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Larval fish, zooplankton community structure, and physical dynamics at a tidal front

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Physical, chemical, and biological measurements at the Akpatok Shallows, Ungava Bay, Québec, in September 1985 confirmed the existence of a front predicted earlier from the Simpson–Hunter h/u^3 stratification parameter. Temperature, salinity, and nutrient data indicated a combination of tidal advection, upwelling and mixing at the front. Nitrate concentrations of ~5 µg at l^{-1} were found in the deeper stratified water near the front. Chlorophyll *a* concentrations of ~4 µg l^{-1} occurred on the stratified side of the front. The macro-zooplankton community was horizontally delineated by the extent of vertical stratification. Jellyfish, *Limacina* spp. and *Clione* spp. were concentrated at the front in contrast to amphipods, mysids, and euphausiids which were concentrated in the stratified water, and decapod larvae in the mixed water. Chaetognaths and larval fish showed similar distributions on either side of the front, but were rare at the front. The spatial distributions of the major larval fish taxa were either consistent with (Cottidae) or contrary to (Cyclopteridae) the retention hypothesis. Distributions of cyclopterid and gadoid larval sizes illustrated enhanced survival and/or growth on the stratified side of the front.

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Introduction

A prevailing hypothesis in fisheries research is that population fluctuations are directly related to early life history processes. Several studies have demonstrated that variation in recruitment of marine stocks is correlated with abiotic factors, primarily water mass dynamics that influence early-life history (Chadwick *et al.*, 1977; Leggett, 1977; Nelson *et al.*, 1977; Bakun and Parish, 1980; Bailey, 1981; Leggett *et al.*, 1984; Crecco and Savoy, 1984; Sinclair *et al.*, 1985; Peterman and Bradford, 1987). These findings are consistent with the saltatory development of most fish larvae and imply critical thresholds (Balon, 1984). Various hypotheses, directly related to Hjort (1914, 1926), have proven difficult to address because of insufficient sampling at appropriate time and space scales, logistical restrictions, and the masking effect of physical processes on population dynamics (Taggart and Leggett, 1987a, b, c). Defining the interrelationships of biological and physical variables is fundamental to making significant advances in the study of fish population dynamics (Rothschild, 1981, 1986).

Coastal and shallow-sea fronts occurring between stratified and mixed water offer advantages over open marine systems for testing various early life history hypotheses. Fronts are generated by physical processes (Bowman, 1978) and are characterized by sharp horizontal discontinuities in temperature and/or salinity, and by distinct productivity levels and floral and faunal aggregations (Pingree, 1978; Pingree *et al.*, 1975; Pingree and Griffiths, 1978; Bowman, 1978; Bowman and Esaias, 1978; Simpson *et al.*, 1978, 1979; Fournier *et al.*, 1979, 1984; Allen *et al.*, 1980; Fiedler, 1983; de Lafontaine *et al.*, 1984; Parsons *et al.*, 1984; Richardson, 1985; Sakamoto and Tanaka, 1986).

Tidal fronts are ideal for studying the influence of physical processes on zooplankton community structure and larval fish populations as their locations are predictable (Simpson and Hunter, 1974), they afford replicate sampling with relatively simple logistics (e.g. Munk *et al.*, 1986; Richardson *et al.*, 1986a, b), and they have been hypothesized to influence larval survival and recruitment (Iles and Sinclair, 1982).

As part of a larger comparative study of relationships between physical dynamics and community structure at a number of tidal, coastal, and shelf-break fronts recently examined in the NW Atlantic, we report on the initial results of a study at a tidal front in Ungava Bay (Canada) in September 1985. Our overall objective is to test the hypotheses that: (a) the scale-dependent distribution and abundance of local zooplankton populations are predictable from the physical characteristics of the local water masses, and corollary (b) the distribution, growth, and mortality of local fish larvae are also predictable from the physical structure as mediated through the dynamics of the zooplankton populations.

Methods and materials

Study area

Ungava Bay is a large embayment bounded by the eastern Hudson Strait and northern Québec (Fig. 1). The bathymetry consists of a submerged plateau (<150 m deep) cut by a channel (200–400 m deep) extending southwest from northern Labrador and curving north and west of Akpatok Island. The plateau east and south of this island is the Akpatok Shallows. The region experiences strong tides with 3 to 4 m elevations and 0.5 to 1 m s^{-1} currents.

The location of tidal fronts within the bay were predicted by Griffiths *et al.* (1981) from a numerical model of the M_2 tides and the Simpson and Hunter (1974)

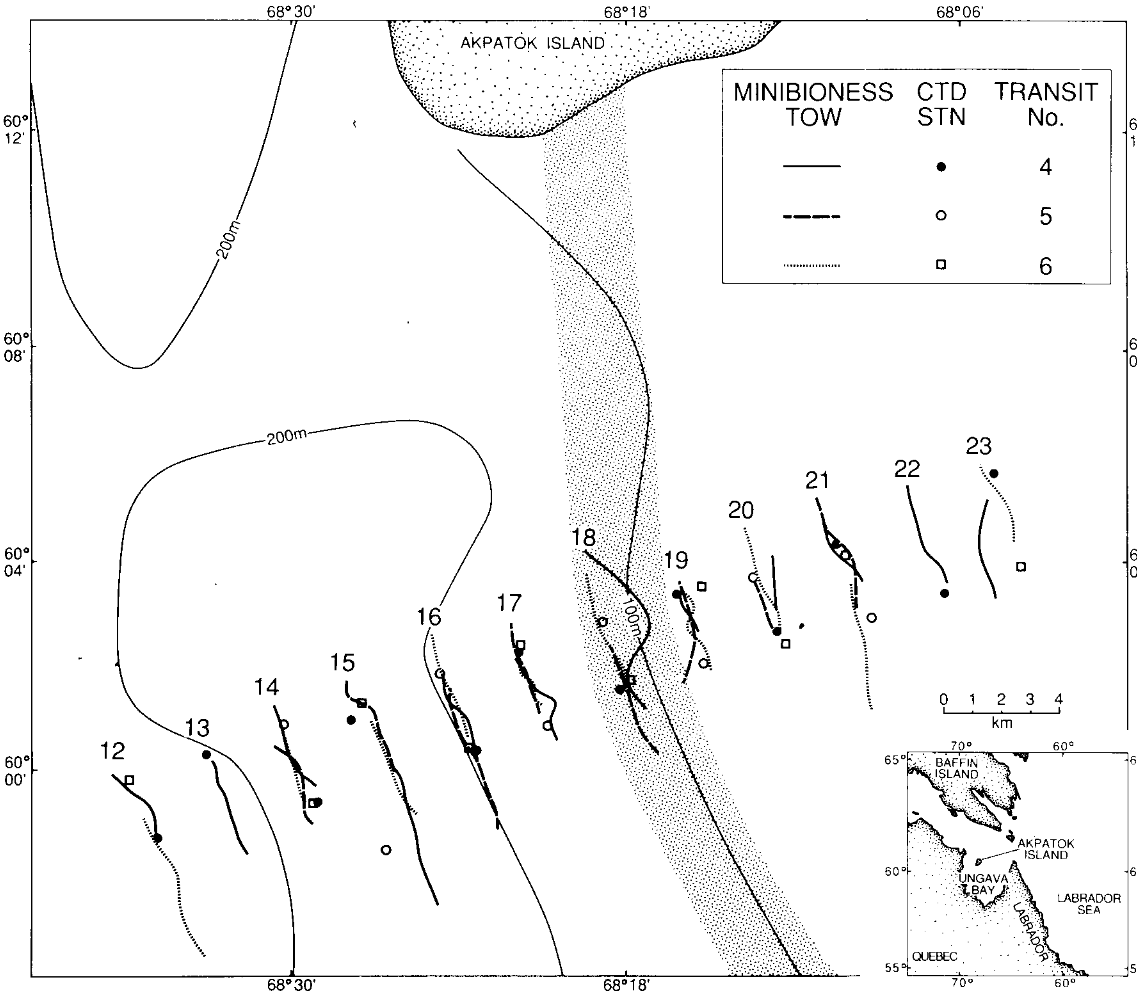

Figure 1. Bathymetric chart showing the location of Ungava Bay (inset) and the location of CTD and bottle sampling stations and miniBIONESS tow paths (stations 12 to 23) on Transits 4 to 6 between the eastern Akpatok Shallows (<100 m) and the western deep channel (>200 m). The stippled area is the frontal region predicted by the h/u^3 stratification parameter.

h/u^3 stratification parameter. Similar predictions for the Hudson Strait area (Griffiths *et al.*, 1981) were later confirmed (Drinkwater and Jones, 1987), but no data were available prior to our study to evaluate the predictions for Ungava Bay. Our study was located across a steep bathymetric gradient 20 km south of Akpatok Island where a front between mixed water on the shallows and stratified water in the deep channel was predicted to occur (Fig. 1).

Sampling

On 18–19 September, 1985, we collected vertical temperature and salinity profiles at a series of stations along a transect extending from the shallows to the deep channel (Fig. 1) using a Guildline digital conductivity, temperature, depth sensor (CTD) mounted on a Niskin bottle sampling rosette. The presence of a front was confirmed and two additional CTD transits were made to assess the extent and short-term variability of the frontal region. On 19–21 September, a series of three additional transits (4, 5, 6; Fig. 1) were sampled using a small scale version (miniBIONESS) of the Bedford Institute of Oceanography Net and Environmental Sampling System (Sameoto *et al.*, 1980). This multiple opening and closing net sampler was fitted with seven 0.25 m^2 area nets, an Extended Applied Microsystems CTD–12, two (internal and external) Tsurumi–Seiki digital TSK flowmeters, digital pitch and roll sensors (see Frank (1986) for details), and was towed at ~ 1 m s^{-1}. Internal and external flowmeter and pitch data provided volume and filtering efficiencies used to correct abundance estimates. Prior to each miniBIONESS tow a CTD profile was made and Niskin bottle samples were drawn from every second cast for nitrate, phosphate, silicate, and chlorophyll *a* analyses. Ten samples were taken at each station at representative depths throughout the water column.

MiniBIONESS tows ($\sim$4.5 km in length and at $\sim$3 km intervals) were made parallel to the front to reduce smearing of any cross-frontal pattern (Fig. 1). The sampling transect comprised a total of 12 stations (numbered 12 to 23). A total of 30 station tows were made as not all stations were occupied on each transit. Over the shallows (Stn. 19–23) the water column was sampled in three 15 m depth strata between 0 and 45 m (on descent with 333 μm-mesh nets and on ascent with 80 μm-mesh nets). In the transition zone (Stn. 16–18) four 15 m strata were sampled between 0 and 60 m (on descent using 333 μm-mesh nets and on ascent the upper three strata were sampled with the 80 μm-mesh nets). Over the deep region (Stn. 12–15) five 15 m strata between 0 and 75 m were sampled (on descent with 333 μm-mesh nets followed by a 75 to 45 m depth integrated stratum with a 333 μm–mesh net, and finally with one 80 μm-mesh net through the 45 to 0 m depth stratum). Each net was towed for a 5 to 7 min period.

After completing the first seven stations on Transit 4, and while on Station 16, the 80 μm-mesh nets were destroyed. Subsequently a single 80 μm-mesh net was used to sample the 0 to 45 m depth stratum at all stations and six 333 μm-mesh nets were used in a manner similar to that outlined above.

At the end of each tow the nets were thoroughly rinsed and the codend contents were preserved in 4% formalin buffered with sodium borate. In the laboratory each sample was sorted for fish larvae and macro-zooplankton. Fish larvae were removed, enumerated, measured, and identified. Macro-zooplankton were enumerated and identified to taxa (chaetognaths, amphipods, jellyfish, euphausiids, decapods, mysids, ctenophores, *Limacina* spp., and *Clione* spp.). The remainder of samples collected with the 80 μm-mesh nets were filtered through a 1050 μm-mesh screen and the filtrate was enumerated in fifteen equivalent spherical diameter (esd) size classes (64, 80, 101, 128, 161, 203, 256, 322, 406, 512, 645, 812, 1024 μm average esd) with a Coulter Counter TA–II (Taggart and Leggett, 1987a). Volume and depth weighted biomass estimates were calculated from the particle size class data by assuming a density of 1 g cm^{-3}. Abundance estimates for all macro-zooplankton taxa were expressed as number per unit volume and density distributions were objectively calculated using the Kriging method (see Ripley, 1981) with minimal smoothing (5%) in the Golden Graphics System (Golden Software Inc., Golden, CO).

Results

Physical characteristics

A front was observed separating mixed water over the Akpatok Shallows from stratified water in the deep channel (Fig. 2). The stratified water consisted of a shallow (10 to 20 m deep) surface layer, a pycnocline region (20 to 60 m), and a bottom layer of weaker vertical gradients. Temperature in the stratified water varied from -1 to 1°C with the majority of the water <0°C. Salinity ranged from 31.4 to 32.5. Water over the shallows was relatively warm (>1°C) and less saline (<31.4). Density (σ_t) differences were primarily due to salinity at the low temperatures observed.

The horizontal gradient of vertical density differences between the surface (10 m) and near-bottom showed the front to be consistently located between Stations 15 and 18 (Fig. 3). Consequently the front overlay the break in topography between the ledge at 130 m and the deep channel (Fig. 2). Vertical density differences calculated to a fixed depth of 60 m showed the same pattern as shown in Figure 3.

The general characteristics of the front were similar for all transits, but some variability was observed. For example, the σ_t surfaces in the vicinity of Stations 17

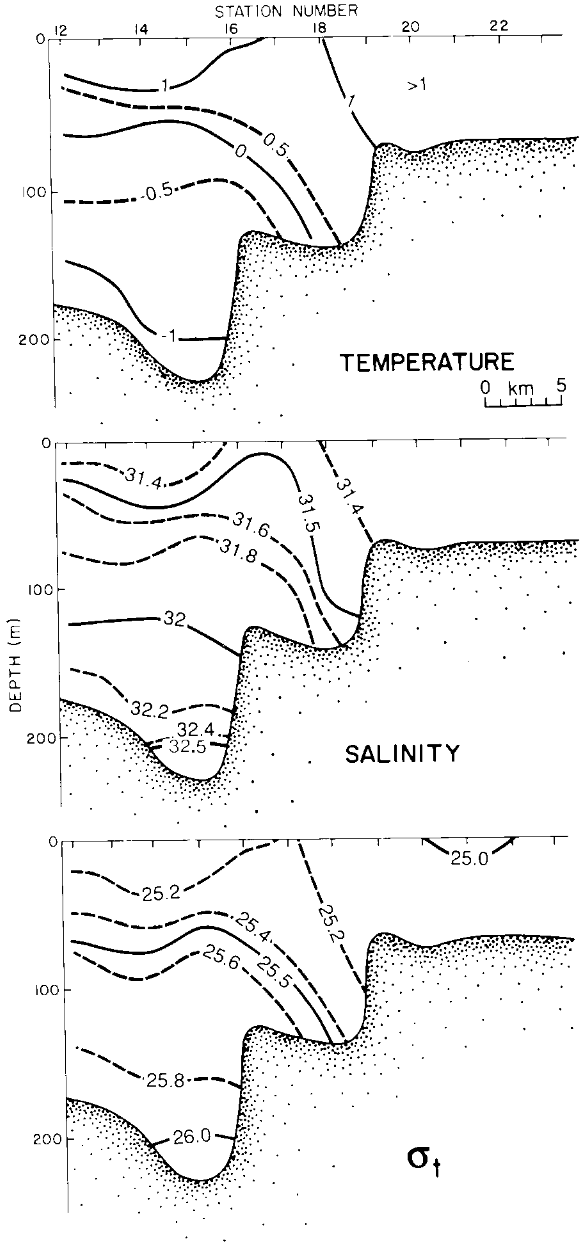

Figure 2. Temperature (°C), salinity, and density (σ_t) isopleths from CTD Transit 4. Horizontal gradients of marked vertical changes separate stratified water (Stn. 12–15) from mixed water (Stn. 19–23).

and 18 (notably 25.4 and 25.6) on Transit 5 were steeper relative to Transit 4 (Fig. 4). Furthermore, between Transits 5 and 6 the 25.2 σ_t surface was displaced eastward. We suggest that these changes were primarily associated with tidal advection. Stations 16 through 18 on Transits 4 and 5 were occupied during ebbing and flooding tides, respectively. The occupation of stations over the shallows on Transit 6 occurred near low water when the higher density water (25.2 to 25.6 σ_t) over

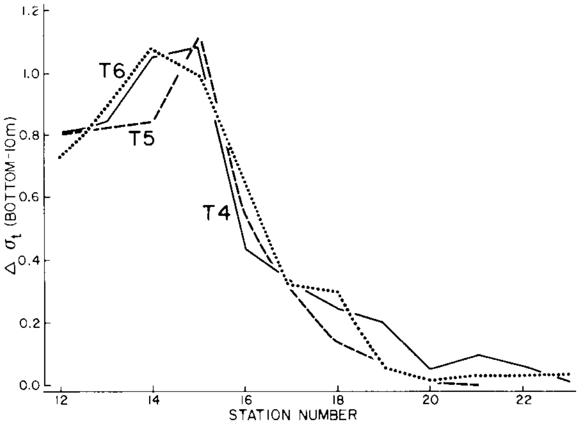

Figure 3. Horizontal gradient of vertical density differences ($\Delta\sigma_t$) between the surface and 10 m above bottom during Transits 4, 5, and 6. The front (largest gradient) occurs between Stations 15 and 17.

the topographic step would be expected to be at its maximum eastward extent (in Ungava Bay the tide resembles a standing wave such that slack tide occurs near the time of high and low water). In the frontal region (Stn. 16) and on the topographic step (Stn. 18) the degree of stratification, as measured by the difference in σ_t between the surface and 100 m, increased toward the time of low water providing further evidence of tidal advection. Nevertheless, tidal advection did not significantly displace the location of the front (Fig. 3).

The low density surface water on either side of the front, the shallowing of the isopycnals from the deep side toward the front, and well-mixed water over the shallows are features consistent with those of the classical mixing/upwelling front (Pingree *et al.*, 1978).

Nutrients and chlorophyll distribution

Nitrate concentrations in the mixed water showed a vertically uniform distribution between 1 and 2 μg at l^{-1} in contrast to the stratified water where nitrates in the surface layer were low ($\sim$1 μg at l^{-1}), and increased with depth to a maximum of $\sim$8 μg at l^{-1} (Fig. 5). Nitrate isopleths shallowed in the frontal region in a manner consistent with the isopycnals and provided further evidence of upwelling and cross-isobath advection. Silicate (1 to 21 μg at l^{-1}) and phosphate (0.4 to 1.6 μg at l^{-1}) concentrations showed similar patterns to those of nitrates. Chlorophyll *a* concentrations (2 to 4 μg l^{-1}) were maximum near the base of the surface mixed layer on the stratified side of the front (Fig. 6). Concentrations were typically 1 to 2 μg l^{-1} in the mixed water, and in the deeper water the concentrations were consistently <1 μg l^{-1}.

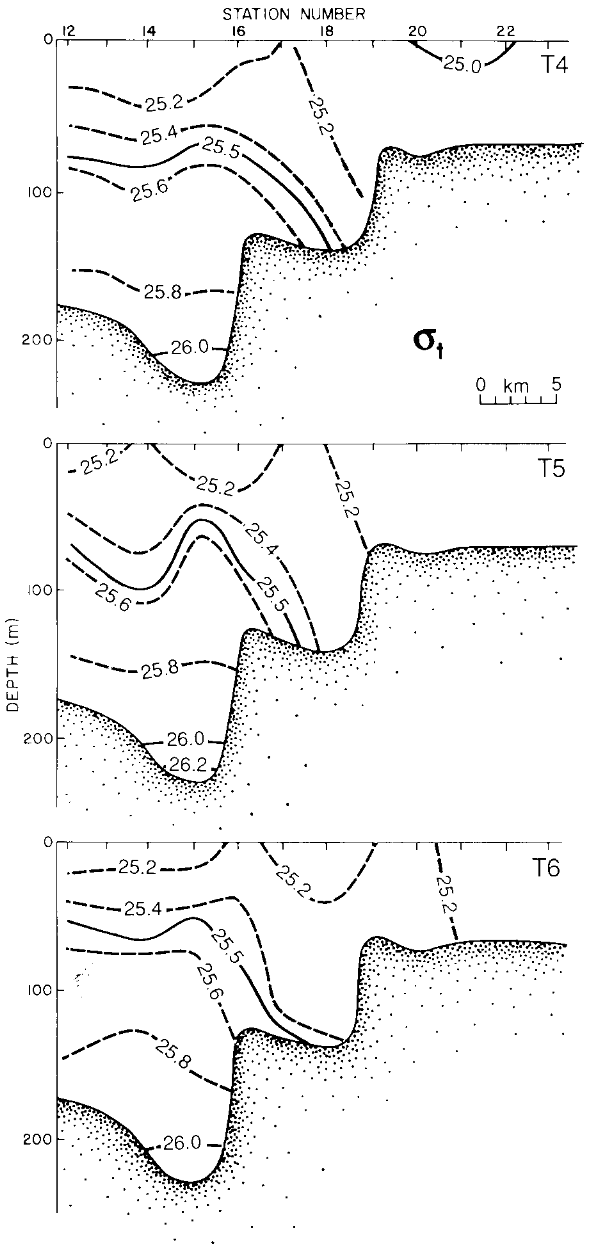

Figure 4. Evolution of cross-sectional σ_t surfaces from Transit 4 through Transit 6 at the Akpatok Shallows frontal region.

Meso-zooplankton distribution

The distribution of the meso-zooplankton biomass was primarily influenced by the distribution of the meso-zooplankton size classes in association with the frontal-region water masses. On all transits the largest size classes (512 to 1024 μm esd) dominated near the front and the smaller size classes (64 to 101 and 128 to 203 μm esd) dominated in the stratified water (Fig. 7). This resulted in the proportional distribution (arcsin square root transform) of the largest and smallest size classes being significantly and inversely correlated ($r = -0.82$; $p < 0.05$) across the region. The size-class distribution in the mixed water was variable among transits, although on Transit 6 the largest size class was dominant on the mixed side of the front.

Macro-zooplankton distribution

As with the meso-zooplankton biomass, the macro-zooplankton community structure was well defined by

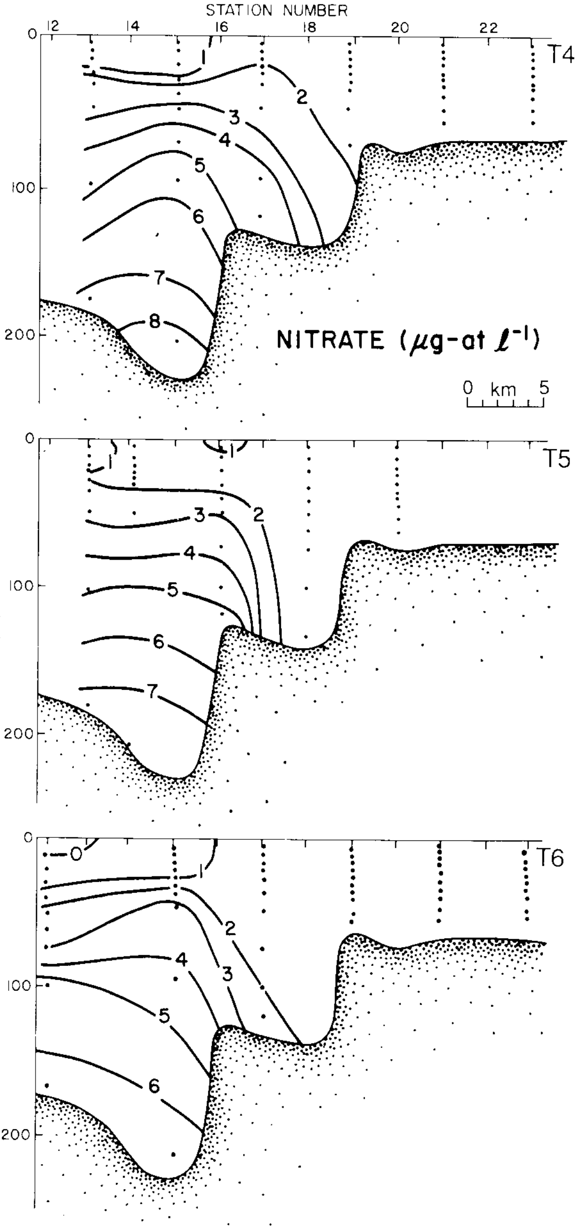

Figure 5. Isopleths of nitrate concentrations (μg-at l^{-1}) at the Akpatok Shallows frontal region on Transits 4, 5 and 6. Depths of bottle samples are noted (●).

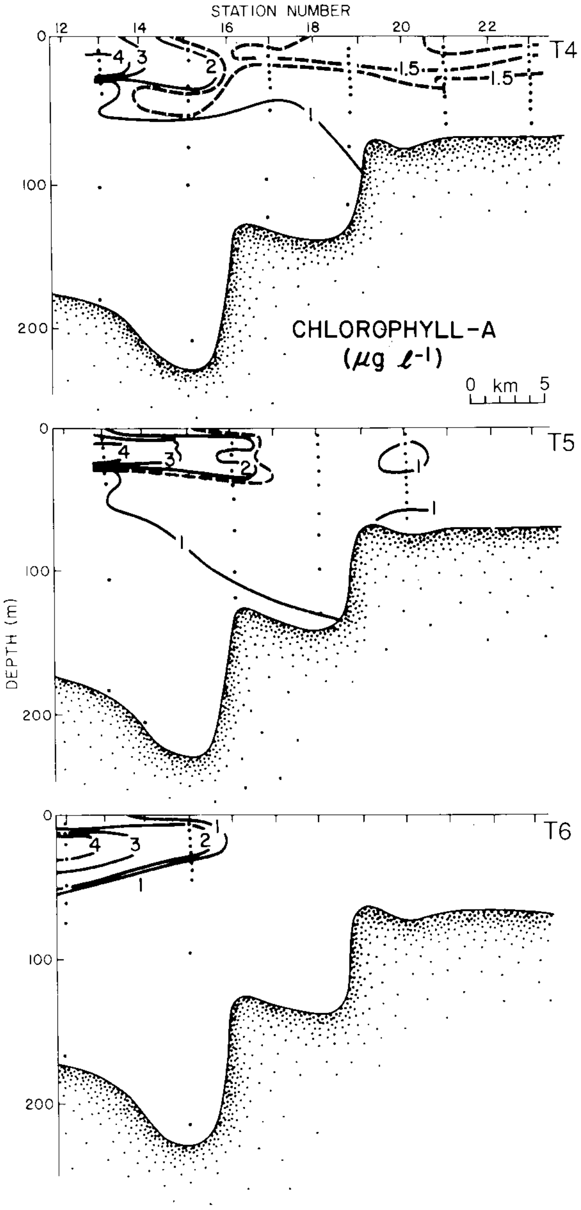

Figure 6. Isopleths of chlorophyll *a* concentrations ($\mu g\ l^{-1}$) at the Akpatok Shallows frontal region on Transits 4, 5, and 6. Depths of bottle samples are noted (●). No data were available for Stations 17–23 on Transit 6.

the physical structure of the regional water masses. Amphipods, one of the more abundant taxa, were concentrated in the stratified water (Fig. 8a). This pattern was apparent for all three transits. The distributions of the less abundant mysiid and euphausiid taxa were virtually the same. In contrast, decapod larvae were primarily limited to the mixed water (Fig. 8b). There were few decapods in the stratified water, and they were virtually absent from the front. This distributional pattern was similar from Transits 5 and 6, though the areas of high concentration were closer to the front (Stn. 20, Transit 5; Stn. 18, Transit 6). None of the other macro-zooplankton taxa showed similar distributional patterns.

Jellyfish were strongly aggregated at the front (Fig.

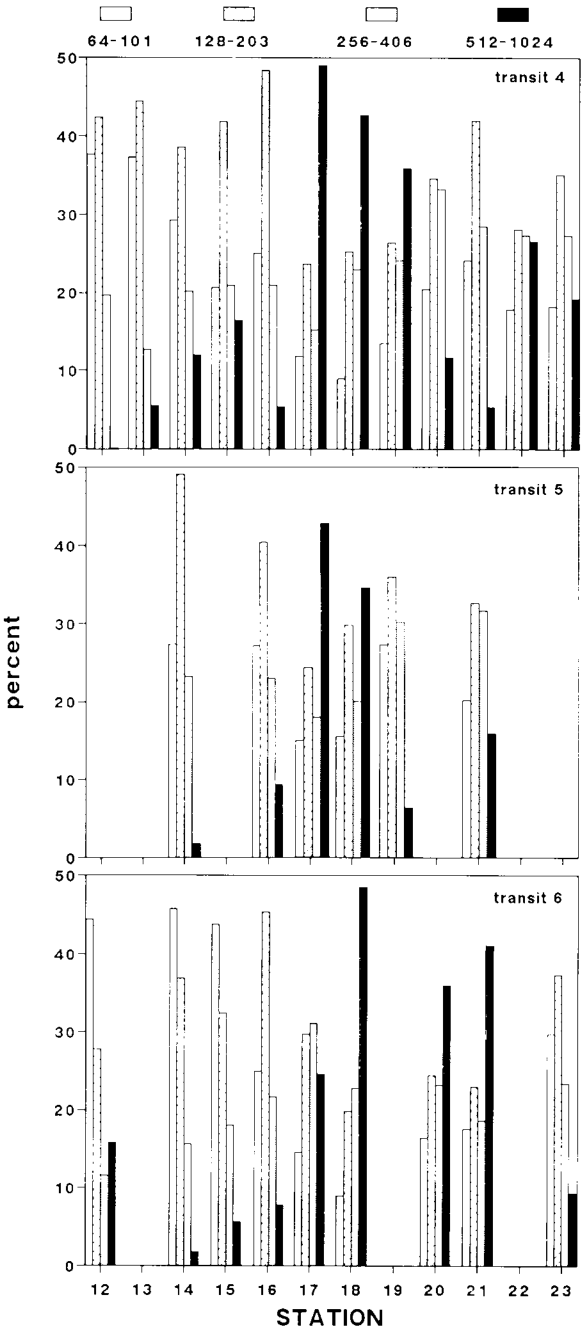

Figure 7. Percentage distribution of meso-zooplankton biomass by size classes (64–101, 128–203, 256–406, and 512–1024 µm esd) as a function of geographic position for each of Transits 4, 5, and 6 across the Akpatok Shallows frontal region.

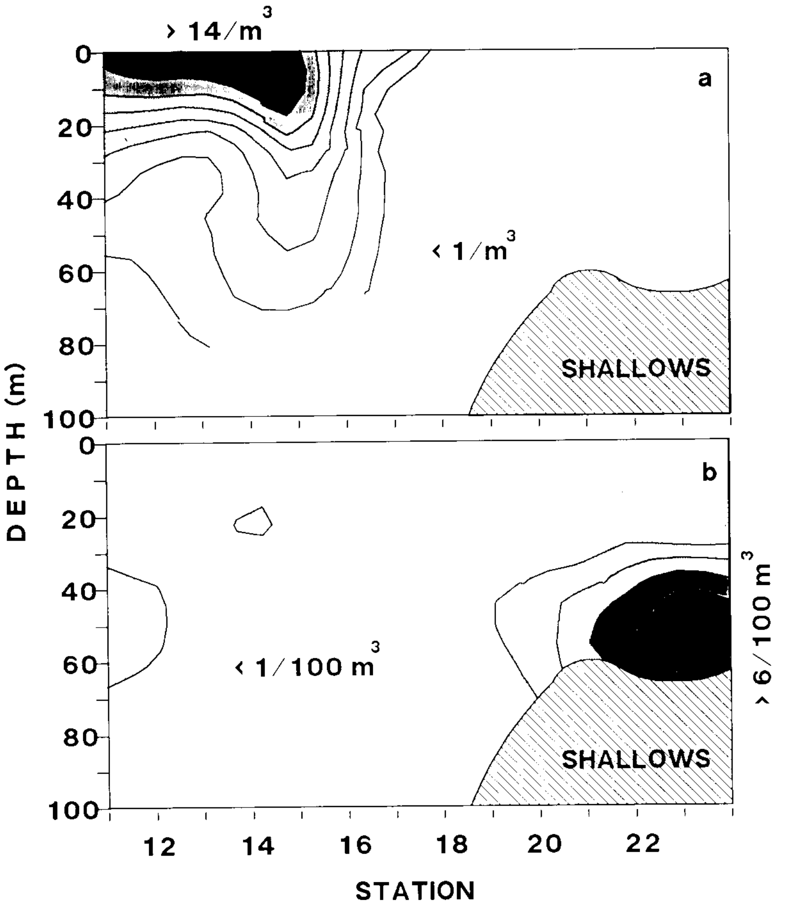

Figure 8. Representative concentration isopleths of (a) amphipods (>1050 μm) from Transit 6, and (b) decapods (>1050 μm) from Transit 4 at the Akpatok Shallows frontal region in September 1985.

9a). Although the horizontal distribution of *Limacina* sp. and *Clione* sp. (not illustrated) showed a very similar pattern to that of the jellyfish in their horizontal distribution among all three transits, the vertical distribution of these taxa showed higher concentrations at greater depths on Transits 5 and 6.

Chaetognaths were the most abundant taxa ($>1\ m^{-3}$ at 40 to 60 m in mixed and stratified water) but their distribution was not as clear as that shown by the other taxa. Chaetognaths were sparse near the front (0.15 to $0.5\ m^{-3}$) on all three transits, but the limits were not as distinct as with the other taxa.

Larval fish distribution

A total of 368 larval fish were captured during the study and provided an overall average abundance of ~2 larvae $100\ m^{-3}$. Sculpins (Cottidae) and lumpfish (Cyclopteridae) dominated the larval fish community (40% and 37%, respectively; Table 1). The remainder of the community was represented by shannies and blennies (Stichaeidae 10%), alligator fish and sea poachers (Agonidae 5%), cod (Gadidae 4%), and northern sandlance (*Ammodytes dubius* 4%).

The larval fish community appeared to be less influenced by regional water mass structure than did the other zooplankton taxa. Larval abundance on Transit 6 near the front was low and their vertical distribution was restricted (Fig. 9b). Larvae were more abundant in the mixed and in the stratified water and their vertical distribution was less restricted. Distributions on Transits 4 and 5 were similar with the lowest concentrations (0.01 to $0.015\ m^{-3}$) consistently observed at the front. However, in both Transits 4 and 5 the high concentrations over the shallows (Fig. 9b) were further west and closer to the front.

Separating the larval fish community into its family parts revealed distributions that were more complex than the composite illustrated in Figure 9b. Sculpin larvae averaged 22.2 mm total length (TL); their length frequency distribution was skewed toward larger individuals (Table 1), and the taxon was virtually absent from the front and from the stratified water (Fig. 10a). The apparent increase in the lengths of larval sculpin from mixed to stratified water was not significant ($p = 0.64$; length data normalized with log transform). In contrast, lumpfish larvae averaged 24.6 mm TL, showed a broader size frequency distribution that was skewed

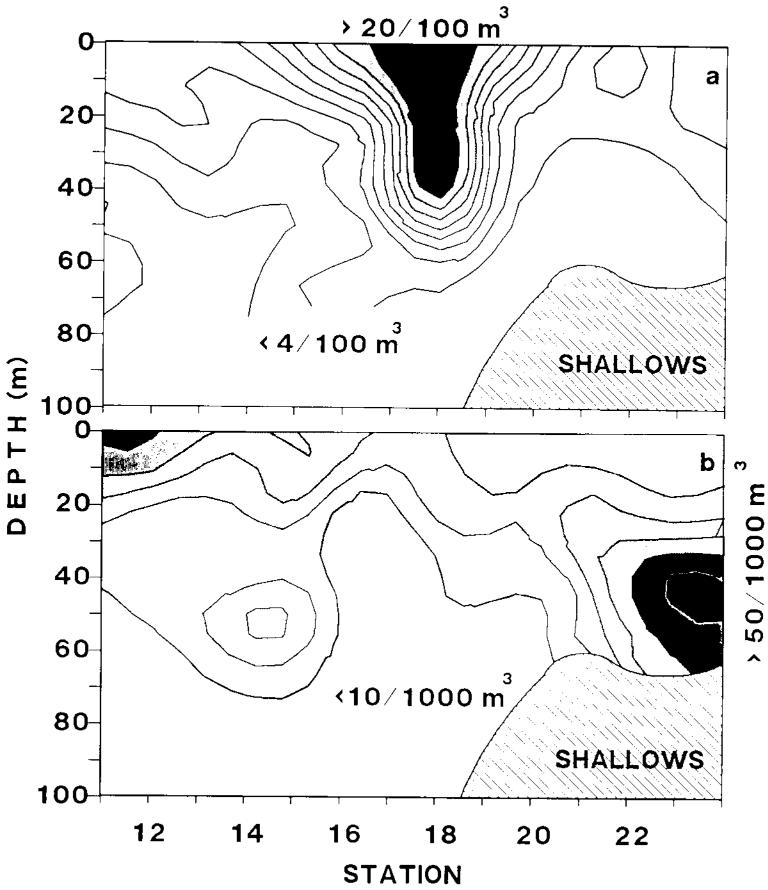

Figure 9. Representative concentration isopleths of (a) jellyfish (>1050 μm) from Transit 4, and (b) larval fish from Transit 6 at the Akpatok Shallows frontal region in September 1985.

toward smaller individuals (Table 1), and were found throughout the region (Fig. 10b). The increase in length (arithmetic and log transformed) of lumpfish larvae across the front into stratified water was highly significant ($p < 0.0001$). The less abundant stichaeid larvae averaged 29.5 mm TL with a relatively narrow length frequency distribution (Table 1), and there was no significant relationship between length and their occurrence in the regional water masses ($p = 0.32$). However, stichaeids were virtually absent from the front (Stn. 16, 17; Fig. 10c). Cod larvae were rare (14 *Gadus morhua* and 2 *G. ogac*), averaged 37.5 mm TL (Table 1), and despite their rarity showed a significant ($p = 0.02$) trend in increased length across the front to stratified water (Fig. 10d). The equally rare agonidae larvae showed a length and water mass location pattern similar to that shown by cod, and along with cod and stichaeids they were extremely rare or absent in the vicinity of the front

Table 1. Statistical distribution parameters for lengths (mm) of the major larval fish taxa collected in September 1985 in Ungava Bay.

	Taxon			
	Cottidae	Cyclopteridae	Stichaeidae	Gadidae
Sample size	144	134	37	16
Average	22.2	24.6	29.5	37.5
Mode	19.0	23.0	20.0	34.0
Median	21.1	25.0	28.0	33.3
Range	28.2	23.1	65.0	77.5
Sd	4.7	4.9	10.6	21.5
Skewness	1.3	−0.7	3.2	1.9
Kurtosis	2.0	1.5	15.4	3.1
Cv	21.2	16.1	35.9	57.2

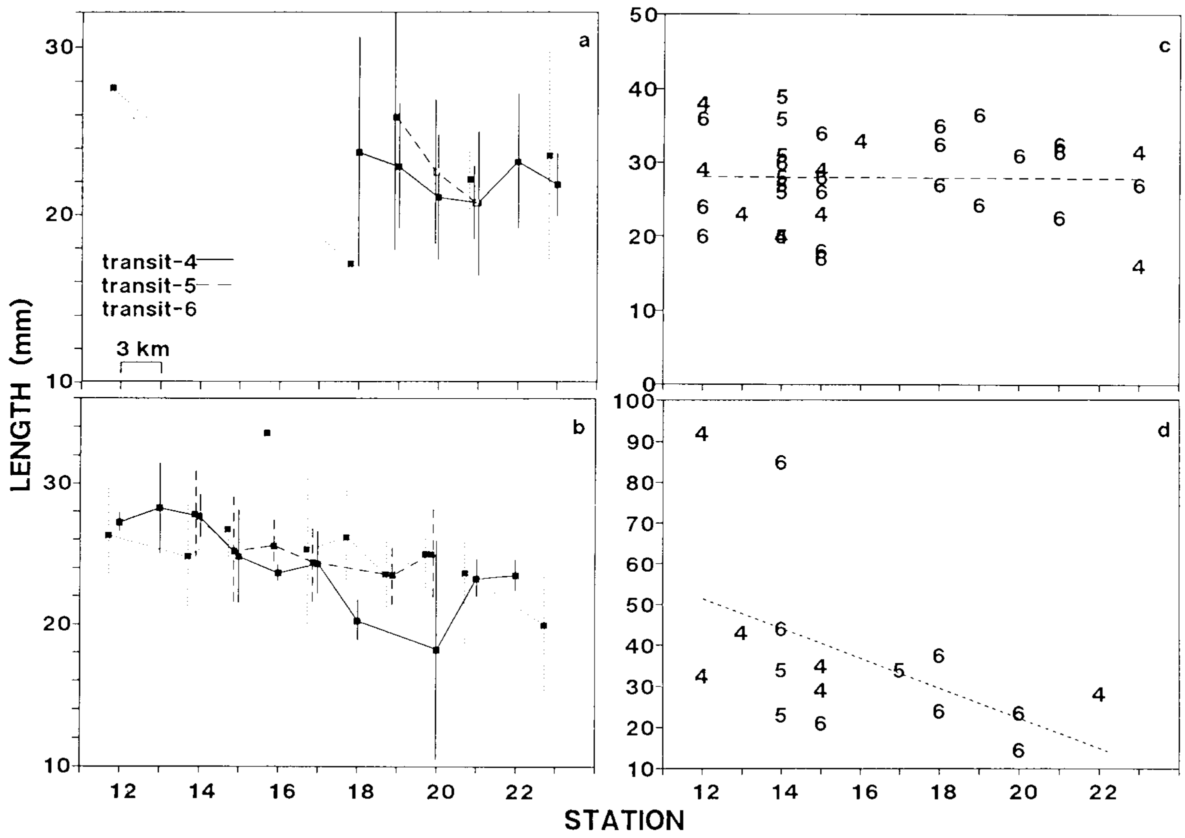

Figure 10. Cross-frontal distribution of station-averaged (± 1 s.d.) larval lengths for (a) cottid larvae, (b) cyclopterid larvae, and individual lengths of (c) all stichaeid larvae, and (d) all gadoid larvae collected on each of Transits 4, 5, and 6 at the Akpatok Shallows frontal region in September 1985. See text for interpretation.

(Stn. 16–18). Sandlance were captured in mixed and stratified water as well as at the front and showed no length related pattern.

Discussion

The results of our study, drawn from three transits of the frontal transect at the Akpatok Shallows, are consistent with the hypothesis that the general structure in the local biological community, ranging from chlorophyll, meso-, and macro-zooplankton to larval fish, was a function of variations in local water mass structure. Our sampling protocol did not fully resolve variations at tidal frequencies and this may have resulted in some spatial and temporal aliasing of the data, and the short duration of our study prevents us from making robust inferences about the long-term variation in the observed patterns.

The location of the Akpatok Shallows front was precisely in the region predicted by Griffiths *et al.* (1981) using tidal mixing arguments. The front was well defined by changes in density structure that were determined mostly by salinity. The lowest salinities observed during our study were at the easternmost stations over the shallows. Observations made in September of 1986 (K. Drinkwater, unpubl. data) revealed the lowest salinity water over the center of Akpatok Shallows. We suggest the likelihood of a long residence time of low salinity water over the shallows subsequent to ice-melt in July, although advection of low salinity water from Hudson Strait or from nearshore Ungava Bay cannot be ruled out.

Observed changes in the local density structure are thought to be primarily due to cross-isobath tidal advection possibly influenced by deep-water upwelling and along-front advection. The cross-isobath tidal excursions in the region are in the order of 10 km over the shallows and 6–8 km over the channel (Chandler *et al.*, 1985). Stratified water is advected toward the shallows during an ebb tide while the mixed water is carried toward the channel during a flood tide. The steepening of isopycnals (Fig. 4) and of nitrate concentration isopleths (Fig. 5) is consistent with this interpretation, as were variations in the position of concentration maxima of decapods and fish larvae among transits. In addition, changes in the relative dominance of meso-zooplankton subclasses are consistent with cross-isobath advection and mixing. Larger meso-zooplankton, dominant at the front on Transits 4 and 5 were subsequently found in the mixed water (Transit 6; Fig. 7). Along-front variations and advection may also account for the observations. However, the variations were too large and too rapid to result from biological processes (predation/production, etc.). Analysis of acoustic-profiling current-meter data collected during the study is currently underway and should enable us to resolve the relative importance of cross-frontal and along-front advection.

The observed shallowing of the isopycnals and nitrate isopleths on the stratified side of the front were consistent with upwelling, as were the distributions of *Limacina* spp. which showed a continuum from the deep water up into the frontal region. We suggest that the deep water in the channel is a nutrient source for the waters at the front supplied through a combination of upwelling and mixing. High chlorophyll *a* concentrations on the stratified side of the front were similar to those seen in other studies (e.g. Pingree, 1978) and infer that the increased stability relative to the mixed water resulted in a higher standing crop.

The small-scale distributions of the various larval fish taxa with respect to the front provided perhaps the most interesting results from our study. Cottids and cyclopterids are benthic spawners in shallow water and it is reasonable that the larvae of both taxa originated from the Akpatok Shallows on the mixed side of the front. The trend in increased length for some taxa from mixed to stratified water can be most simply explained by either of two competing hypotheses: (1) the observations were a result of progressive westward displacement (older and larger larvae found further off the shelf) assuming that all larvae were of similar geographic origin and growth and mortality was spatially and temporally invariant; or (2) the observations resulted from differential growth and mortality and that larvae closer to the front and in stratified water had higher growth and survival. The data are insufficient to test rigorously either hypothesis. It is notable that total (64 to 1024 μm esd) meso-zooplankton biomass (larval food) was generally higher at the front and smaller zooplankton (64–101) biomass was higher in the stratified water. However, all larval fish taxa with the exception of the cottids were absent or extremely rare at the front where *Limacina* spp. and jellyfish (potential larval fish predators) were concentrated. High concentrations of chaetognaths and decapod larvae (potential predators) in the mixed water are consistent with the second hypothesis. Stichaeid larvae showed no significant pattern with respect to stratification, cottids appeared to be retained in mixed water, and cyclopterids showed no evidence of retention within mixed water. Kiørboe *et al.* (1988) showed that herring larvae tend to concentrate at fronts, consistent with the retention hypothesis (Iles and Sinclair, 1982). Our observations show that only cottid larvae were consistent with the retention hypothesis. This implies that there are strong behavioural differences among taxa and that the concept of frontal retention cannot be generalized to all pelagic fish larvae.

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