Pergamon

Deep-Sea Research II, Vol. 43, No. 7–8, pp. 1855–1873, 1996
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0967–0645/96 $15.00+0.00

PII: S0967–0645(96)00055–0

Distributions of copepod nauplii and turbulence on the southern flank of Georges Bank: implications for feeding by larval cod (*Gadus morhua*)

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(*Received* 14 *October* 1994; *in revised form* 29 *November* 1995; *accepted* 2 *May* 1996)

Abstract—The vertical distributions of copepod nauplii and water properties were sampled at well-mixed and stratified sites on Georges Bank using a pumping system, CTD and *in vivo* fluorometer during a four day period in late May 1992. At each stratified station at least one sample was taken within the thermocline and the fluorescence maximum, which usually co-occurred. Well-mixed sites had low average concentrations of nauplii, *ca* 4 l^{-1}, and showed little variation of abundance with depth. Stratified sites had from 4 to 16 times the integrated (0–50 m) abundance of nauplii compared to well-mixed sites and showed strong vertical patterns of distribution. Maximum concentrations of nauplii, up to 160 l^{-1}, were associated with the thermocline at 7 of the 9 stratified stations. At the two remaining stratified sites the naupliar maximum was in the upper mixed layer, sampled at 5 m depth. The encounter rate between early feeding cod (*Gadus morhua*) larvae and their naupliar prey was calculated with and without turbulence. Turbulence was estimated from two sources: wind stress in the upper layer (calculated from wind observations during our cruise) and tidal shear in the lower layer (estimated initially from a tidal mixing equation). We ultimately replaced the lower layer estimates with turbulence data from a series of measurements made in 1995. The latter are more robust and had the advantage of providing dissipation rates for the pycnocline as well as the lower layer. Theory predicts an increase in encounters between a predator and its prey with the addition of turbulence parameters into standard models of encounter. We combined turbulence profiles with the vertical distribution of nauplii to examine the potential contribution of turbulent kinetic energy to predator–prey encounter rates at various depths in stratified and mixed water columns. Our calculations suggest the following increases due to turbulence at stratified sites on Georges Bank during our cruise: from 34 to 219% in the upper mixed layer, depending on wind speed and depth; approximately 8% in the pycnocline; and approximately 110% below the pycnocline. Mixed sites experience increases of at least 110% (tide only), but greater increases (118–192% in this study) occur when the wind blows because of the combined (spatially overlapped) effects of wind and tidal mixing at these sites. The absolute values for encounter rates and their modification by turbulence are sensitive to a number of assumptions in the models. We used a series of stated assumptions to generate estimates that range from 0.6 to 26.5 prey h^{-1}, depending on geographical location, physical forcing and depth. Copyright © 1996 Elsevier Science Ltd

INTRODUCTION

This paper examines the potential prey field for early feeding cod (*Gadus morhua*) larvae on the southern flank of Georges Bank during spring 1992. We consider that portion of the zooplankton community retained by 40 μm mesh sieves after sampling at selected depths with a submerged pump and preserving with formalin, focussing our attention on the size, distribution and abundance of copepod nauplii. We describe the abundance and vertical

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distribution of copepod nauplii in relation to hydrographic conditions and *in vivo* fluorescence in stratified and well-mixed regions of the bank and compare prey "availability" in the two regimes and at various depths using standing stock and turbulence-modified calculations. We contrast results from two different approaches to sampling the stratified region: a Lagrangian drifter and a fixed mooring site. Finally, we compare pump and 10 l Niskin bottle samples for the abundance, size and taxonomic composition of small (40–1700 μm body length) zooplankton.

Cod spawn on Georges Bank over a period of 6–8 months, from November to June, but most spawning is concentrated over the northeastern portion from February into April. Eggs drift southwestward with the residual, anticyclonic circulation, and hatch within 2–3 weeks (Lough, 1984). Larvae begin feeding within about a week, at 4–5 mm standard length (SL), and feed heavily on copepod nauplii through their first several weeks of growth, to about 8 mm SL (Auditore *et al.*, 1993; Lough and Mountain, 1996). Early feeding larvae are expected over the southern portion of the bank in significant numbers in May (GLOBEC, 1992; Lough, 1984). During the present study, a second research vessel sampled cod larvae and found most to be 5–10 mm SL at the mixed site and 5–7 mm at the stratified site (Lough *et al.*, 1996). Larvae were more abundant at the mixed site and were caught in significant numbers to 40 m depth, the closest nominal sampling depth to the bottom. Vertical distribution in the stratified region could not be described as thoroughly because of the small number of larvae caught, but higher concentrations between 20 and 30 m were indicated (Lough *et al.*, 1996). Earlier studies (Lough, 1984; Buckley and Lough, 1987; Lough and Potter, 1993) showed that most cod larvae $\leq$8 mm SL were within the pycnocline during stratified periods. Buckley and Lough (1987) suggested that the larval distributions might be related to the vertical maximum abundance of copepod nauplii, which also occurred in or near the pycnocline in their study. According to Lough and Potter (1993), larvae of this size do not undertake detectable diel vertical migrations. Werner *et al.* (1993) showed that the thermocline may provide for the maximum retention of larvae on the bank, furnishing an additional, or perhaps alternative, explanation for the relative abundance of cod larvae at that depth.

Numerous organisms other than copepod nauplii may be important in the early development of feeding behavior in fish larvae (Noakes and Godin, 1988; Ohman *et al.*, 1991), and certainly the energetics of growing larvae demand a shift to larger prey over time (Kane, 1984; Lough and Mountain, 1996). Nonetheless, it generally is agreed that there is a period in the early growth of many marine teleost larvae when feeding on copepod nauplii is extremely important, if not critical, to survival. Hence, much attention has been given to the abundance and vertical distribution of these small organisms (Owen, 1989; Incze *et al.*, 1990; Lough and Potter, 1993; Incze and Ainaire, 1994; Tiselius *et al.*, 1994) and the behavior and capability of fish larvae to prey on them (e.g. Blaxter, 1986). A considerable body of useful literature has resulted, but is based largely on a static view of prey abundance. When turbulence has been considered, it has been mostly with regard to the dilution of prey items (Buckley and Lough, 1987; Incze *et al.*, 1990) or to the secondary effects that mixing has on production (Wroblewski and Richman, 1987). Recent studies have shown that the historical focus on concentration (number per unit volume) of prey does not adequately represent the predator–prey relationship in the sea. Rothschild and Osborn (1988) developed a model that showed how turbulence would enhance the contact rate between a predator and its prey. Implications of this model have been explored for planktonic recruitment (Davis *et al.*, 1991) and substantiated by experimental studies with copepod grazers (Saiz *et al.*, 1992) and field studies with larval Arcto-Norwegian cod (Sundby and Fossum, 1990) and larval herring (Muelbert *et al.*, 1994). It is possible that the relationship between turbulence and feeding success is hyperbolic, but MacKenzie *et al.* (1994) suggest that this may happen for cod larvae at higher levels of turbulence than we found in this study.

On Georges Bank, turbulence derives chiefly from two sources. In the mixed region, generally shallower then 60 m in spring, tidally generated turbulent kinetic energy (TKE) is sufficient to mix the entire water column, conforming to predictions of the tidal stirring parameter, $u^3 h^{-1}$, of Bowers and Simpson (1987). Seaward is a stratified region in which the pycnocline becomes increasingly well defined as shelf depth and/or seasonal warming increase. Turbulence in the lower layer is caused by tidal shear along the bottom and decreases with distance (height) above bottom. Turbulence in the upper layer is caused primarily by wind stress and convective mixing which occur sporadically and with varying intensity during spring over the entire bank. Breaking waves contribute to turbulence during the passage of storms, but the depth- and wind-dependence of wave-induced turbulence is unclear. MacKenzie and Leggett, 1993 found little evidence that turbulence at depths of 0–5 and 0–10 m in the presence of breaking waves was higher than expected from a simple model based on wind. The pycnocline represents a region of poorly understood, but certainly much reduced, mixing compared to the bottom tidally mixed, or upper wind-mixed layers. Previous studies concerning the potential effect of turbulence on larval feeding have not attempted to deal with the vertical profile of turbulence through the pycnocline (MacKenzie and Leggett, 1991, 1993). A hydrodynamic model of circulation in the Gulf of Maine and Georges Bank (Lynch *et al.*, 1996) indicates that turbulent dissipation rate (taken to be equivalent to TKE) in the pycnocline is reduced by at least two orders of magnitude from upper and lower mixed layer values (D. Lynch, personal communication, 1995; Werner *et al.*, 1996), and this has been corroborated by recent measurements (Horne *et al.*, 1996; Oakey, unpublished data, 1995). Theoretical calculations (MacKenzie and Leggett, 1991) and field studies (Sundby and Fossum, 1990) suggest that levels of turbulence on Georges Bank are sufficient to substantially alter our interpretation of prey availability. Although much remains to be understood about the distribution of turbulent energy and the behavior of prey and foraging larval fish under turbulent conditions, it is necessary to start thinking in these terms when presenting field data on prey abundance. Therefore, our standing stock estimates of naupliar prey densities are adjusted by approximations of the turbulent kinetic energy impact on prey "availability" (predator–prey encounter) in our study.

METHODS

Samples were collected from R.V. *Endeavor* on the southern flank of Georges Bank over shelf depths ranging from 44 to 83 m, from 21 to 24 May 1992. A standard CTD and *in vivo* fluorometric profile of the water column preceded each sample collection. The CTD was returned to the deck and redeployed with a pumping system that consisted of a submersible pump and 60 m of reinforced plastic hose of 5.7 cm inside diameter. The system delivered 5.2 $m^3 min^{-1}$ to the deck through an additional 10 m of hose and had a clearance time of ~40 s. The hose intake was attached near the pressure sensor of the CTD and lowered to nominal sampling depths of 5, 10, 15, 20, 30 and 50 m and allowed to clear for 1 min. Displayed hydrographic and fluorescence data were monitored continuously during the cast, and one or more of the aforementioned depths was adjusted slightly, or other depths were added, in order to sample the pycnocline and fluorescence maximum. On board the research vessel, a small volume of flow (15.5 l min^{-1} ± 0.7% range during calibration) was tapped from the main return line, passed through a thermistor and a second fluorometer to confirm its origin (vs the CTD data), and then made available for sampling. An in-line digital flow meter in one of the discharge lines was used to watch for possible variations in flow rate. Zooplankton was sampled by directing the small volume flow for 1 min through 40 μm mesh samplers, rinsing into 4 oz ($\sim$ 120 g) glass storage containers and preserving in 5% buffered formalin. The mesh size is small enough to retain naupliar prey of larval cod (Kane, 1984). At one station in the mixed area, sampling by the pump and by 10-l Niskin bottles was compared. Bottles were on the CTD rosette sampler, while the pump was deployed from a separate winch more than 10 m away on the same side of the vessel. One bottle was closed at the beginning of each of three sequential 30 s (*ca* 7.7 l) pump samples. All samples were analyzed using a video- and computer-assisted stereomicroscope system (Incze *et al.*, 1990). Extracted chlorophyll measurements (Phinney and Yentsch, 1985) were used to calibrate the CTD fluorometer. Converted fluorometric data were used to plot chlorophyll profiles. Conductivity data had unresolved irregularities at several of the casts, so we used temperature data here instead of σ_t density. Since density is dominated by temperature on Georges Bank during spring, temperature structure is a reasonable proxy for density structure (cf. Flagg, 1987: Fig. 10.17).

Samples were collected along an across-isobath transect where bottom depths were 83, 70, 50 and 44 m; at a well-mixed site (50 m); at a stratified site ($\sim$80 m); and following a Lagrangian drifter in the stratified region. The drifter used LORAN-C positioning data, was drogued at 15 m, and passed over bottom depths of 80 to $<$60 m during the course of sampling (Fig. 1).

Turbulent kinetic energy was calculated as the dissipation rate, ε, in units of $\mathrm{W\,kg^{-1}}$ (some papers use $\mathrm{W\,m^{-3}}$, which is $\mathrm{W\,kg^{-1}} \times 10^3$). We estimated turbulence from two sources. For tides:

$$\varepsilon = (6.0 \times 10^{-6}[u^3 h^{-1}]) \tag{1}$$

where u is the M2 depth-averaged tidal velocity ($\mathrm{m\,s^{-1}}$) and h is the height (m) of the bottom mixed layer (= height of the water column at the mixed sites: Bowers and Simpson, 1987). We also used values from recent measurements by Dr Neil Oakey from an area close to our original study sites. (N. Oakey, Bedford Inst. of Oceanography, Dartmouth, NS, Canada, unpublished data from R.V. *Seward Johnson* cruise 9508, June 1995. See methods in Oakey, 1982; Horne *et al.*, 1996.) Characteristic values were obtained by inspection of data for that portion of the lower layer where we sampled for nauplii. For wind:

$$\varepsilon = (5.82 \times 10^{-9} W^3/z) \tag{2}$$

where W is wind speed ($\mathrm{m\,s^{-1}}$) and z is the depth of sample (m) (from MacKenzie and Leggett, 1993, modified for different units). Equation (2) underestimates ε under calm conditions with surface cooling because it ignores convective mixing. Similarly, for wind speeds exceeding 7.5 $\mathrm{m\,s^{-1}}$, it fails to account for turbulence caused by breaking waves (Pond and Pickard, 1983). Neither factor was considered to play a major role in this study. In the pycnocline turbulence decays to some small value compared to conditions in the upper and lower mixed layers, but there is no straightforward relationship that describes this (Lough and Mountain, 1996; Werner *et al.*, 1996). Recent measurements from Oakey (as above, unpublished data, 1995) were used.

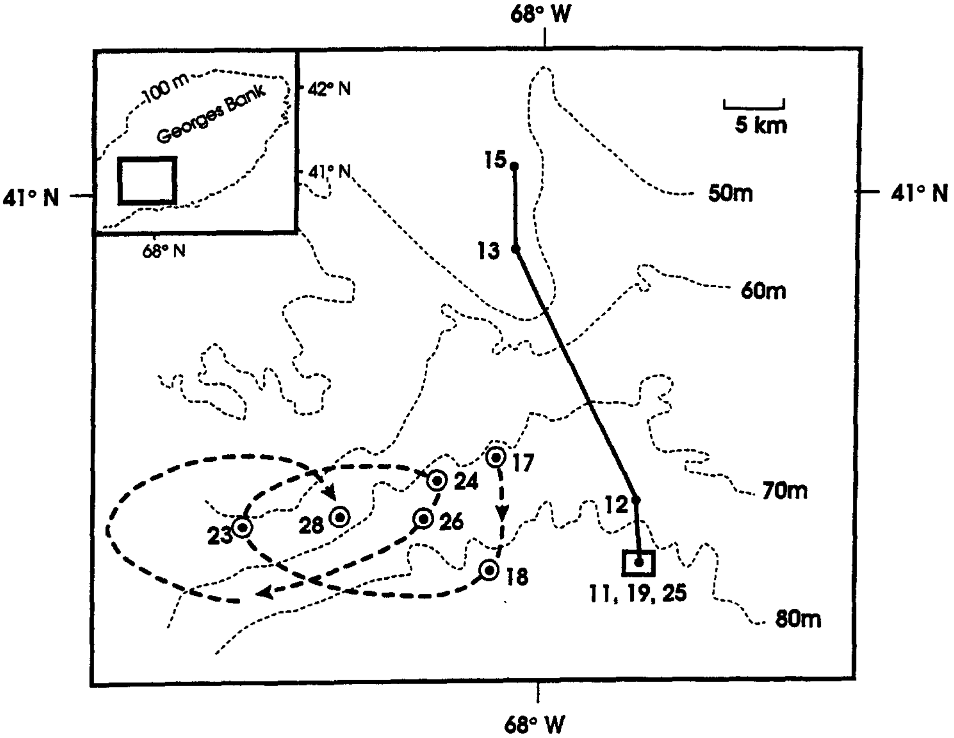

Fig. 1. Study area showing sampling stations for copepod nauplii and other small zooplankton on the southern flank of Georges Bank and the mooring location (open square). Dashed line is a schematic of the drifter trajectory. Drifter stations 17, 24 and 28 were sampled approximately 24 h apart (details in Table 1).

Following Rothschild and Osborn (1988), we use our calculated values of ε to derive a turbulent velocity, w, under various conditions:

$$w^2 = 3.615(\varepsilon r)^{2/3} \tag{3}$$

where r is a length scale for turbulence appropriate to the predator–prey interaction. We used two values for this scale. First, we followed Rothschild and Osborn by setting r equal to the average separation distance between prey, approximated by $N^{-0.333}$, where N is the number of prey per m^3. Second, we followed more recent arguments that r should equal the radius of detection of prey by the predator (Evans, 1989; Denman and Gargett, 1995; MacKenzie and Kiorboe, 1995). Turbulent velocity, in units cm s^{-1}, becomes a component of the relative speed, A, between a predator and its prey. Following Evans' (1989) modification of the original Rothschild and Osborn equation, we calculate:

$$A = (u^2 + v^2 + 2w^2)^{1/2} \tag{4}$$

where u is the swimming velocity of the prey; v is the swimming velocity of the predator (both in cm s^{-1}) and w^2 is from Equation (3).

From Gerritsen and Strickler (1977), the "contact" or encounter rate, C, between a predator and its prey can be written:

$$C = (\pi R^2 N)A \tag{5}$$

where C is expressed as prey s^{-1}; R (cm) is the encounter radius (also called the perceptive distance or reactive distance) of the predator, and N is the number of prey per unit volume. Since R almost certainly is not equal in all directions or under all conditions, C is used here only as a standard for comparison, referring to the frequency with which the anterior end of the predator (larval fish) and a potential prey (nauplius) come within a fixed distance, R, of each other (note formulation in Equation (5)). We do not attempt to quantify the frequency of detection, pursuit or success in capturing and ingesting prey within the specified volume, all of which may be influenced by a variety of factors including light, predator satiation, predator pre-occupation with another encounter, or turbulence itself.

In Equation (1) we used a tidal velocity of 70 cm s^{-1} (Butman and Beardsley, 1987) and thickness of the bottom layer as determined for each station by the CTD data. In the mixed area we used height of the water column. In Equation (2) we used a mean of the hourly averages of wind speed for 6 h prior to sampling (the last hour overlapped with sampling in some cases). From field measurements we use values of ε equal to 10^{-6} W kg^{-1} for a tidally mixed water column or layer and 10^{-8} W kg^{-1} in the pycnocline. In the stratified region our deepest observations for nauplii (50 m) were 20 m or more above bottom at almost all stations; therefore they were out of the region of rapidly decaying Epsilon values. In Equation (4) we use $u = 0.0125$ cm s^{-1} for copepod nauplii (Sundby and Fossum, 1990) and $v = 0.20$ cm s^{-1} for an early feeding cod larva (cf. Lough and Mountain, 1996: their Table 3). These are similar to values used by MacKenzie and Leggett (1991) in their theoretical development. In Equation (5) we use $R = 0.26$ cm (*ca* 0.5 body length), and we hold it constant because its possible variations due to turbulence, light and other factors are not well known. This is slightly less than the perceptive distance relationship worked out by Laurence (1985) for larval haddock, equal to $2/3\ \pi$ $(0.75 \text{ body length})^2$. Finally, we use observed naupliar vertical distributions from our field sampling and compare vertical profiles of theoretical contact rates derived with and without turbulence.

RESULTS

Naupliar concentrations at stratified sites varied from 6.9 to 80 l^{-1} in the upper mixed layer and 22 to 160 l^{-1} within the thermocline. Concentrations in the mixed area were markedly lower, never exceeding 6 l^{-1} at the two stations (Table 1). The across-shelf transect was sampled in just under 27 h and ranged over shelf depths from 83 to 44 m (Fig. 1). Wind speeds were low (mean = 3.7 m s^{-1}) for 6 h prior to sampling the offshore station, increased to 8.2 m s^{-1} for 6 h before the second station, and then gradually increased to a 6 h average of 9.2 m s^{-1} for the shallowest station (Table 1). Temperature and naupliar abundance profiles showed decreasing stratification between the first two stations (83 and 70 m, respectively) and virtually no stratification at the two shallowest sites (50 and 44 m; Fig. 2). Integrated naupliar abundance was similar within each of the two groups of stations but differed by a factor greater than 4 × between them. At the two stratified stations (11P and 12P), 0–50 m trapezoidal integration gave 5.0 and 5.4×10^5 nauplii m^{-2}; the mixed sites were both 1.2×10^5 m^{-2} (Fig. 2). The steeper thermocline gradient at the deepest site was associated with a more pronounced vertical structure in the naupliar distribution compared to the second, more weakly stratified, site. Although the standing stocks of nauplii were similar at the two stratified sites, differences in vertical distribution resulted in

Table 1. *Summary of station data*

Area/Station	Day of Year	Depth (m)	Time	Naupliar Maximum No. l^{-1}	Naupliar Maximum Depth (m)	Max. Layer	Wind 6 h mean ($m\ s^{-1}$)	Wind Range of hourly means
Stratified Area								
Drifter								
17P	143	70	17:20	38.1	15	T	9.3	5.8–11.3
18P	143	85	19:49	36.8	15	T	9.0	5.8–10.5
23P	144	80	17:31	21.9	10	T	11.3	9.4–13.3
24P	144	67	21:43	70.1	10	T	10.7	9.4–13.3
28P	145	70	17:55	80.0	5	U	11.0	7.8–20.4*
Transect								
12P	143	70	05:39	22.9	5	U	8.2	6.8–10.3
Mooring								
11P	142	83	09:00	43.8	10	T	3.7	1.6–4.4
19P	143	81	10:07	31.2	20	T	8.8	5.7–10.5
25P	145	75	00:17	160.4	15	T	10.3	9.0–11.8
Mixed Area								
13P	143	50	08:32	5.7	15	NA	8.4	5.1–10.0
15P	143	48	11:48	6.0	20	NA	9.2	8.4–10.0

Time is local (EST); naupliar maximum shows the concentration (no. l^{-1}) and depth of the maximum as well as the layer in which the maximum was found (U: upper mixed layer; T: thermocline; NA: not applicable). Wind speed was averaged over 6 h preceding sampling; the range of hourly averages over the 6 h period is given in the last column.

*20.4 was the mean for the hour immediately preceding sampling.

nearly a 2 × difference in peak naupliar concentration (Table 1). Chlorophyll concentration was low at all sites, with variable patterns of vertical distribution.

Data from the mooring site in the stratified region ($z = 80$ m) were collected over a 3.5 day period. The first station (Fig. 3) is the same as that illustrated in Fig. 2 for the transect, but plotted at a different scale. Temperature profiles changed substantially between days. Chlorophyll concentration, while always low, showed some vertical structure at each cast, with a deeper maximum in the latter two samples. Naupliar concentrations were maximum within the thermocline and coincident with, or close to, the depth of the chlorophyll maximum, but note that sampling was directed at the chlorophyll maximum and that vertical resolution is *ca* 5 m for nauplii (pump samples) and 1 m for chlorophyll and temperature (averaging interval for fluorometric and CTD data). Integrated (0–50 m) chlorophyll changed only a little between casts, but integrated naupliar abundance changed by a factor of 3.7. The maximum naupliar concentration (May 23: 160 l^{-1} at 15 m) was associated with comparatively high concentrations of nauplii at all depths ≤ 20 m at that station. CTD profiles (Fig. 3) changed noticeably during this period.

The quality of LORAN-C buoy fixes was variable, but sufficient for general tracking (Manning *et al.*, 1995). Our Fig. 1 therefore shows only a schematic of the trajectory, but sampling station positions are accurate. Drifter stations had more consistent temperature profiles than the fixed mooring site (Fig. 4; details of comparison are shown in Fig. 5). In particular, the thermocline gradient was steeper, and the depth of maximum change, at

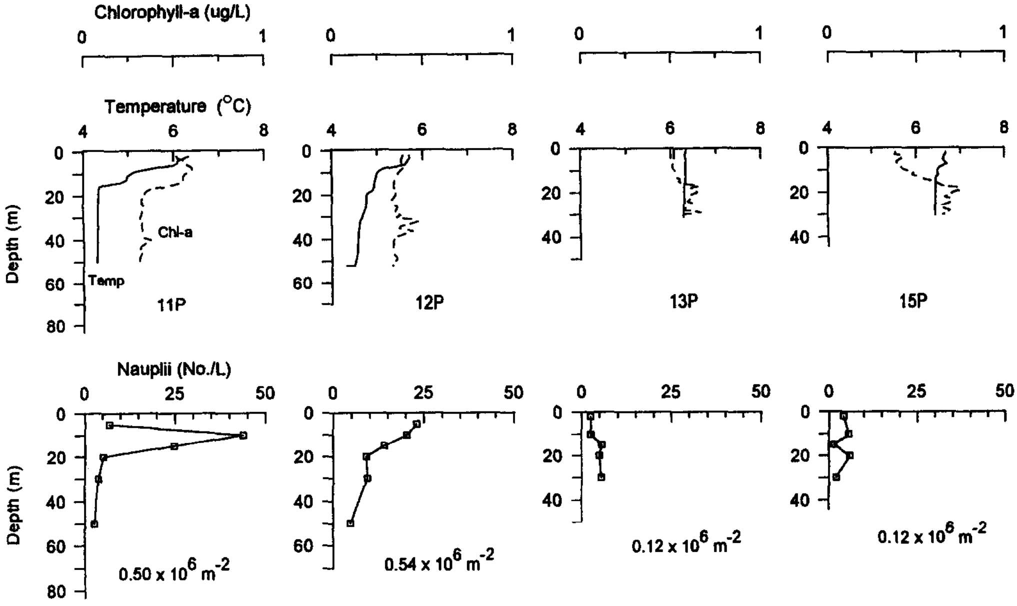

Fig. 2. Across-shelf transect of temperature, chlorophyll-*a* and naupliar concentrations measured at stations 11P–15P, shelf depths from 83 to 44 m (Table 1). Temperature (solid line) and chlorophyll-*a* (broken line) are 1 m-averaged data; nauplii are from discrete depths indicated by the open symbols. The number given at the bottom of each naupliar depth profile is the integrated abundance of nauplii (no. m^{-2}) to the lowest depth sampled.

approximately 8 m, was less variable. Chlorophyll profiles showed a maximum below the thermocline at 3 of the 5 sites: 18P, 23P and 28P, similar to 19P and 25P at the mooring site. Station 23P had the greatest vertical separation between the fluorescence peak and the steepest temperature gradient. At other stations there was either little structure (17P) or generally elevated values in the upper layer (24P, similar to 11P at the mooring). Naupliar distributions and integrated abundances varied substantially and fell into three cases. (i) At 17P and 18P, there was a well-developed maximum at least 5 m thick located in the thermocline (the two casts were only 2.3 h apart: Table 1). The fluorescence peak, which occurred only at 18P, was coincident with the naupliar abundance maximum. (ii) At station 23P the naupliar maximum did not appear to be as thick as at the previous two stations; it was nearer the surface, of lower magnitude, and associated with the thermocline, not with the fluorescence maximum. Sea surface temperature (SST) was warmer by > 1°C. (iii) At 24P and 28P there were far more nauplii than at any of the prior stations, and high concentrations extended well into the upper mixed layer, not showing the type of decrease seen elsewhere in the series (cf. Figures 2–4, Table 1). They also were in warmer (by *ca* 2°C) surface water than the earlier samples. The changes did not take place monotonically and were particularly pronounced between 23P and 24P, sampled only 4 h apart (Table 1). Stations 17, 24 and 28 (Fig. 1) were located over similar shelf depths and were each sampled approximately 24 h apart.

Theoretical encounter rates, *C*, between larval cod and copepod nauplii are shown in Table 2 with and without turbulence. For calculating turbulence in the upper layer, average wind speed over the 6 h prior to sampling ranged from 3.7 to 11.3 m s^{-1} (Table 1). At 2.5 m,

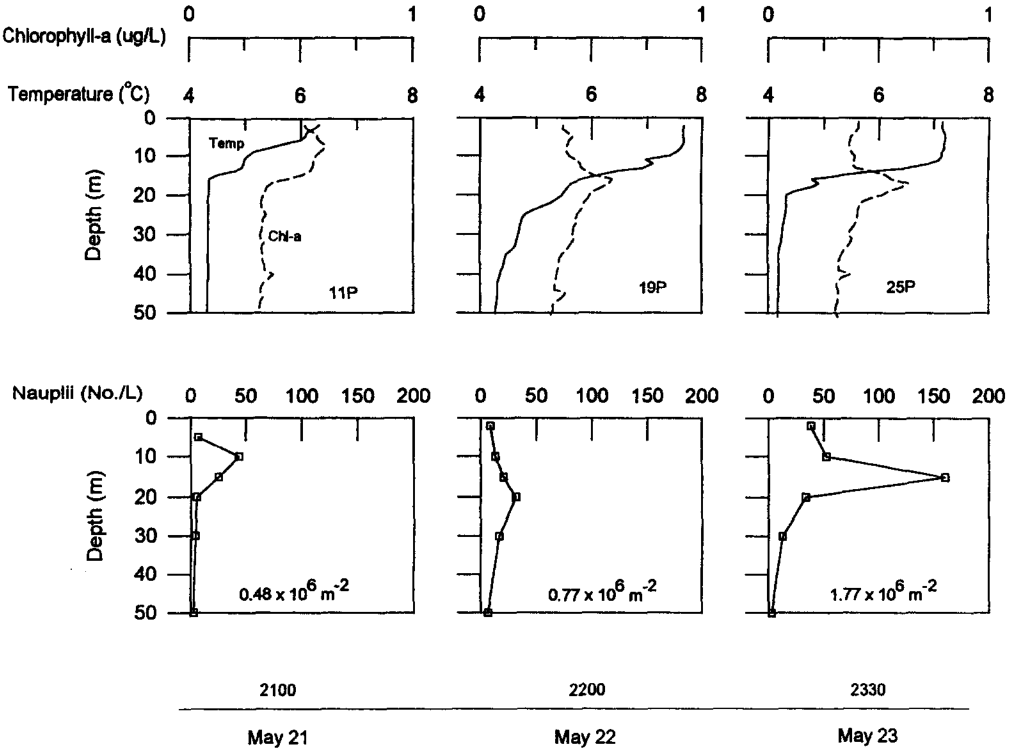

Fig. 3. Information as in Fig. 2, but for the mooring site, stations 11P, 19P and 25 P (Table 1). Day and time of sampling are shown at the bottom.

the median depth of samples in the upper mixed layer (Table 2), the observed 6-h average wind speeds generated dissipation rates from 4.3×10^{-7} to $3.8 \times 10^{-5}\,\mathrm{W\,kg^{-1}}$. For the lower layer, the tidal mixing Equation (1) gave turbulent dissipation rates from 3.1 to $5.3 \times 10^{-8}\,\mathrm{W\,kg^{-1}}$, depending on depth of the bottom layer. These values are much lower than those shown by Horne *et al.* (1996) and measured in the study area in 1995 by Oakey (unpublished data). We used our characterization of the recently measured dissipation rates from Oakey for estimating turbulence impacts because Equation (1) has recognized limitations for this application, and because measurements provided a reasonable scaling of turbulence in the pycnocline ($1 \times 10^{-8}\,\mathrm{W\,kg^{-1}}$) relative to the lower layer ($1 \times 10^{-6}\,\mathrm{W\,kg^{-1}}$). Results shown in Table 2 are based on calculations where the turbulence scale (Equation (3)) is equal to the perceptive field and not to the average separation distance between prey. We deal with the sensitivity of the model to this scaling in the Discussion.

In the stratified area, the highest values shown for the ranges of naupliar concentrations and encounter rates are nearly all due to the influence of three stations: 24, 25 and 28. These stations had the four highest values in the upper layer, the five highest in the thermocline, and eight of the nine highest in the bottom layer. These stations had only a small effect on median values for "naupliar concentration", "$C-1$" and "$C-2$" in the upper layer and pycnocline. In contrast, bottom layer values were affected substantially: removing the three stations reduced the medians to approximately one half of the values listed in Table 2. We

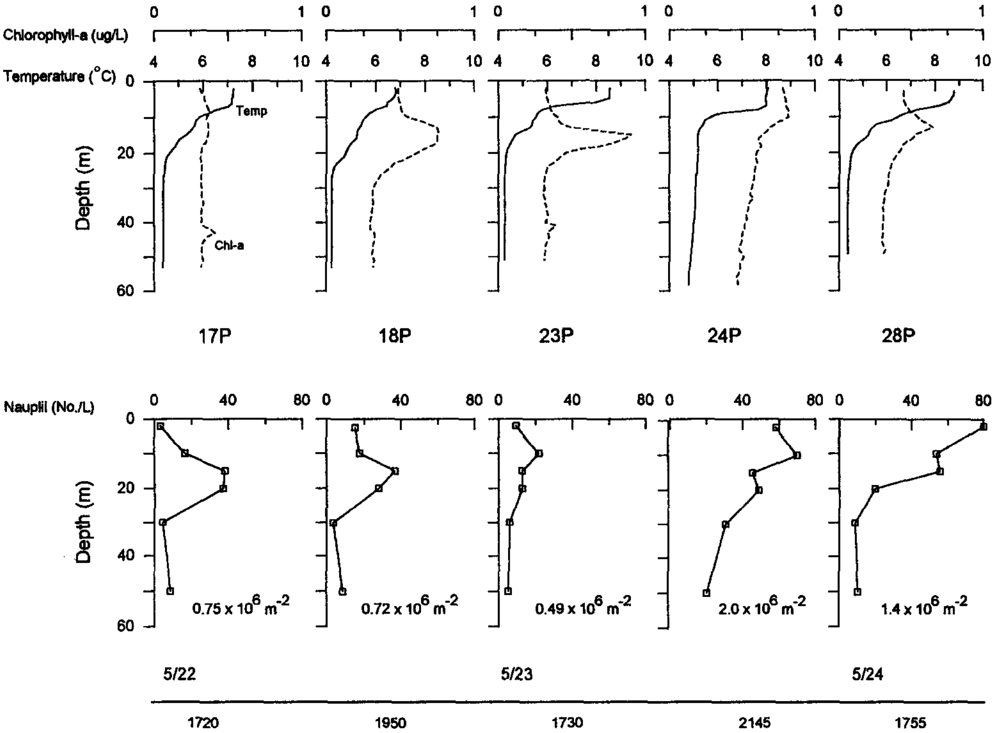

Fig. 4. Information as in Figs 2 and 3, but for the drifter stations. Date and time of sampling are shown at the bottom; details are in Table 1.

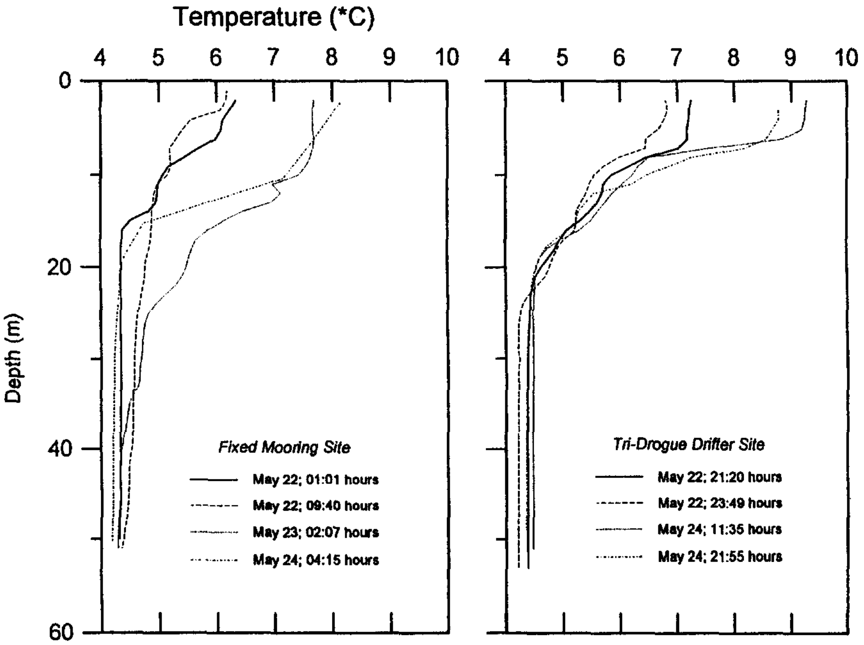

Fig. 5. Changes in temperature profile at the mooring and drifter stations over a two-day period.

Table 2. Prey field conditions and theoretical encounter rates at stratified ($n = 9$) *and mixed* ($n = 2$) *sampling stations*

Area/Layer	Number of Samples	Depth (m)	Nauplii (No. l^{-1})	$C-1$	$C-2$	
Stratified						
Upper	13	2.5 (2–10)	15.0 (5–80)	0.30 (0.10–1.60)	0.59 (0.17–5.04)	
Thermocline	15	15.0 (10–20)	32.5 (13–160)	0.65 (0.25–3.22)	0.77 (0.30–3.46)	
Bottom	23	30.0 (15–50)	9.0 (3–49)	0.17 (0.05–0.98)	0.36 (0.12–2.06)	
Mixed	10	15.0 (2–30)	4.5 (2–6)	0.09 (0.03–0.12)	0.14 (0.05–0.22)	Wind
					0.19 (0.07–0.25)	Tide
					0.22 (0.07–0.27)	Both

Encounter rates (C: prey cm^{-2} s^{-1} × 100) are shown without ($C-1$) and with ($C-2$) turbulence for various portions of the water column. Data include the number of samples per layer and the median (range) of values for each grouping of data. $C-2$ values are shown separately for wind and tidal forcing in the mixed area as well as for the combined forcing.

did not pursue separate analyses with these stations because of the small sample size that would have resulted.

Turbulence calculations produced increases in C as follows: from 34 to 219% in the upper mixed layer, depending on wind speed and depth; approximately 8% in the pycnocline; and approximately 110% below the pycnocline. These increases modified the vertical profile of contact rates by decreasing the difference between the two mixed layers and the pycnocline (Table 2). Without turbulence, the pycnocline had the maximum contact rates at seven of the nine stratified stations; with turbulence the pycnocline had a clear maximum at only four of the nine. The wind-mixed layer had the maximum in all other instances. At two stations the bottom layer had predicted contact rates similar to or greater than the pycnocline, a prediction that did not exist in the absence of turbulence. Contact rates in the mixed area were lower than most estimates for the stratified area when tides or winds were considered alone. Combining dissipation rates from the two sources of mixing increased the predicted contact rates, but these remained low relative to the stratified area (Table 2). Converting from the units in Table 2 by using the predator cruising speed (as previously, $v = 0.2$ cm s^{-1}) gives rates up to 2 prey h^{-1} in the mixed area and from 0.8 to 15.7 h^{-1} below the pycnocline in the stratified area. Minimum and maximum theoretical contact rates for the upper layer occurred at stations 11P and 28P due to combined effects of naupliar concentration and wind speed (1.1 and 38.5 prey h^{-1}, respectively). Within the pycnocline the range of contact rates was 2.3–26.5 prey h^{-1}.

Most nauplii were in early stages, NI or NII, and most were between 190 and 225 μm total body length. Differences in size distribution between stratified and mixed sites were minor and possibly attributable to the smaller sample size at well-mixed stations. At stratified stations, there were no notable differences in size distribution with depth except at 50 m, where there was often a more homogeneous distribution of sizes (Fig. 6).

The size frequency distribution of organisms sampled by pump ($n = 176$ organisms counted and measured) and bottle ($n = 151$) were very similar (Fig. 7), differing mostly at 50–150 μm body length. There were no statistically significant differences in the binned size–frequency distribution for each bottle-pump pair (t-test, $P < 0.05$). A taxonomic comparison of the pooled bottle vs pump samples (Fig. 8) indicates that most taxa were sampled with

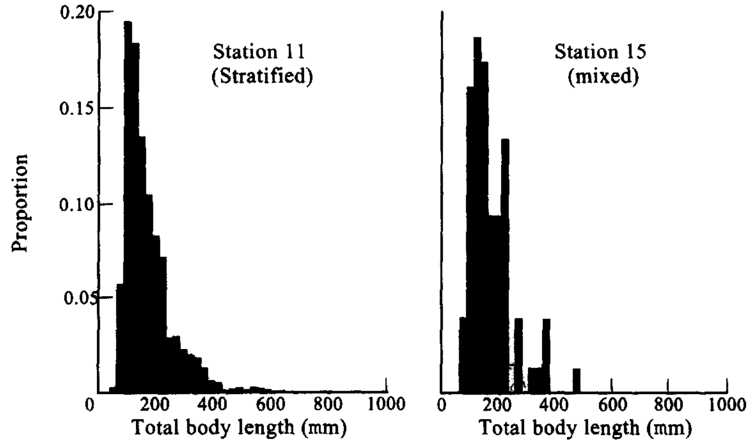

Fig. 6. Size (total body length) frequency distribution of copepod nauplii at a stratified and mixed station.

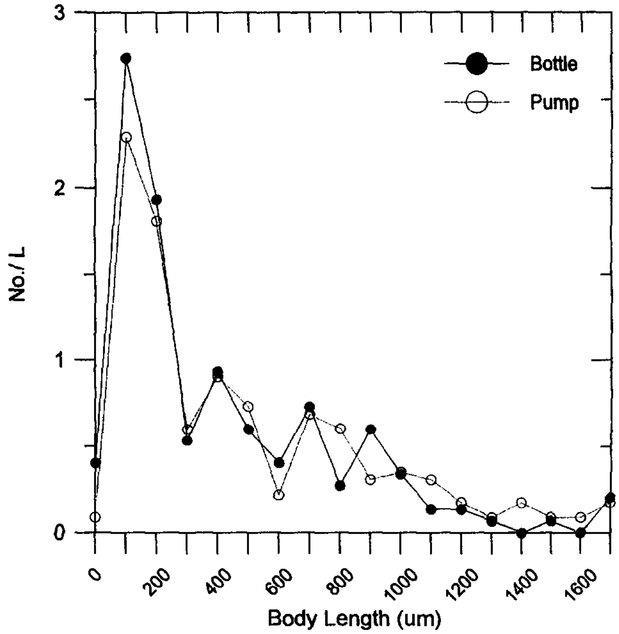

Fig. 7. Frequency distribution of all organisms in 100 μm length groups, comparing pooled pump and bottle estimates.

similar efficiency, although the numbers of some were too low for independent evaluation. Bivalve larvae were the only organisms that showed a clear and consistent bias in the data between pump and bottle collections. This group comprised an average of 5.6% of organisms in the bottle samples (range =2.6–8.9%) but 21.1% of pump samples (range = 18.8–22.9%). Concentrations of copepod nauplii sampled by the two methods were as follows, as no. l^{-1} for each bottle–pump pair: 4.2 vs 3.4; 3.2 vs 1.7; and 3.4 vs 3.2—all

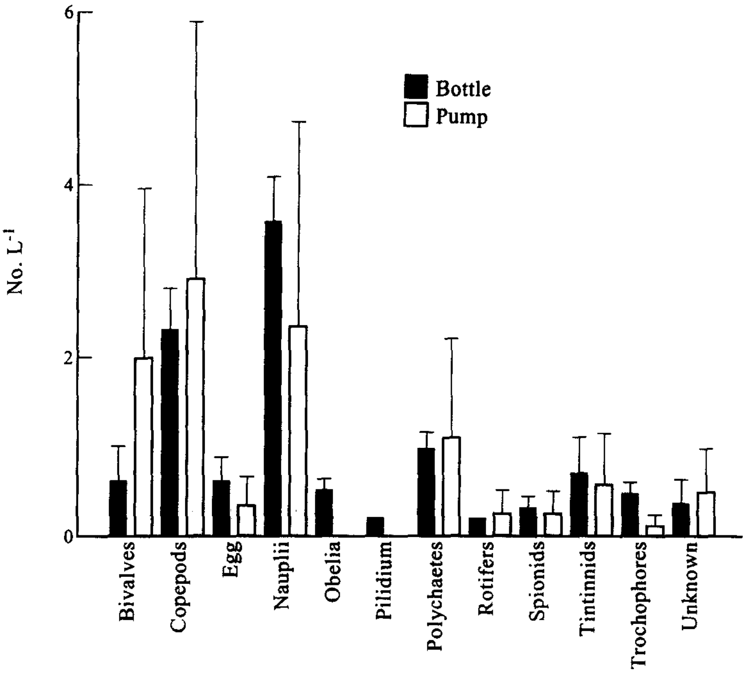

Fig. 8. Taxonomic comparison of pump and bottle samples from three sequential samples (mean + 1 standard deviation are shown).

quite close except in the middle pair. The low pump concentration in the middle pair applied to total organisms as well, which were (no. l^{-1}): 11.2 vs 12.5; 11.2 vs 6.2; and 7.8 vs 10.3.

DISCUSSION

For many years studies have focussed on the abundance of prey organisms as an important environmental factor affecting the growth and survival of larval fish (Peterman and Bradford, 1987). Most laboratory work has indicated that prey are needed at concentrations much greater than found in the field. As a result, much effort has been focussed on resolving potential experimental artifacts and considering the possible effects and importance of prey patches, including those created by vertical distributions of prey organisms. The first approach was predicated on the assumption that laboratory results overestimated larval needs; the second recognized that field concentrations could be locally higher than most sampling efforts reveal. Both considerations have been shown to be valid, but recent theoretical (Rothschild and Osborn, 1988) and field (Sundby and Fossum, 1990) studies of the role of turbulence in feeding relationships add to the list of factors that must be considered. These studies call for modifying how we interpret vertical patterns of larval fish and their prey, as well as other trophodynamic relationships. MacKenzie and Leggett (1991, 1993) provided useful theoretical treatments of turbulence-induced effects on larval feeding conditions and showed that the formulation for wind-induced turbulence works well over the range of wind velocities encountered in this study. In this paper we have used some of these concepts to examine the feeding environment for larval cod on Georges Bank using actual wind speeds, average tidal velocities, turbulence dissipation rate measurements, and observed naupliar concentrations. Our estimates include upper and lower mixed layers and the pycnocline, thanks to the availability of suitable data for the latter two (Horne *et al.*, 1996; Oakey, unpublished data). The earlier work of Sundby and Fossum (1990) on Arcto-Norwegian cod larvae was confined to the wind-mixed layer because that is where their larvae occurred, and MacKenzie and Leggett (1991, 1993) did not attempt to include the added complication of a pycnocline in their model development. Lough and Mountain (1996) estimated turbulence for all three layers following a separate series of derivations. They obtained a decrease of turbulent dissipation rates in the pycnocline of 1–2 orders of magnitude, but in general had values that were lower than ours. Werner *et al.* (1996) used a three-dimensional model of circulation on Georges Bank (Lynch *et al.*, 1996) and obtained turbulence estimates close to ours: generally greater than 10^{-6} W kg^{-1} within the bottom boundary layer and never less than that value in the well mixed area. They had values as high as 10^{-5} W kg^{-1} where water depth was 40 m or less, but our shallowest sites were still slightly deeper at 44 and 50 m.

On Georges Bank, cod larvae can be very abundant in the pycnocline and they occur both above and below it, so it was necessary to consider how feeding conditions might vary from one layer to the next. Our calculations show that differences in turbulence levels increase the theoretical contact rates in the upper and lower layers relative to the pycnocline, although the latter appears to remain important for feeding because of generally elevated prey concentrations. While the trends are quite clear, the absolute values of our estimated contact rates are tentative for several reasons, of which the following are prominent. First, instantaneous profiles of turbulence are extremely variable (Horne *et al.*, 1996). We have used average values that permit general comparisons in the vertical. Because larval nutrition integrates feeding success over periods of several hours or more, this averaging may be reasonable for purposes of this paper, but it clearly ignores the richness of the underlying dynamics.

Second, within the lower mixed layer dissipation rate decreases away from the bottom boundary. Our use of a single value for ε ignores this pattern and systematically underestimates the potential enhancement of contact rates closer to the bottom, although our application remained distant enough (20 m or more) from the bottom to avoid the most severe problems. The single value is perhaps low for the mixed area (Werner *et al.*, 1996) and ignores time-dependent changes due to tidal phase (Horne *et al.*, 1996) and movement over variable bottom depths.

Third, the swimming and feeding behaviors of larvae and prey are over-simplified in our equations, which use a single cruising speed instead of a pause–travel mode of predation (Skiftesvik, 1992; MacKenzie and Kiorboe, 1995). The velocity we have used for a cruising cod larva may be low as an absolute speed, but may not be so bad considering that we have not included feeding activity in our budget of the larva's time. Calculations using our data readily show (also MacKenzie and Leggett, 1993) that predator swimming speed has a significant effect on the absolute rate of predation [equations (4) and (5)]. As larval swimming speed decreases, contact rates also decrease, but turbulent velocity assumes a greater role in mediating those rates. Consequently, turbulence has a greater impact on vertical profiles of C for slower-swimming larvae. Errors in the assignment of prey swimming speed produce a minor effect in Equation (4), but the treatment ignores possible escape responses outside the predator's radius of detection.

Fourth, the encounter rate as we have used it is merely an expression of "near approach" that focusses on the spatial relationship. We purposely avoided the many biological parameters, involved in prey detection and successful pursuit, that are poorly known and almost certainly are highly variable. From the viewpoint of encounter probability, turbulence enhances feeding only when prey density is below levels supporting maximum feeding activity by the predator. Absolute, as opposed to relative, rates of encounter and feeding success are needed before the true role of turbulence can be evaluated. Thus, while our comparisons indicate that apparent prey densities are modified by turbulence, an understanding of how these turbulence-modified profiles of relative encounter rate translate to vertical patterns of feeding success will require much further work. The patterns of distribution of nauplii and larvae result from behaviors we know relatively little about, and there may be things about the pycnocline, for instance, that provide advantages for larvae that are not revealed by simple models of encounter.

Finally, the population-level impact of differences in potential encounter rate depends on the vertical distribution of cod larvae during periods when they feed. On this matter we have some population mean data (e.g. Lough and Mountain, 1996), but almost no insight at the level of individual survivors. We know, for example, that cod larvae show a variety of vertical distributions (Lough *et al.*, 1996) and that prey also exhibit a variety of distributions (Fig. 4, this paper), but concurrent data on predators and prey are comparatively scarce. Mean data, whether describing prey separation distances, larval swimming speeds, predicted encounter rates or turbulence, likely skew our prediction of biologically important interactions.

Another issue with our treatment of turbulent velocities in the model is the scaling of biological interactions and their relationship to turbulence. We mention three important aspects here. First is the appropriate length scale for calculating turbulent velocities. Selecting the average prey separation distance (instead of reactive distance) as the relevant scaling factor greatly increases the relative importance of turbulence to the encounter rate, more so as prey concentration decreases because the distance (length) scale for turbulent input increases. This can be seen by making appropriate substitutions in Equation (3) and following them through subsequent calculations. The relationship of various mixing length scales to encounter rates needs further development, as the processes at the various scales are interconnected. Second is the appropriate statistical distribution of these distances. The mean separation (Poisson distribution) ignores patchy distributions and may lead to significant over-estimation of the distances involved in many interactions [Equations (3) and (5), this paper; see Rothschild, 1992]. We noted a similar problem above with the use of single "characteristic" values of epsilon for the pycnocline and lower layer. While not technically accurate, we felt that this approximation served the purposes of this paper acceptably. That it ignores the possible relationship between prey patches and turbulence as well as the interrelationship between these conditions and larval feeding should be noted. The patchiness of prey distributions and turbulence at time and space scales relevant to cod larvae and their prey is too dynamic to map simultaneously with current methods, but it may be possible to treat the interactions statistically (Rothschild, 1992). Third is the question of whether turbulent eddying motions are involved in the encounter rate of the particles being considered (Hill *et al.*, 1992, Denman and Gargett, 1995). The Kolmogorov scale (η) is used to express the smallest eddy size in a fluid:

$$\eta = (v^3/\varepsilon)^{0.25}$$

where v is the kinematic viscosity ($\sim 1.05 \times 10^{-2}\,\mathrm{cm\,s^{-1}}$) and ε is the turbulent dissipation rate, as above. The Kolmogorov length scale for interactions between particles differs from this scale such that:

$$K_\eta = 2\pi\eta^{-1}$$

(Denman and Gargett, 1995). The Kolmogorov length scale for the lowest dissipation rate used in our study is 0.20 cm, a value close to the length scale (reactive distance) we used for interacting predator and prey: $R = 0.26$ cm. A recent behavioral study by MacKenzie and Kiorboe (1995) gives a larger reactive distance for small cod larvae: $R = 0.43$ cm for larvae of 0.52 cm SL. This would substantially increase the encounter rates we calculated [Equations (3) and (5)]. Equation (5) may not properly represent the volume of effective search, however, and the calculated encounter rate is sensitive to this parameter as well. With these uncertainties in mind, it is clear that our estimations remain suggestive. Variations in encounter rates and turbulent enhancement of those rates are extremely dependent on refinement of the biological parameters used. Our extremes of data, including all depths sampled, suggest possible encounter rates between cod larvae and copepod nauplii in the stratified area ranging from 0.8 to 38.5 prey $\mathrm{h^{-1}}$ and, in the mixed area, from 0.6 to 2.0 prey $\mathrm{h^{-1}}$. The range spans more than one order of magnitude in the vertical at individual stratified stations, a similar amount in the horizontal among the various layers at stratified sites, and a similar amount between stratified and mixed areas. The two mixed sites showed only small differences between them or in the vertical. That cod larvae in the mixed area were in apparently good condition at the time of our sampling suggests that they were relying on other prey (Lough *et al.*, 1996).

Although the Lagrangian drifter showed less evidence of change in hydrographic conditions than the mooring site, there appears to have been considerable slippage of the upper 10 m, as evidenced by both temperature and nauplii. The changes did not occur at a constant rate or even in the same direction (increase or decrease) through the series. It is interesting that the pycnocline population of nauplii remained fairly consistent for most of the series, but 23P was a clear anomaly in many respects and we don't have enough information to offer an explanation.

Our comparison of pump and bottle samples shows that pumping can be used for sampling small zooplanktonic taxa when there is advantage to it, for example when one wishes to sample larger and rarer organisms at the same time (e.g. Rahkola *et al.*, 1994). Another advantage, not used in this study, is that sampling casts could be repeated more quickly and/or frequently than with bottles, and pumped samples are amenable to automated recording and counting techniques. In our study, the pump enabled us to sample from a larger volume of water than the Niskin bottles while maintaining accurate control over depth (sea state permitting) and sampling volume, which is more time-consuming and difficult to do with a towed net. In fact, the *ca* 15.5 l that we sampled is a subsample of a much larger volume, *ca* 5.2 $\mathrm{m^3}$, that could not be handled by nets or bottles as quickly as we did here. The greater variance from the pump sample resulted from the middle cast. The CTD was not raised and lowered each time a bottle was closed, and it is possible that the bottles were not as sensitive to spatial/temporal differences in plankton when compared with the pump intake, which was always fully exposed to any relative motion between the vessel and surrounding water. The differences in sampling of bivalve larvae were not necessarily related to the added waiting period between bottle closings, as even the first bottle contained comparatively few. The first bottle followed normal sampling procedures in that there was little delay between arrival at depth and closing.

Because of its considerable diameter, the large volume hose was limited in high wind and sea state, and this prevented us from sampling through the wind event that began at Station 28P. A smaller diameter hose, or modified methods of deployment, might have advantages in extending the capability of this method.

Acknowledgements—We thank J. Green for help with pump deployments, J. Shaffer and D. Phinney for chlorophyll analysis, and J. Churchill, A. Epstein and J. Manning for providing CTD data. R. G. Lough shared preliminary data on larval cod lengths and vertical distributions. N. Oakey provided turbulence data and, with D. Hebert, engaged in helpful discussions about turbulence. Our manuscript was improved by comments from two anonymous reviewers and B. MacKenzie. This is contribution no. 63 of the U.S. GLOBEC program, funded jointly by the National Oceanic and Atmospheric Administration and the National Science Foundation.

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