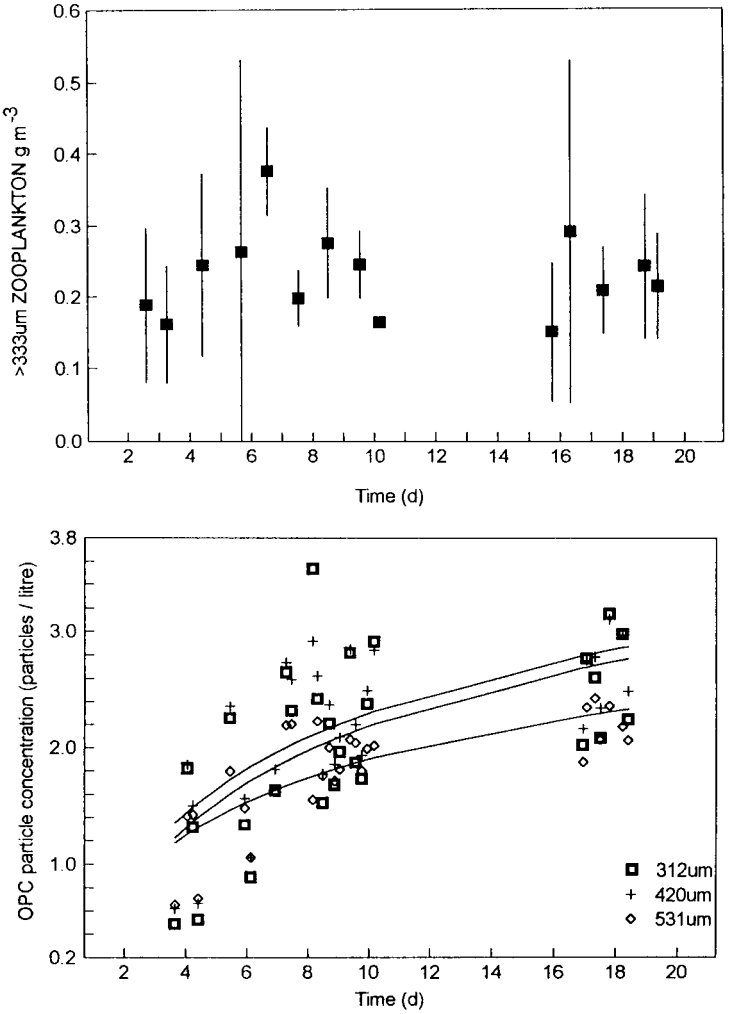

Figure 8. Time series of (a) daily average (± 2 one standard deviation) estimates of > 333 μm size zooplankton wet biomass (g m^{-3}); and (b) set-by-set estimates of zooplankton particle concentrations of different size classes as measured by the Optical Plankton Counter (OPC) in the tracked crest water (CW) on Western Bank.

length range based on our 'hatch window' and the age-length relationship used here (T. Miller, Chesapeake Biological Laboratory, P.O. Box 38, Solomons, Maryland 20688). For this reason, we have confidence in our analyses.

Sample concentration estimates were adjusted according to the proportion of larvae from a sample which belonged to the previously defined cohort (proportion of sample from the cohort × sample concentration = cohort concentration). Larval cod concentrations generally decreased through time and we estimated an instantaneous loss rate (z) of 0.24 using regression analysis on all set concentrations through time (Proc GLM, SAS 1989, $r^2 = 0.50$) and assuming that loss followed the exponential decay function:

$$N_t = N_o e^{-zt} \tag{1}$$

where N_t is the abundance at time t and N_o is the initial abundance. The variability in concentration estimates was considerable (Fig. 9), so to further examine the loss rate

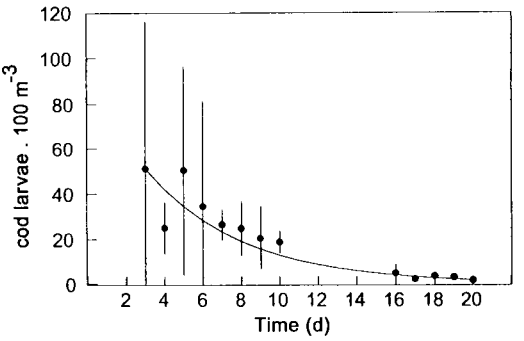

Figure 9. Average (± 2 SE) observed cohort concentration of cod larvae in the tracked crest water (CW) on Western Bank and the exponential decay (mortality) curve fitted to the mean concentration through time ($z = 0.2$).

we determined the daily median and daily mean larval concentration to estimate z. A regression of the daily median concentration against time showed a similar loss rate of 0.24 ($r^2 = 0.7$), and the daily mean showed a somewhat lower rate of $z = 0.2$; $r^2 = 0.9$ (Fig. 9).

4 DISCUSSION

To our knowledge, this is the first time that a data assimilative hydrodynamic model has been used in real-time to guide the biological sampling effort during the study of a larval fish cohort within its advective environment. Previously, drifters were used to mark water masses and patches of larvae. If the patch was large enough, drifters remained within the patch for reasonable lengths of time. However, when the patch was small relative to the difference in drift between larval fish and drogued drifters, contact would be lost in a few hours or days. If an Eularian approach was adopted, samples were collected on relatively large spatial scales in order to ensure that the moving patch remained within the sampled area. This resulted in the expenditure of considerable effort in areas of low interest. The model predictions of future positions of past and present sampling locations allowed us to focus our attention where sampling was most effective and eliminate the bias of relying purely on drifter positions to predict patch location. The benefit of sampling with the aid of a hydrodynamic model was illustrated by our ability to accurately predict the location of a remnant of the original larval patch despite a 5 day sampling hiatus due to inclement weather. A survey of the crest region following the storm showed that although there were other local larval concentration maxima, only the position where the model predicted the patch was, had water properties (SST, salinity) and larval concentrations consistent with previous observations within the patch (Griffin & Thompson 1995). Sorting, identification, and data entry at sea allowed preliminary analyses which also guided sampling efforts. An example of this feedback loop was the observation of increased concentrations of larvae (3-4 times) in certain samples. The combination of those observations with physical properties of the water at those stations, and model predictions of past, present and future locations of those stations revealed a thermohaline front bounding the tracked water parcel (Lochmann et al. 1995). We used this opportunity to conduct some simple investigations of frontal features.

This study was not designed to examine the effects of storms on survival of larval cod. Nevertheless, there is no evidence to suggest that concentrations of the zooplankton (large and small) prey field of the cod larvae decreased during the storm. It is clear that prior to the storm concentrations of smaller zooplankton increased with time. The loss rate of larvae from the CW displayed a classic exponential decay typically observed in most larval fish studies, although the fitted relationship (Fig. 9) indicates that there was a higher than expected loss (mortality) of larvae during the storm period, as shown by the majority of positive residuals in the daily averaged larval concentrations prior to the storm period (days 5, 6, 7, 8, 9 and 10).

Cod larvae, zooplankton wet biomass, and zooplankton (312, 420, and 531 μm ESD) were most concentrated in a narrow frontal region between the well-mixed CW that we tracked and the stratified CFW near the crest of Western Bank. One explanation for these differences may be related to differential mortality (i.e. higher concentrations of cod larvae were found at the front because larvae elsewhere were dying at a faster rate). McLaren and Avendano (1995) showed that 3-6 mm cod larvae on Western Bank fed on particles ranging from 80 to 480 μm ESD. Although the mesh size of the plankton nets (333 μm) and the lower limit of the resolution of the OPC (250 μm) do not cover this entire range, the 266-357 μm size class (geometric mean 312 μm) certainly was a measure of larval cod food. The elevated levels of plankton in this size class at the front are consistent with resident larvae being provided with a relatively enhanced prey field and thus a better potential for survival. Analyses of the SL of larvae within the CW and within the frontal region showed no differences, and thus no indication of enhanced growth within the front. A complementary study shows no evidence that larvae in the frontal region were in better biochemical condition than larvae in CW (Lochmann et al. 1995).

The observed absence of larger (older) individuals in CFW may have resulted simply from the sampling effort relative to the low concentrations. When sampling a fixed volume, size groups present at low concentrations will have a lower probability of being collected. Our sampling effort was focused on CW so few samples were collected from CFW. Alternatively, larger (older) larvae may have been advected out of the study region by subtidal flow to the west and north of the Bank (Griffin & Thompson 1995).

An alternative explanation for the elevated concentrations of larvae and zooplankton at the front is a purely physical one – convergence. This process would concentrate buoyant zooplankton and larval cod at the front, which was, based on drifter trajectories, convergent (Lochmann et al. 1995). Simple approximations suggest that an individual larva might reside at the front for a period of 2-2.5 days before it is swept back into the interior CW or lost to the exterior CFW and advected away (Lochmann et al. 1995). The relatively short estimated residence time and the similarity of larvae from CW and the frontal region implies frequent exchange between the two locations. The CW and the frontal region had higher levels of zooplankton than CFW. Larvae entrained into the frontal region from CFW, and recirculated within this semi-closed system (CW and the frontal region), may benefit in the long term through retention at the crest where the prey field appears to be beneficial to larvae (McLaren & Avendano 1995).

Our observations are consistent with the observations of O'Boyle et al. (1984), who proposed that a permanent clockwise gyre situated over the western crest of

Browns Bank acted to retain larvae. Suthers & Frank (1989) further suggested that variability in the integrity of the Browns Bank gyre determined the interannual distribution of later stages of cod larvae. Furthermore, the geographic location of the feature we describe is consistent with the location of maxima in egg and larval concentrations described by O'Boyle et al. (1984) and Brander & Hurley (1992) for Western Bank.

The importance of gyre-like water masses and their associated frontal features which allow early stage fish to remain on or near banks has been discussed in detail by Iles and Sinclair (1982), and although simple observations of the concentration field are insufficient to distinguish between physically driven retention and differential mortality, our observations clearly suggest it is physically driven retention that is responsible for the high concentrations of cod larvae within a relatively small area on the crest of the Bank.

The member/vagrant hypothesis (Sinclair 1988) suggests that a marine fish population can lose members through geographic displacement from a distributional area. The semi-closed system and convergent front we describe appears to have important life history consequences for cod. Inter-annual variability in the integrity of the frontal system and the associated gyre-like feature may account for some of the recruitment variability observed in Western Bank cod.

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