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Zooplankton biomass gradient off south-western Nova Scotia: nearshore ctenophore predation or hydrographic separation?

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Abstract. A persistent large-scale cross-shelf gradient in zooplankton biomass >1050 μm was evident off south-western Nova Scotia during annual spring surveys between 1985 and 1987, with relatively low levels inshore and higher levels offshore. Conversely, the abundance of the tentaculate ctenophore *Pleurobrachia pileus* was the greatest inshore, and distributed reciprocally to zooplankton >1050 μm. The principle prey of both adult ctenophores and post-larval cod is zooplankton >1050 μm (primarily calanoid copepods), and cod growth rates are strongly influenced by prey biomass. Ctenophore predation appears to have been responsible for the low nearshore zooplankton biomass, whereas the influence of hydrographic factors on the zooplankton gradient was minimal. On a smaller scale, persistent, abrupt changes in zooplankton biomass >1050 μm and ctenophore density existed 3–30 km from shore, in contrast to linear gradients in water density (σ_t) during a 5 week sampling period in spring 1987. Ctenophores were confined to depths <55 m and zooplankton >1050 μm predominantly occurred at depths >55 m. High concentrations of chlorophyll and phaeopigment were evident at depths <55 m also suggesting intense predation by ctenophores on large herbivores. The relatively high proportion of smaller zooplankton (153–308 μm) in the nearshore is also consistent with the predation hypothesis. The reduced growth experienced by post-larval cod inshore appears generated by ctenophore predation of a common prey resource.

Introduction

Recent field studies using growth and condition indices to examine the survival of marine fish larvae have revealed the importance of food limitation (O'Connell, 1980; Leggett, 1986; Theilacker, 1986; Buckley and Lough, 1987). In particular, the dependence of growth and survival on prey abundance extends well into the post-larval and pelagic juvenile phase (Peterman, 1987; Suthers *et al.*, 1989), and it is believed that small variations in survival of the later ontogenetic stages can greatly influence year class strength (Sissenwine *et al.*, 1984; Bjørke and Sundby, 1987).

Analysis of the inter-annual patterns of post-larval cod (*Gadus morhua*) dispersal off south-western Nova Scotia revealed that in each year varying proportions of the larvae were advected from the offshore spawning areas (Browns Bank) to nearshore areas (Suthers and Frank, 1989). Recent growth of post-larval cod (defined as the width of the outer 14 daily growth increments of the otolith), was positively correlated with the abundance of large zooplankton (Suthers *et al.*, 1989), and it is known from previous studies that the diet of post-larval cod is dominated by *Calanus* >1 mm length (Marak, 1960; Kane, 1984; Budgey, 1987). The nearshore (<55 m depth) biomass of large zooplankton

was, on average, 75% lower than offshore (>100 m depth), which was opposite to the gradient in microzooplankton in the 80–153 μm size range (Frank, 1988). Consequently, the lowest recent growth of cod post-larvae was recorded inshore, and the highest offshore including Browns Bank. The spatial pattern in growth was, therefore, coincident with the distribution of their prey.

The low biomass of zooplankton observed inshore has not been explained, although several observations suggest it may be due to grazing by ctenophores. For example, high concentrations of the ctenophore *Pleurobrachia pileus* typify the nearshore waters of south-western Nova Scotia, with densities from 1975 to 1982 ranging between 1 and 16 m^{-3} during the spring, and up to 69 m^{-3} during the summer (Milne and Corey, 1986). Ctenophores also occur offshore (e.g. on Browns Bank; Frank, 1986), although their abundance on the bank relative to the nearshore generally appears to be low. Adult *P.pileus* are known to consume large zooplankton (>1050 μm, Hirota, 1974; Sullivan and Reeve, 1982; Frank, 1986; Greene *et al.*, 1986), and are capable of severely depleting the standing stock of zooplankton when they are abundant (Deason and Smayda, 1982; Frank, 1986; Greve and Reiners, 1988; Roff *et al.*, 1988). High ctenophore densities in the nearshore and relatively low levels offshore could be responsible for the observed gradient in zooplankton abundance off south-western Nova Scotia.

Other explanations for the inverse distributions of ctenophores and their prey are possible. Zooplankton and ctenophores could be restricted to different current regimes or water masses. For example, the distribution of capelin larvae and their small zooplankton prey, compared with the distribution of gelatinous predators in the nearshore waters off eastern Newfoundland, were spatially separated as a result of occupying different water masses (Frank and Leggett, 1982). Reciprocal oscillations in the abundance of capelin larvae and gelatinous predators were apparent at a fixed sampling site, resulting not from biological interactions but through wind driven coastal water mass replacement (Frank and Leggett, 1985). In another example, the fortnightly abundance of ctenophores at a fixed station in the Kiel Bight was positively correlated with salinity (Schneider, 1987). Seasonal advection of more saline, ctenophore dominated water from the Kattegat appeared responsible for the observed seasonal fluctuation. In many field studies reporting reciprocal ctenophore–zooplankton distributions (Deason and Smayda, 1982; Feigenbaum and Kelly, 1984; Williams and Collins, 1985; Roff *et al.*, 1988), the contribution of water mass advection to the variation in ctenophore abundance was not included in the analysis. Thus caution must be exercised in the interpretation of distributional patterns of potential predators and prey. Off south-western Nova Scotia, an inshore–offshore gradient in temperature and salinity is observed during summer and winter (Fournier *et al.*, 1984a,b). The possibility exists that ctenophore and zooplankton distributions could be determined by water mass characteristics, rather than biological interactions.

The aim of this study was to determine the extent to which the horizontal distribution of zooplankton biomass during the spring in south-western Nova Scotia was influenced by differential grazing pressure exerted by ctenophores

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and horizontal pattern in water mass characteristics (temperature, salinity). The null hypothesis was that ctenophore abundance was not significantly correlated with zooplankton biomass. A second null hypothesis was that the water density (σ_t) was not significantly correlated with zooplankton biomass.

Comparisons of the large-scale distribution of zooplankton and ctenophores were derived from spring and early summer surveys in the shelf waters of south-western Nova Scotia during 1985–1987. On a finer scale, the spatial and temporal distributions of zooplankton and ctenophores were examined from April 26 to June 1, 1987 in the nearshore area of south-western Nova Scotia, to further examine the two hypotheses, and to explore in detail the influence of physical features on the distributions of zooplankton and ctenophores.

Methods

Study area, and cruise dates

The circulation off south-western Nova Scotia is dominated by strong semi-diurnal tides, with tidal currents up to 100 cm s^{-1}, and a northerly surface residual current >10 cm s^{-1} (Garrett *et al.*, 1978). A permanent clockwise gyre occurs on Browns Bank to the south (Figure 1) (Smith, 1983, 1989). The nearshore region is highly productive, owing in part to upwelling (Smith, 1983) and, during summer and fall, to the presence of a tidal front (Fournier *et al.*, 1984a).

Four large-scale spring and summer ichthyoplankton surveys were conducted from 1985 to 1987 (Suthers and Frank, 1989; Suthers *et al.*, 1989, Table Ia), when collections of zooplankton and ctenophores were made using either the mini-BIONESS (0.25 m^2, 333 μm mesh, as described in Frank, 1988), or a 0.5 m ring net (405 μm mesh, Table Ia). The mini-BIONESS sampled up to seven discrete depths to 55 m, which were combined as a weighted (by volume) average at each station. The 0.5 m net was towed in an oblique haul from 15–25 m to the surface. The mean was calculated for any stations that were replicated. Further details of the sampling protocol are provided in Frank (1988) and Suthers *et al.* (1989).

Nearshore sampling was conducted from April 26 until June 1, 1987, at stations 9 km apart along 43.75°N (transect 2), perpendicular to the coast off Yarmouth, Nova Scotia (Figure 1, Table Ib). Additionally, two parallel transects were sampled on May 11 and 13 along 44.0°N and 43.5°N (transects 3 and 1 respectively, Figure 1, Table Ib). The three nearshore transects sampled on May 11, 13 and 14 were treated as synoptic. All nearshore sampling was conducted during daylight, except for the final sampling date of June 1–2 (from cruise 87-2), which was conducted at night.

Nearshore sampling procedure

A 0.5 m ring net (405 μm mesh) was deployed on eight dates during the 5 week period to sample zooplankton and ctenophores (Table Ib). The gear was towed in an oblique haul to a depth of 15 m, at 1.5 m s^{-1} for 15 min (approximate
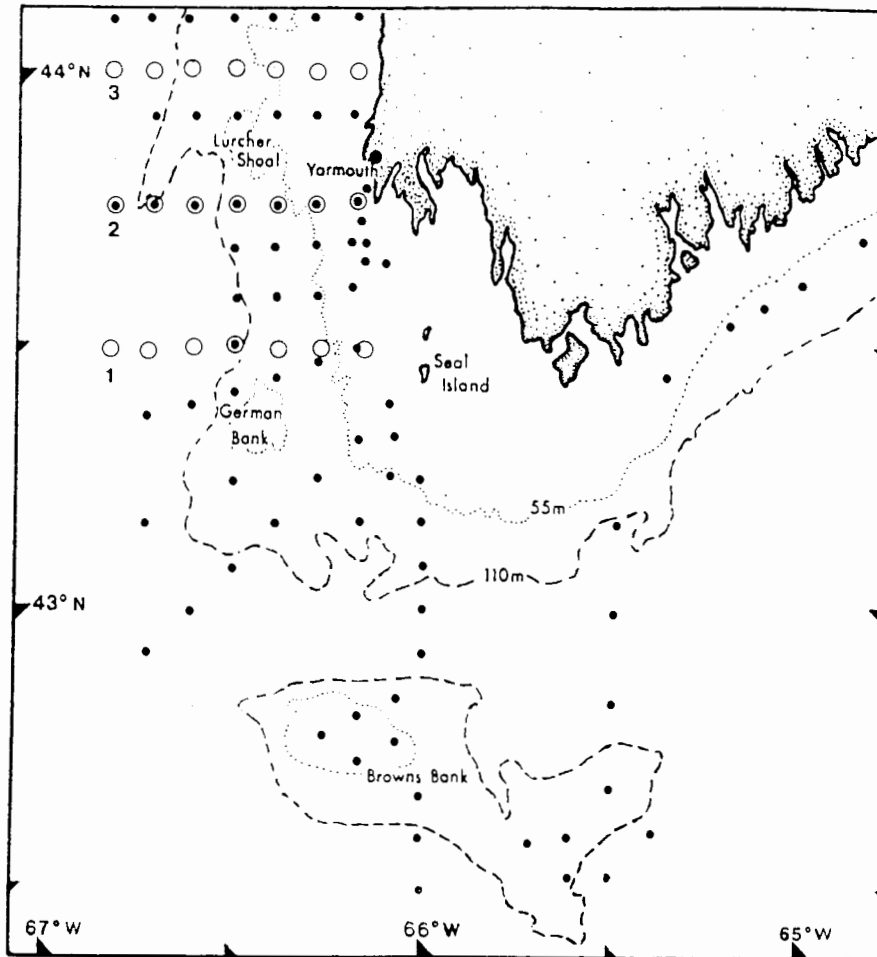
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Fig. 1. Map of study area sampled off south-western Nova Scotia, with the bathymetry and geographic landmarks referred to in text. Circled stations refer to those sampled nearshore on cruise 87-1 (transect number beneath the offshore station).

volume of 300 m^3). The gear on June 1–2 was a mini-BIONESS (from cruise 87-2, Table Ia). During the 5 week period, microzooplankton was sampled at every alternate station with a 0.6 m ring net (80 μm mesh) except at the most nearshore station due to quantities of suspended sand.

Treatment of samples

All samples were rinsed through a 10 mm mesh sieve to exclude macrozooplankton, before preservation in 5% formalin in freshwater. Ctenophore abundance >500 ml volume was estimated by counting three to six 100 ml subsamples of the total volume collected. Zooplankton (mostly calanoid copepods) was separated into four size fractions; 308–602, 602–860, 860–1050 and >1050 μm

Table I. (a) Cruise summary of the four large scale surveys off south-western Nova Scotia, 1985–1987

Year	Date	Cruise	No. stations	Gear
1985	May 9–21	85-1	30	BN
	May 13–26	85-2	15	HM[a]
1986	May 10–18	86-1	35	BN
	May 14–23	86-2	20	HM[b]
	June 5–11	86-3	54	HM[c]
1987	June 28–4	87-2	54	BN

[a] Salinity not determined.
[b] Zooplankton abundance not estimated.
[c] Ctenophore abundance estimated from a Tucker trawl.

(b) Cruise summary of stations sampled in spring 1987 (cruise 87-1). Transects 3, 2 and 1 are along latitudes 43.5°N, 43.75° and 44.0°N respectively. BN, mini-BIONESS; HM, 0.5 m ring net

Date	Transect	No. stations	Gear deployed
April 26, 27	2	8	HM
May 3	2	7	HM
May 10	2	5	HM
May 11	3	7	HM
May 13	1	7	HM
May 17	2	7	HM
May 18	2	7	HM
June 1, 2	2	7	BN[a]

[a] From cruise 87-2.

after Frank (1988), which were then oven-dried to a constant weight (± 0.1 mg). The microzooplankton collections sampled with the 80 μm mesh net were separated into 80–153, 153–308 and >308 μm size fractions, of which only the 153–308 μm fraction is considered here.

Water density, pigment analysis

During the nearshore sampling, temperature and salinity profiles were recorded at the completion of each tow with a Guildline CTD (Conductivity–Temperature–Depth). Water densities were calculated from temperature and salinity using the UNESCO 1980 formulation and expressed as σ_t (kg m^{-3}). A stratification parameter was calculated as the difference in water density between the surface and 10–15 m from the bottom (σ_{tob}). Phytoplankton standing stock and phaeopigment (the latter considered an index of herbivore grazing; Lorenzen, 1967) was determined at each station from three replicate 200 ml water samples collected at a depth of 3–4 m, following the procedures contained in Holm-Hansen and Rieman (1978).

Analysis

Previous analyses have shown that biomass of the largest size fraction

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(>1050 μm) was significantly and positively correlated with the two smaller size fractions (602–860, 860–1050 μm), but was not correlated with the 308–602 μm fraction (Frank, 1988). Therefore zooplankton analysis was restricted to the >1050 and 308–602 μm fractions. The distributional pattern of zooplankton biomass >1050 μm was initially assessed by linear regression, with the logarithm of distance from shore as the independent variable. To interpret the pattern observed with distance, zooplankton >1050 μm was then re-analysed using multiple regression, incorporating water density (σ_t) and ctenophore abundance. Zooplankton biomass and ctenophore abundance (plus 1 to remove zero values) were converted to logarithms as normality plots indicated this was an appropriate transformation, and water density was transformed to ($\sigma_t - 24$). The scale for the expanding symbol plots was standardized at 50, 25, 10 and 5% of the maximum station abundance. Contouring was not used (as in the nearshore results) due to the irregular boundary of the sampling grid. Nearshore distributions of the physical variables and abundances of zooplankton and ctenophores were contoured with respect to distance from shore and date, using the Kriging method (see Ripley, 1981). Contours were standardized for ctenophore abundance at ~50, 25, 10, 5 and 2.5% of the maximum station abundance observed during the 5 week period.

Results

Inter-annual zooplankton and ctenophore distributions

During May 1985 the biomass of zooplankton >1050 μm was positively correlated with distance from shore, and negatively correlated with ctenophore abundance. Conversely, ctenophore abundance was negatively correlated with distance from shore (Table II, Figure 2). A horizontal gradient in σ_t existed with low values inshore and slightly higher values offshore. The lowest zooplankton biomass (>1050 μm) was observed in the nearshore off Seal Island and Yarmouth, which coincided with the highest densities of ctenophores (Figure 3). The highest zooplankton (>1050 μm) biomass occurred on Browns Bank and to the north-west. Contrary to large zooplankton, the distribution of smaller zooplankton (308–602 μm) was not significantly correlated with distance from shore, nor with ctenophore density (Table II).

During May 1986, zooplankton biomass >1050 μm was positively correlated with distance from shore; ctenophore abundance was negatively correlated with both distance from shore and zooplankton >1050 μm (Table II, Figure 4). Sigma-t increased linearly with distance (Figure 4). The highest biomass of zooplankton >1050 μm occurred on Browns Bank and to the north-west at stations beyond the 100 m isobath (Figure 5a), while the greatest densities of ctenophores occurred at a few isolated stations on the western cap of Browns Bank, and at several contiguous stations landward of the 60 m isobath (Figure 5b). The biomass of smaller zooplankton (308–602 μm) was not significantly correlated with distance from shore, nor with ctenophore density (Table II).

Three weeks later during June 1986, zooplankton biomass >1050 μm was again positively correlated with distance from shore. And similar to May 1986
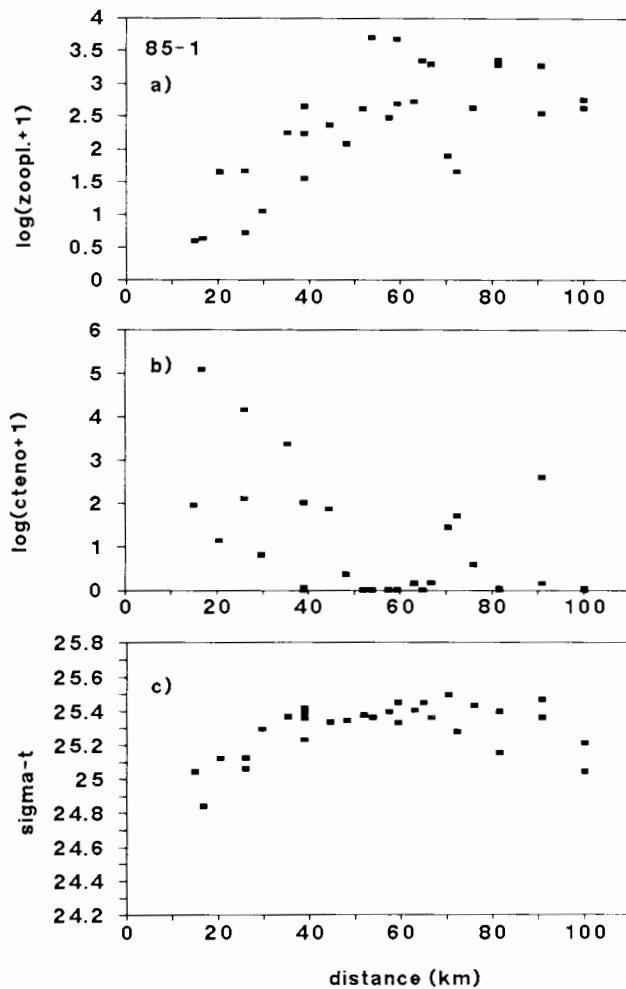
Fig. 2. Plot of (**a**) zooplankton biomass >1050 μm (mg m^{-1}), (**b**) ctenophore abundance (no. 100 m^{-3}) and (**c**) water density (σ_t) with respect to distance from shore during cruise 85-1.

ctenophore abundance was negatively correlated with both distance and zooplankton >1050 μm (Table II, Figure 6). Relatively low values of σ_t occurred inshore, and between 80 and 100 km offshore (corresponding to stations on Browns Bank), which as in other cruises, did not reflect the distribution of zooplankton >1050 μm (Figure 6c). The spatial distribution of zooplankton >1050 μm showed the highest biomass on Browns Bank, while lower biomass occurred inshore of the 100 m isobath (Figure 7a) where the greatest densities of ctenophores were observed (landward of the 60 m isobath, Figure 7b). In contrast to large zooplankton, the biomass of smaller zooplankton (308–602 μm) was not significantly correlated with distance from shore, nor with ctenophore density (Table II).

Table II. Matrix of Spearman rank correlation coefficients of zooplankton biomass >1050 μm and 308–602 μm, ctenophore density, σ_t and ln distance from shore

Cruise (n)		z1050	z308	Ctenophore	σ_t	Distance
85-1 (30)	z1050	1				
	z308	0.27	1			
	Ctenophore	−0.64**	−0.16	1		
	σ_t	0.49*	0.12	−0.36*	1	
	Distance	0.65**	0.17	−0.41*	0.39*	1
86-1 (36)	z1050	1				
	z308	0.22	1			
	Ctenophore	−0.48*	0.29	1		
	σ_t	0.51*	0.04	−0.51*	1	
	Distance	0.63**	−0.14	−0.67**	0.77**	1
86-3 (54)	z1050	1				
	z308	0.23	1			
	Ctenophore	−0.58**	−0.06	1		
	σ_t	0.23	0.08	−0.44*	1	
	Distance	0.78**	0.22	−0.59**	0.35*	1
87-2 (54)	z1050	1				
	z308	0.04	1			
	Ctenophore	−0.51**	0.60**	1		
	σ_t	−0.08	0.15	0.31*	1	
	Distance	0.70**	−0.13	−0.54**	−0.21	1

n = No. of stations; *, $0.001 < P < 0.05$; **, $P < 0.001$.

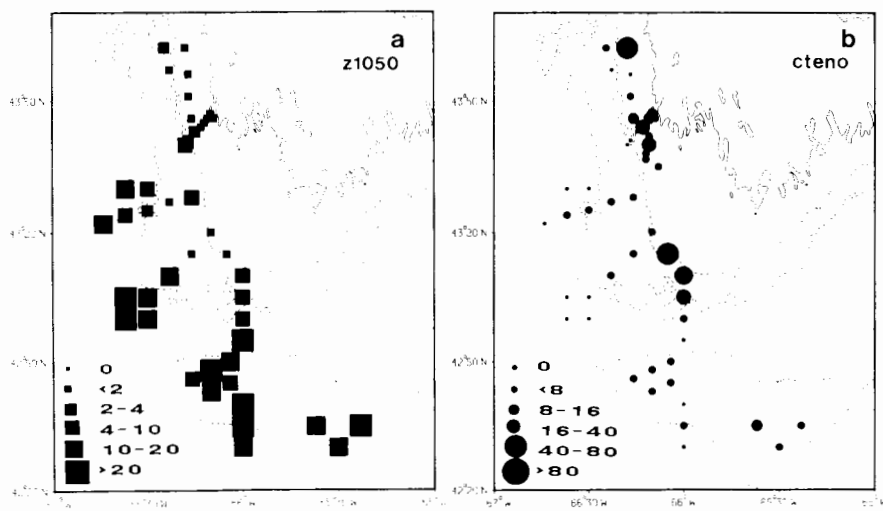**Fig. 3.** Distribution during cruise 85-1.2 of (a) zooplankton >1050 μm (mg m^{-3}) and (b) *P.pileus* (no. 100 m^{-3}). Expanding symbols are standardized at >50, 25–50, 10–25, 5–10 and <5% of the maximum station density.
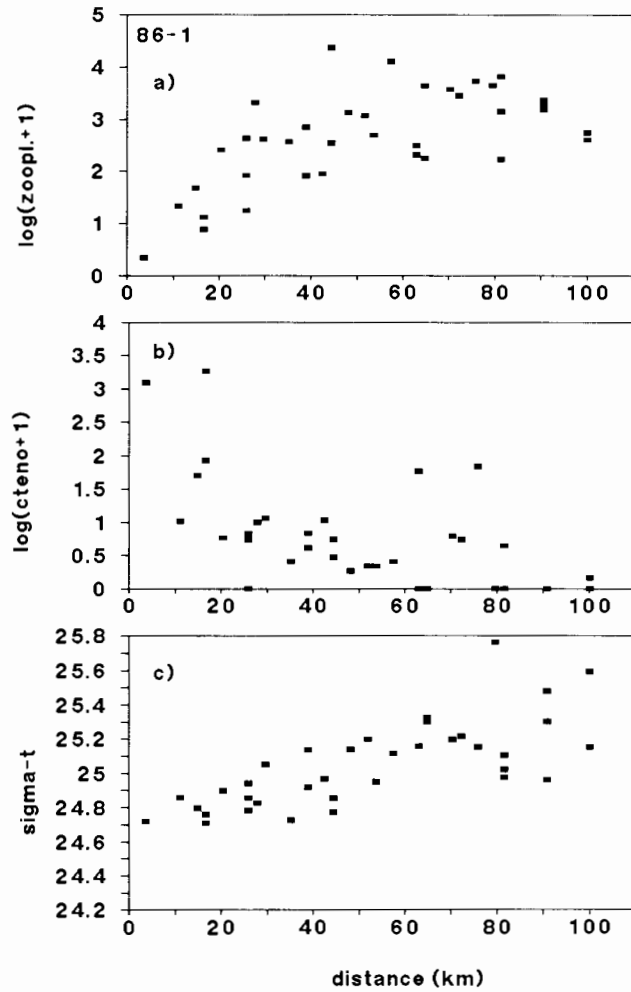
Fig. 4. Plot of (**a**) zooplankton biomass >1050 μm (mg m^{-3}), (**b**) ctenophore abundance (no. 100 m^{-3}) and (**c**) water density (σ_t) with respect to distance from shore during cruise 86-1.

In May 1987, zooplankton biomass >1050 μm, and ctenophore density were significantly correlated with distance from shore but in an opposite fashion, while in contrast to the earlier cruises, there was no significant horizontal trend in σ_t (Table II, Figure 8). Zooplankton >1050 μm was, once again, negatively correlated with the abundance of ctenophores. High zooplankton biomass >1050 μm occurred on Browns Bank and offshore beyond the 100 m isobath (Figure 9a). Ctenophore densities were 1–2 orders of magnitude greater than in previous years, occurring on the western cap of Browns Bank and inshore of the 100 m isobath between German Bank and Seal Island (Figure 9b). The smaller zooplankton biomass (308–602 μm) was not correlated with distance, as in other cruises, and was positively correlated with the abundance of ctenophores.
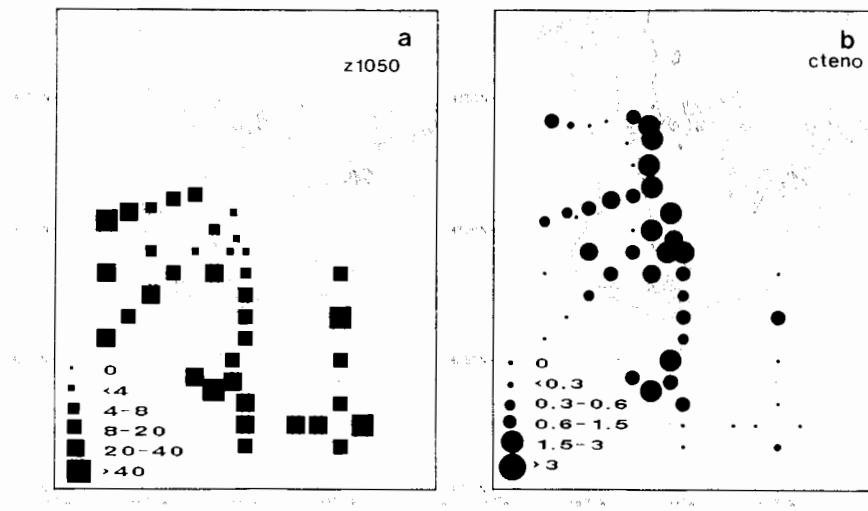
Fig. 5. Distribution during cruise 86-1,2 of (**a**) zooplankton >1050 μm (mg m^{-3}) and (**b**) *P.pileus* (no. 100 m^{-3}). Symbols as in Figure 3. Zooplankton not measured for cruise 86-2.

As expected from the rank correlation analysis, there was a highly significant relationship between zooplankton biomass >1050 μm and distance from shore for each cruise, accounting for ~55% of the variance in zooplankton (Table IIIa). In the multiple regression analyses of zooplankton biomass >1050 μm, ctenophore density was a significant factor in all cruises. Only in cruise 85-1 was σ_t (water density) an additional significant factor (Table IIIb). Also, the coefficients did not change by reversing the order of the variables in the regression. Although ctenophore abundance and σ_t were correlated (Table II), the multiple regression was not confounded in any cruise as indicated from multicollinearity diagnostics (Systat Inc., 1988, Evanston IL). During cruises 85-1 and 86-1, the proportion of the variance in zooplankton >1050 μm explained by distance from shore, was similar to that explained by ctenophore density and σ_t (r^2 in Table IIIb).

Nearshore environmental conditions in 1987

The fine-scale, nearshore sampling revealed a uniform inshore–offshore gradient in surface salinity and water density (σ_t), ranging between 31 and 32‰ and 24.6 and 25.2 kg m^{-3} (Figure 10). The temperature–salinity (T–S) signature indicated that nearshore waters were well mixed and of relatively low salinity compared with stations beyond 30 km (the fourth station) from shore. There appeared to be no cross-shore gradient in sea-surface temperature, although over the 5 week interval, temperature increased from ~2 to 6°C (Figure 10).

Nearshore ctenophore and zooplankton distributions

The biomass of zooplankton >1050 μm was significantly and positively

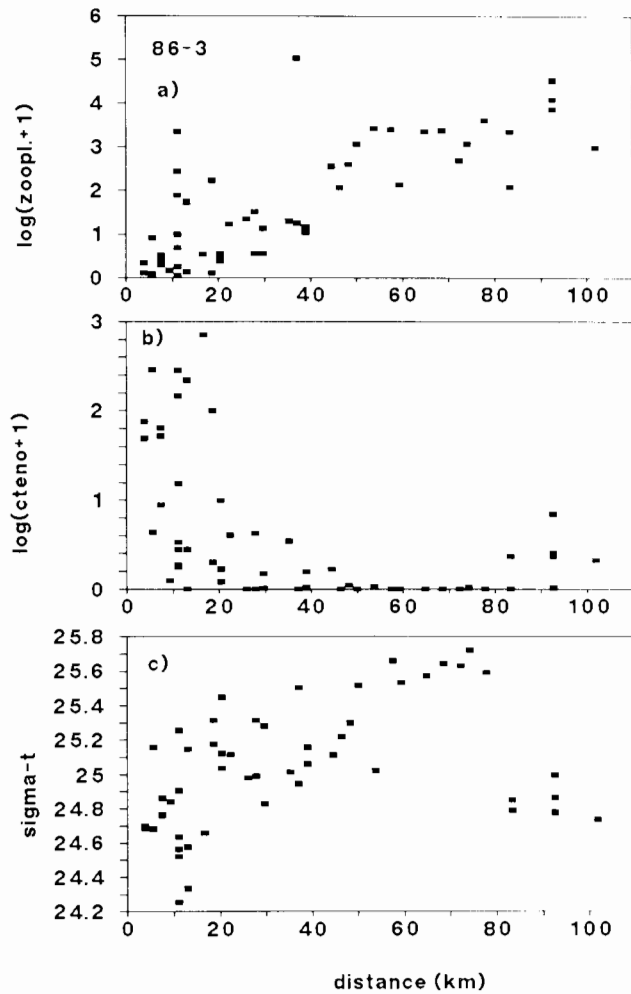**Fig. 6.** Plot of (a) zooplankton biomass >1050 μm (mg m⁻³), (b) ctenophore abundance (no. 100 m⁻³) and (c) water density (σ_t) with respect to distance from shore during cruise 86-3.

correlated with the biomass of 860–1050 and 602–860 μm zooplankton ($r = 0.63$, and $r = 0.65$ respectively), but was not significantly correlated with the biomass of smaller zooplankton 308–602 and 153–308 μm ($r = -0.15$, and $r = -0.27$ respectively). This is consistent with zooplankton biomass distributions observed on a larger scale (Frank, 1988). The distribution of the >1050 μm biomass fraction, and the smaller microzooplankton (153–308 μm) were therefore inversely distributed throughout the 5 week sampling period (Figure 11a and b). Compared with the physical gradients (Figure 10), zooplankton biomass >1050 μm sharply increased beyond the 55 m isobath (20–40 km from shore, Figure 11a). Biomass of the 153–308 μm size fraction tended to increase
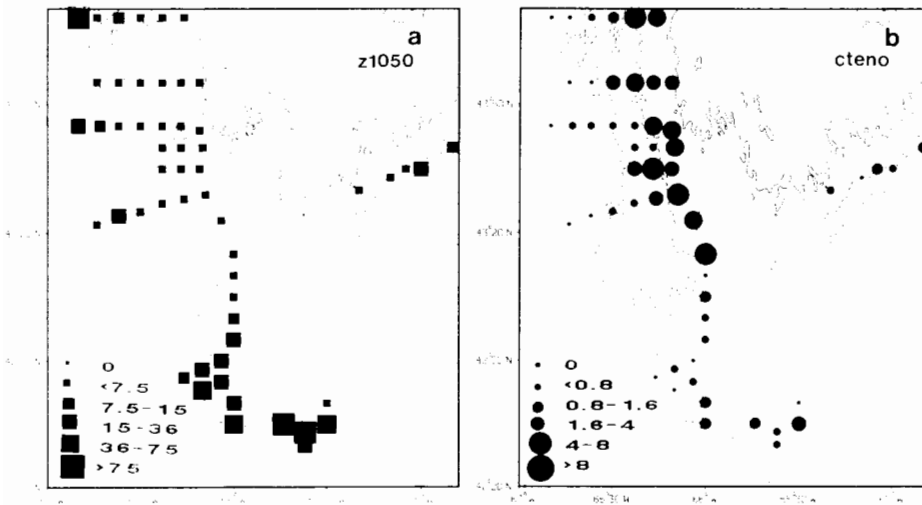
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Fig. 7. Distribution during cruise 86-3 of (a) zooplankton >1050 μm (mg m⁻³) and (b) *P.pileus* (no. 100 m⁻³). Symbols as in Figure 3.

inshore with maximum values occurring in the region of high ctenophores (Figure 11b).

Pleurobrachia generally persisted within the coastal, well-mixed water 10 km from shore inside the 55 m isobath. During early June their distributions extended further offshore, corresponding with an associated decline in zooplankton biomass >1050 μm (Figure 11c).

The greatest concentrations of chlorophyll and phaeopigment occurred at the coastal stations throughout the sampling period, in the same location as the ctenophores and zooplankton in the 153–308 μm size range (Figure 11d and e). In particular, chlorophyll was the lowest offshore, where the greatest biomass of zooplankton >1050 μm occurred.

Spatial distributions over the three transects on May 11–14 reflected a similar pattern to that along transect 2. Zooplankton >1050 μm concentrated in a band ~30 km from shore (Figure 12a) which roughly corresponded to the offshore edge of the ctenophore and phaeopigment distribution. Phaeopigment and *Pleurobrachia* were concentrated inshore (Figure 12b and c), inside the well-mixed zone (Figure 12d). These results corresponded well with the distributions seen during the April–June sampling period.

Discussion

Large-scale zooplankton biomass distribution

The null hypothesis, that ctenophore density was not significantly correlated with zooplankton biomass during spring in south-western Nova Scotia was rejected. However, the second null hypothesis, that water density was not significantly correlated with zooplankton biomass was accepted (Table III). The
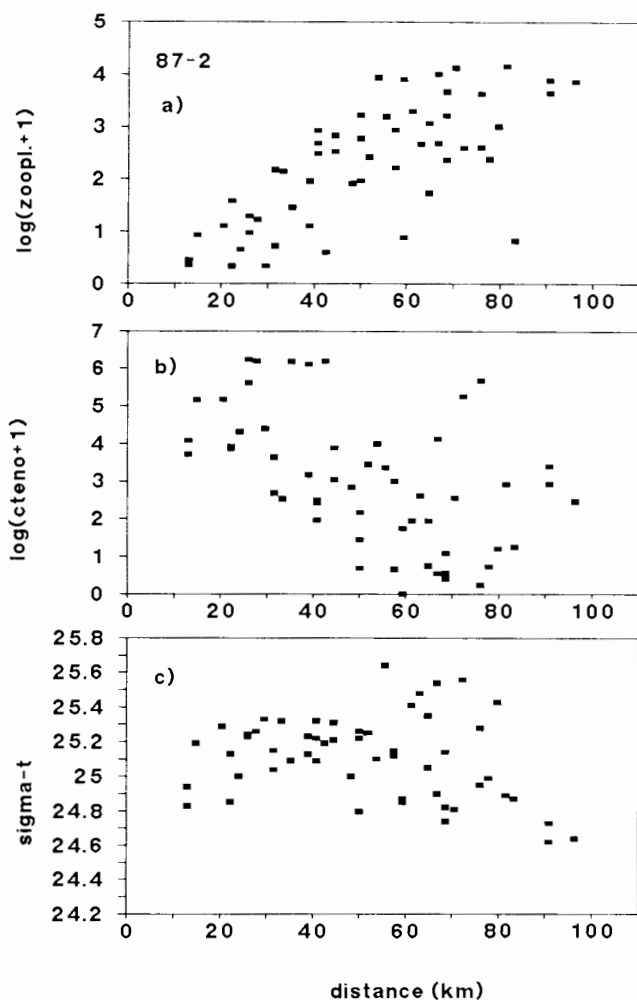
Fig. 8. Plot of (**a**) zooplankton biomass >1050 μm (mg m⁻³), (**b**) ctenophore abundance (no. 100 m⁻³) and (**c**) water density (σ$_t$) with respect to distance from shore during cruise 87-2.

large-scale surveys consistently revealed that zooplankton and ctenophores were inversely distributed, with ctenophore densities generally greater inshore, and zooplankton biomass >1050 μm greater offshore and on Browns Bank. On the other hand, the large-scale surveys did not reveal a consistent pattern in the spatial distribution of σ$_t$, particularly during cruise 87-2 when there was no trend with distance from shore. Post-larval cod sampled offshore exhibited higher growth (Suthers *et al.*, 1989), where the regional average biomass of zooplankton >1050 μm was up to 10-fold greater. The predation by ctenophore hypothesis is consistent with the low or significant positive correlation between zooplankton biomass in the 153–308 μm size range and ctenophore abundance, a size range of zooplankton largely unaffected by adult *Pleurobrachia* grazing.
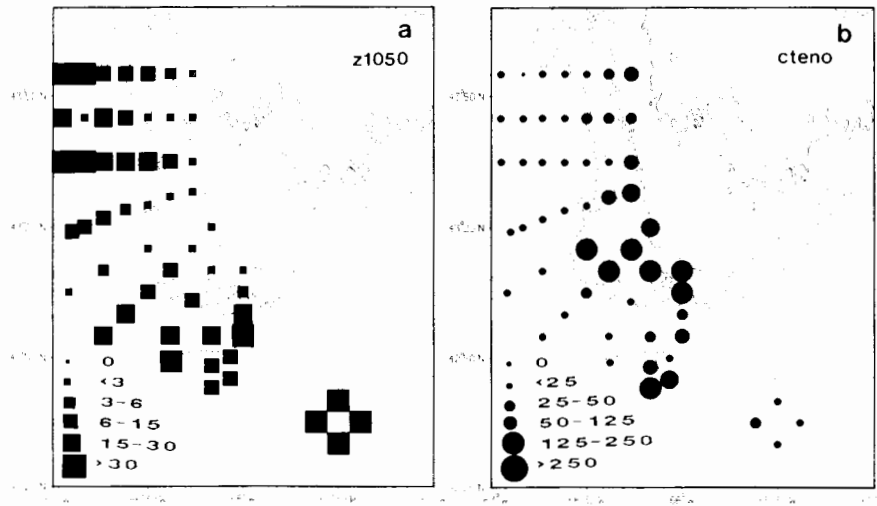
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Fig. 9. Distribution during cruise 87-2 of (**a**) zooplankton >1050 μm (mg m^{-3}) and (**b**) *P.pileus* (no. 100 m^{-3}). Symbols as in Figure 3.

Table III. (a) Summary statistics of the regression of log zooplankton biomass on log distance from shore: (b) the multiple regression model of log zooplankton biomass on log ctenophore abundance (lc) and water density (σ_t −24)

Cruise		Variable	Estimate (SE)	P	r^2
(a)	85-1	Constant	−2.49 (0.82)	0.01*	
		Distance	1.24 (0.21)	<0.00*	0.56
	86-1	Constant	−0.87 (0.56)	0.13	
		Distance	0.93 (0.15)	<0.00*	0.54
	86-3	Constant	−1.83 (0.47)	<0.00*	
		Distance	1.12 (0.14)	<0.00*	0.55
	87-2	Constant	−4.17 (0.83)	<0.00*	
		Distance	1.68 (0.21)	<0.00*	0.54
(b)	85-1	Constant	−0.45 (1.16)	0.70	
		lc	−0.25 (0.10)	0.01*	
		σ_t	2.36 (0.85)	0.01*	0.51
	86-1	Constant	2.07 (0.68)	0.16	
		lc	−0.55 (0.17)	<0.00*	
		σ_t	0.95 (0.57)	0.10	0.42
	86-3	Constant	1.86 (0.57)	<0.00*	
		lc	−0.88 (0.21)	<0.00*	
		σ_t	0.46 (0.49)	0.36	0.31
	87-2	Constant	2.98 (0.66)	0.00*	
		lc	−0.34 (0.08)	<0.00*	
		σ_t	0.30 (0.61)	0.62	0.26

*, $P < 0.05$.

Frank (1986) and others have established that adult *Pleurobrachia* consume zooplankton >1050 μm, although smaller size fractions are consumed by larval ctenophores, and occasionally by adults when large zooplankton is absent (Stoecker *et al.*, 1987; Bell, 1988).
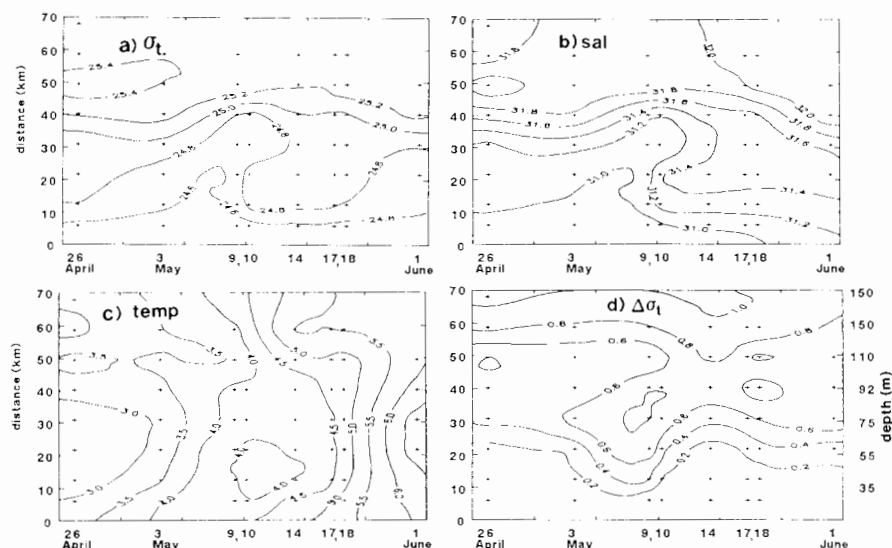
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Fig. 10. Horizontal distribution along transect 2 from April 26 to June 2, 1987 of (**a**) water density (σ_t, kg m^{-3}), (**b**) surface salinity (‰), (**c**) surface temperature (°C), and (**d**) difference in surface-bottom density, σ_{toB}, with approximate station depths on the right-hand axis.

The positive influence of water density on zooplankton biomass >1050 μm (cruise 85-1, Table IIb) may reflect the timing of the cruise relative to the vernal warming and spring bloom. For example, intra-annual variation in ctenophore abundance has been related to the initial spring zooplankton abundance (Deason and Smayda, 1982), while inter-annual variation of ctenophore abundance in south-western Nova Scotia has been related to the cumulative sea-surface temperature anomalies from January to April (Frank, 1986).

Nearshore distributions of zooplankton and ctenophores

The nearshore survey also showed ctenophores were negatively associated with zooplankton biomass >1050 μm, and that the influence of the horizontal density (σ_t) structure was minimal. The reciprocal gradients in ctenophores and zooplankton >1050 μm were steeper 3–30 km from shore than any linear gradients in σ_t, or temperature and salinity alone. Reciprocal temporal changes in ctenophore and zooplankton abundance occurred (cf. Figure 11a and c), but the magnitude was slight presumably as the water mass does not persist in the sampling area due to the >5 km day^{-1} northerly, residual current. The hypothesis of ctenophore predation is consistent with the high abundance of smaller zooplankton (153–308 μm) inshore, as well as the higher concentrations of phytoplankton observed nearest to shore. Temporal peaks in ctenophores and phytoplankton abundance have been observed together with troughs in zooplankton abundance (Deason and Smayda, 1982; Greve and Reiners, 1988), which under conditions of hydrographic stability suggests a growth response of
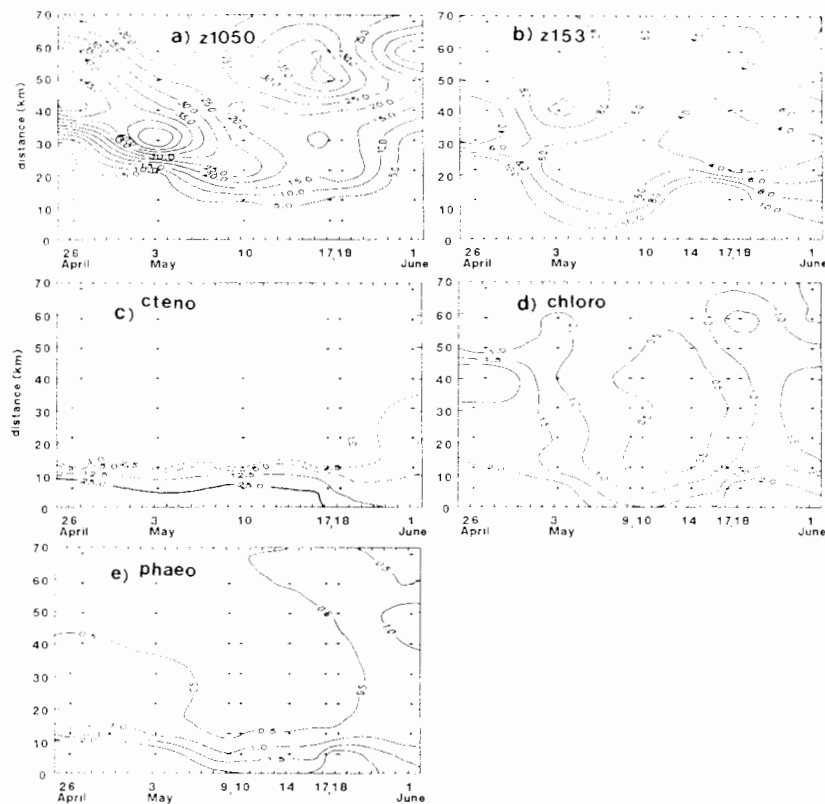
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Fig. 11. Horizontal distribution along transect 2 of (**a**) zooplankton >1050 μm mg m⁻³, (**b**) zooplankton 153–308 μm mg m⁻³, (**c**) ctenophores no. 10 m⁻³ (note scale is 10× previous ctenophore plots), (**d**) chlorophyll and (**e**) phaeopigment μg l⁻¹.

phytoplankton to the predatory removal of herbivorous zooplankton >1050 μm. The concentration of phaeopigment, a digestive breakdown product of chlorophyll shows that considerable herbivory occurred in the nearshore, and yet larger zooplankton were not abundant there, presumably due to ctenophore predation. Alternatively, phaeopigments could have been stirred up from the substrate nearshore, although the spatial pattern is not consistent with depth (Figures 11e and 12b).

The predatory impact on zooplankton biomass >1050 μm by ctenophores may be considerable. For example, *Pleurobrachia* at a concentration of 1 m⁻³ (2.5 contour in Figure 11c) could consume on a daily basis ~4 mg dry wt m⁻³ (Frank, 1986). Large zooplankton such as *Calanus finmarchicus* produce one predominant generation per year with the spring production of ~1 mg dry wt day⁻¹ m⁻³ (McLaren *et al.*, 1989, their Table 3). Therefore the calculated daily predation by *Pleurobrachia* exceeds the production estimate of McLaren *et al.* (1989), and >80% of the standing stock of zooplankton >1050 μm found at the two most nearshore stations (Figure 11a). Other studies have noted that
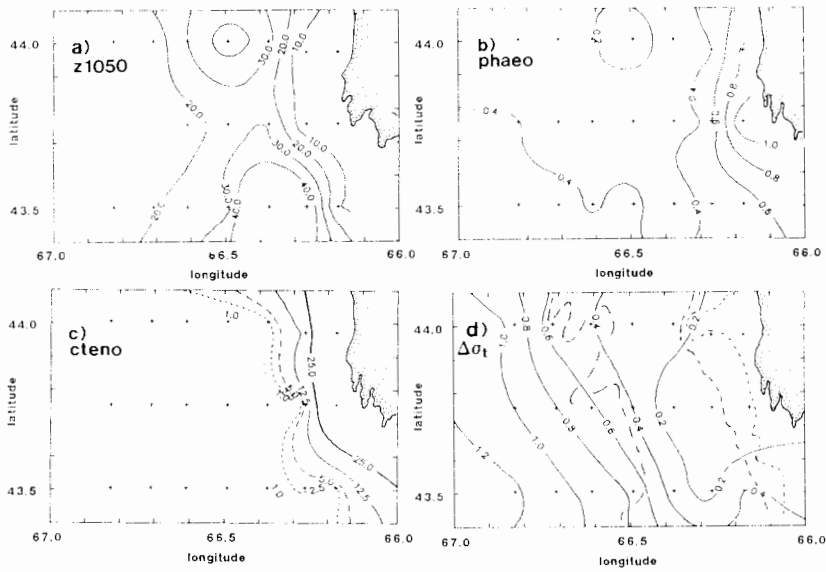
Fig. 12. Spatial distribution over the three transects on May 11, 13 and 14 of (a) zooplankton >1050 μm, mg m^{-3}, (b) chlorophyll μg l^{-1}, (c) ctenophores no. 100 m^{-3}, and (d) $\sigma_{t_{0,8}}$, and the 20, 55 and 110 m isobath.

planktivores other than larval fish can reduce the abundance or production of nauplii by ~20% daily (Dagg *et al.*, 1984; Fortier and Harris, 1989). Fortier and Harris (1989) noted that the vertical distribution of some fish larvae was indicative of density dependent competition for food, and yet the observed larval fish abundance could have only slight impact on the prey density. The effect of the predatory planktonic community was therefore invoked to account for the appearance of density dependence. The effect of larval fish on their prey resource may indeed be slight (Cushing, 1983), but should be considered in the light of their potential competitors.

The role of turbulence nearshore

The distribution of ctenophores appeared restricted to shallow areas particularly in the nearshore and on Browns Bank. The distribution of ctenophores tended to follow the bathymetry offshore around Trinity Ledge (Figure 12). One process that may account for the restricted distribution is the year-round tidal mixing that occurs inshore. Ctenophore feeding is highly dependent upon encounter rates with their prey (Reeve and Walter, 1978), and higher turbulence would enhance their feeding opportunities (Rothschild and Osborn, 1988—a factor also noted by Miller and Daan, 1989). It is significant that many of the higher estimates of ctenophore clearance rates are derived from large volume containers (>50 l), or from studies that included laboratory mixing, or from gut content analysis of field caught specimens (Sullivan and Reeve, 1982; Frank,

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1986; Greene *et al.*, 1986; Monteleone and Duguay, 1988), where conditions of higher micro-turbulence (at the scale of cm) and increased contact rates would be expected (Sundby and Fossum, 1989). Rothschild and Osborn (1988) emphasize the relative velocity of predator and prey rather than their relative densities in estimating predation rates. Further study of ctenophore–zooplankton dynamics should include experimental manipulation in the field of micro-turbulence to test the conclusions of this research.

The predatory impact of ctenophores has been questioned by Miller and Daan (1989) because of inconsistent results in the literature. However other factors besides contact rates confound laboratory-determined clearance rates that have only recently been addressed. These include container volume (Monteleone and Duguay, 1988; Bell, 1988), post-capture trauma, and individual behaviour such as tentacle extension in *Pleurobrachia* (Bell, 1988). Low temporal correlation between ctenophores and zooplankton abundance at a fixed station (as shown by Miller and Daan, 1989) may be expected with patchy ctenophore abundance and more uniformly distributed zooplankton abundance. For example, during the four large-scale surveys, Lloyd's (1967) patchiness indices were between 1.5 and 4.1 for zooplankton biomass $>1050 \mu m$ and 4.1 and 10.1 for ctenophores.

The impact of ctenophore predation on zooplankton biomass and size structure may be general and applicable to other areas. Cross-shelf gradients in zooplankton abundance are observed elsewhere (Frank, 1988), although ctenophore abundance is not provided. However in an analogous situation to south-western Nova Scotia, a zooplankton biomass ($>200 \mu m$) gradient occurs across a tidal front off Northwest Scotland (Kiørboe and Johansen, 1986). The gradient could well be generated by the year-round abundances of *Pleurobrachia* known to occur inshore (Fraser, 1970; Roff *et al.*, 1988).

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