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Relationships among vertically structured *in situ* measures of turbulence, larval fish abundance and feeding success and copepods on Western Bank, Scotian Shelf*

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ABSTRACT

Using vertically stratified data of the abundance of silver hake (*Merluccius bilinearis*) larvae and concentrations of copepods collected in the field, we examine relationships among the vertical distribution of larval fish, their potential prey, feeding success and water column turbulence. Water column turbulence and associated stratification parameters were estimated from: (i) *in situ* measures of turbulent kinetic energy dissipation (ε) provided by an EPSONDE profiler; (ii) *in situ* wind speed; (iii) the Richardson number (*Ri*); and (iv) the buoyancy frequency (N^2). Small (< 5 mm total length) silver hake were more abundant in the least turbulent waters (i.e. at a minimum in the rate of dissipation of turbulent kinetic energy, $\varepsilon < 10^{-7}$ W kg^{-1}; $Ri > 0.25$; $N^2 > 0.001$ (rad s^{-1})^2). Partial correlations amongst ε, N^2 and small hake larvae were significant only for N^2. The abundance of larger (> 5 mm total length) hake larvae was positively correlated with depth and was not associated with either ε or N^2. Vertical distributions of three potential prey (classified by stage) were variable. Early stage copepodids were positively correlated with N^2 and negatively correlated with ε. We found no evidence of diel distribution patterns for small (< 5 mm total length) hake larvae or for any of the developmental stages of the copepods examined. Neither estimate of water column turbulence inferred from wind speed nor from *Ri* was meaningfully related to *in situ* estimates of ε or to larval fish abundance. Feeding success, measured either as prey items (gut)$^{-1}$, average prey length, or total prey volume (gut)$^{-1}$, was not related to predicted encounter rates between days. However, the average prey length (gut)$^{-1}$ was significantly ($P < 0.01$) related to water column turbulence. These conflicting results suggest that the relationship between larval feeding and the environment is more complicated than assumed. We conclude that without substantial high resolution *in situ* examination of the relationship between the vertical distributions of turbulence, larvae and their prey, the growing acceptance in the secondary literature that turbulence has a positive and biologically meaningful effect on trophic interactions between fish and their zooplankton prey (a generalization based largely on modelling and laboratory experiments) is premature.

Key words: feeding success, *Merluccius bilinearis*, silver hake, TKE dissipation, turbulence

INTRODUCTION

Rothschild and Osborn (1988) formalized the general hypothesis that turbulence, generated by wind or other forces, may enhance the survival of planktonic predators in food-limited environments through an increase in the prey encounter rate. They made four specific predictions: (i) both predator and prey may adjust their vertical position to take advantage of turbulence variation in the water column; (ii) the structure of prey patches will depend on the relative velocities and the relative concentrations of predator and prey; (iii) vertical nutrient fluxes will be enhanced in nutrient-limited environments; and (iv) turbulent processes provide a link between large scale oceanographic phenomena (wind speed) and microscale events (feeding success).

Subsequent to the Rothschild and Osborn paper, considerable effort has been expended in extending

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the general hypothesis beyond the original concept (targeted at zooplankton) to the feeding, growth and survival of fish larvae. The effort relates to both theoretical and empirical studies (Sundby and Fossum, 1990; Mackenzie and Leggett, 1991; Mackenzie *et al.*, 1994; Sundby *et al.*, 1994; Kiørboe and Mackenzie, 1995; Mackenzie and Kiørboe, 1995; Mackenzie and Kiørboe, 2000), especially regarding the fourth prediction (above), that is difficult to operationally define and to quantitatively test. In general, field studies have examined measures of larval feeding success as a function of turbulence inferred either from wind mixing (e.g. Sundby and Fossum, 1990; Sundby *et al.*, 1994; Lough and Mountain, 1996; McLaren *et al.*, 1997) or from measures of stratification (e.g. Incze *et al.*, 1996; Dower *et al.*, 1998). The different results showed feeding success sometimes to be a positive function of ε (here the inferred dissipation rate of turbulent kinetic energy), sometimes a negative function, and in some cases ε explained a small proportion of the variation in feeding success (e.g. Sundby and Fossum, 1990; Sundby *et al.*, 1994; McLaren *et al.*, 1997; Dower *et al.*, 1998). For example, McLaren *et al.* (1997) examined feeding in cod (*Gadus morhua*) larvae (mean length 5 mm) over a 23-day period and concluded that feeding success was negatively associated with turbulence (inferred from wind speed) and the latter explained just 1% of the variation in gut content. Dower *et al.* (1998) examined feeding success in relation to prey size and turbulence over a 3-week period. They inferred turbulence from estimates of the Richardson number, *Ri*, the ratio between the vertical gradient in density (that acts as a stabilizing force) and the vertical shear (the gradient in velocity that acts as a source of turbulence), and found that size-adjusted feeding success [prey items $(\text{gut})^{-1}$] decreased under conditions of low *Ri*. However, they also found that the average size of prey in a gut and total volume of prey in a gut increased with low *Ri* and that *Ri* explained ~ 20% of the variation in total volume of prey in a gut.

One important assumption of the 'turbulence hypothesis' (feeding as a function of turbulence) is that plankton must adjust their vertical position in the water column 'to take advantage of permanent, semi-permanent or periodic, localized, turbulent motion to capture prey or avoid predators' (as postulated by Rothschild and Osborn, 1988, p. 472) or to secure some optimal (or average) level of ε that would maximize prey encounter rates. Laboratory experiments have shown that the behaviour of larval fish changes in areas of potentially high prey encounter rate or concentration such that the number, frequency and acuity of turns increases, while the swimming velocity decreases (Dower *et al.*, 1997). A result is that the daily ambit of larvae decrease; possibly leading to aggregations within the water column. A consequence may be a concentration of larvae at the pycnocline or at other discontinuities that exhibit a greater than average prey encounter rate or greater than average prey concentration (Mackenzie and Leggett, 1991; Sclafani *et al.*, 1993). The most striking omission in the study of larval fish feeding as a function of turbulence is the paucity of concomitant *in situ* profiles of turbulence, larval fish and their prey (see Mackenzie, 2000 for most recent review). Turbulence varies with depth (Oakey, 1982). Thus, it seems that vertically structured sampling of a natural environment should be the simplest way to directly examine larvae and their prey in relation to turbulence, and to determine what proportion of the larval population may benefit from the increased turbulence that is predicted to enhance encounter rates (Franks, 2001). Despite the above shortcomings, the turbulence hypothesis, at least as it relates to plankton contact rates, is fast becoming an integral part of numerical modelling (e.g. Davis *et al.*, 1991; Werner *et al.*, 1996; Hannah *et al.*, 1998; Leising and Franks, 1999) and is becoming entrenched in the secondary literature (cf. Mullin, 1993; Bakun, 1996; Mann and Lazier, 1999).

As early as the first attempt to examine the postulates of Rothschild and Osborn (1988), Sundby and Fossum (1990) clearly stated that knowledge of the vertical distribution of the predator, their prey, and turbulence was necessary to address the influence of turbulence on the contact rate between fish larvae and their prey (in their case nauplii). We know of only one study (Gallego *et al.*, 1999) where turbulence was measured directly and *in situ*, although from a biological perspective very broad depth strata and very large mesh-nets were employed and many of the small larvae were likely missed. Missing small larvae matters because, according to theoretical arguments (Mackenzie and Kiørboe, 1995) and empirical observations (Dower *et al.*, 1998), it is the small larvae that should benefit most from enhanced encounter rates. In another study, Sundby *et al.* (1994) examined the feeding ratio of larvae collected at different depths where they were presumably exposed to different degrees of turbulence as inferred from wind speed. Some of their results were ambiguous and they concluded that some aspect of the assumed relationship between the vertical distributions of turbulence, predators and prey were involved, but not resolved. Failure to specifically resolve the vertical distributions will bias any functional relationship implied by conceptual models or imposed by numerical simulations (e.g. Leising and Franks, 1999), and may thus result in ambiguous field tests (e.g. Sundby *et al.*, 1994).

In summary, it appears that several of the postulates above, presented by Rothschild and Osborn (1988), remain untested. Here, we report on a 36-h study involving *in situ* vertical measures of turbulence, larval fish, and potential prey. The data are used in an attempt to test two null hypotheses that stem directly from Rothschild and Osborn (1988): (i) there is no relationship between turbulence and larval fish abundance or size distribution and/or prey concentration; and (ii) the feeding success of small larvae is independent of encounter rate as predicted using a generally accepted encounter model that employs observed variations in turbulence. These hypotheses are evaluated using direct observations of larvae, prey concentrations, larval feeding success and the rate of turbulence kinetic energy dissipation, ε (intensity of the turbulence field, assuming that turbulence energy generation is balanced at small scales by viscous dissipation) estimated using EPSONDE (Oakey, 1988).

METHODS AND MATERIALS

Biological samples and physical measurements were collected over a 36-h period of 8–9 October, 1998 within in a 15 × 15 km area near the crest of Western Bank on the Scotian Shelf in the NW Atlantic (Fig. 1). This region is a known source of high concentrations of larval fish (Reiss *et al.*, 2000). We repeatedly measured hydrographic structure, vertical distributions of plankton (copepods and larval fish) and the dissipation rate of turbulent kinetic energy (ε).

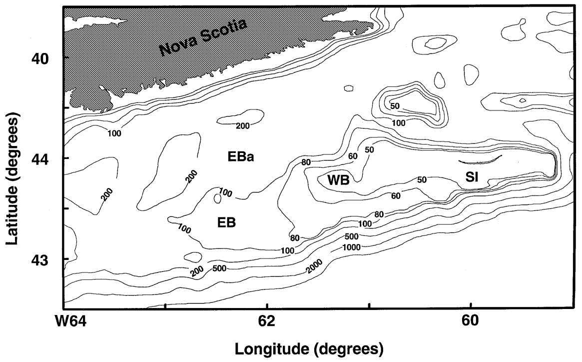


Figure 1. Bathymetric (m) chart of the Scotian Shelf showing Emerald Bank (EB), Emerald Basin (EBa), Sable Island (SI) the location of the meteorological station and Western Bank (WB) the location of the 36-h diel sampling series during the period 8–9 October 1998.

This study was part of the Canadian Global Ecosystems Dynamics (GLOBEC, Canada) program investigation of physical-biological coupling on Western Bank conducted from 28 September to 21 October, 1998 (Hazen and Reiss, 1999). Sampling over the 36-h period occurred in cycles that were repeated every 3–4 h. Each cycle (a total of nine cycles with 37% at night) was represented by a sequence of measurements (as listed below) consisting of: (i) conductivity (C), temperature (T) and depth (D) profiles from which salinity and density profiles were calculated; (ii) turbulent dissipation rate (ε) profiles; (iii) small-mesh depth-discrete net collections of zooplankton; and (iv) large-mesh depth-discrete collections of larval fish and zooplankton.

Hydrographic, current and meteorological data

Each sampling cycle was initiated with a hydrographic cast to within 2 m of the bottom using a CTD (SBE-25, Seabird Electronics Inc., Bellevue, WA) equipped with a fluorometer (Sea Tech Inc., Philomath, OR). CTD data were depth-averaged into 1-m depth strata. Depth-structured currents were estimated using a hull-mounted Acoustic Doppler Current Profiler (ADCP; RDI Inc., 150 *kHz* narrow-band) configured to continuously resolve currents in 4-m depth strata using four pings per ensemble and profiles were averaged and stored at 2-min intervals. Wind speed and direction data were recorded hourly from the ship's mast-mounted sensors. Hourly wind speed and direction data were also obtained from the Sable Island meteorological station (courtesy of the Atlantic Climate Centre, Canada) located ~80 km due east of our sampling site. The latter data were considered more reliable than the measurements from the ship, and were used to compute the surface wind stress, τ ($\mathrm{N\ m^{-2}}$), using the formulation of Smith (1988). Wind energy flux from the atmosphere to the ocean was estimated as $E10 = \tau\, U10$ ($\mathrm{W\ m^{-2}}$), where $U10$ is the wind speed at 10 m above surface (Oakey, 1982).

Turbulence estimates

Estimates of ε (and other turbulence quantities), as a function of depth, were derived from the intensive profiling cycles using EPSONDE (Oakey, 1988), a tethered free-falling profiler (2.4 m long, 0.14 m diameter) equipped with a CTD and sensors to directly measure velocity ($\mathrm{m\ s^{-1}}$) and temperature (°C) microstructure (mm spatial resolution). Velocity microstructure, from which estimates of ε are made, is mechanically measured using airfoil shear-probes built at the Bedford Institute of Oceanography (Neil Oakey, Dartmouth, NS Canada). Temperature microstructure, from which the dissipation of temperature variance (χ;°C^2 s^{-1}) and the vertical heat-flux eddy diffusivity (K_T; m^2 s^{-1}) can be estimated, is measured using two, fast thermistors. The instrument free falls from the surface (at approximately 1 m s^{-1}), outboard of the ship, on a loose Kevlar multiconductor cable. Data were transmitted from EPSONDE to a shipboard PC for data logging and initial signal processing. 'Bursts' of 16–19 sequential profiles were collected during each cycle. The duration of each burst was ~1 h (i.e. one profile every 3–4 min).

Wind speed (U) was used to estimate the depth-averaged rate of turbulent kinetic energy (TKE) dissipation (ε_w; W kg^{-1}) in the upper mixed layer ($\sigma_t < 23.5$) by using the constant stress layer model, where $\varepsilon_w = u^{*3} (\kappa z)^{-1}$, and $u^* = (\tau/\rho_w)^{0.5}$ is the friction velocity, τ is the wind stress, and ρ_w is the density of sea water, κ is von Karmann's constant (0.4) and z is depth (m). Oakey and Elliott (1982) estimated ε over a 7-day period at a range of wind speeds and their measurements indicated that a constant fraction of the wind energy flux dissipated in the mixed layer. Throughout, we will call ε_w the wind-based estimate of turbulence to differentiate it from ε estimated directly from the EPSONDE probe.

The Richardson Number (Ri), a measure of the relative strength of the stabilizing effect of buoyancy to the destabilizing effect of vertical current shear, was calculated as: $Ri = N^2/[(\partial u/\partial z)^2 + (\partial v/\partial z)^2]$; where $N = [(-g/\rho_0)(\partial \rho/\partial z)]^{0.5}$, the Brunt–Vaisala frequency; ρ_0 is a reference density (kg m^{-3}); g is the gravitational constant (m s^{-2}); and u and v are the along- and across-bank current velocities (m s^{-1}) as estimated from the ADCP within each depth stratum. This measure is similar to that used by Dower *et al.* (1998).

Biological sampling

Discrete-depth vertical net tows for collecting zooplankton were made using a 50-cm diameter, 64-μm mesh closing ring net. Five depths were sampled during each of the nine cycles for a total of 45 plankton samples. The open net was attached to a fixed wire-frame, and lowered (codend first) to the bottom of the selected depth stratum and then raised at ~1 m s^{-1} to the top of the stratum where the net was mechanically closed. The volume sampled was estimated by multiplying the area of the net by the depth of the stratum. In general, five depth-strata were sampled (0–7, 7–14, 14–21, 21–28 and 28–35 m) to provide filtered volumes of ~1.7 m^3 stratum^{-1}. These strata were selected to include the upper mixed layer, the fluorescence maximum, and the subpycnocline. Vertical net tows did not extend as deep (35 m maximum, but always below the pycnocline) as the BIONESS (44 m maximum; detailed below). Plankton collected with the ring-net were preserved in 5% (vol : vol) buffered formalin : seawater.

Each sampling cycle was completed with the deployment of a BIONESS (Open Seas Instruments, Musquodoboit Harbour, NS, Canada), a multiple net sampler equipped with sets of 1 m^2 opening/closing 333-μm mesh nets, a Seabird CTD, pitch and roll sensors, and internal and external flowmeters (General Oceanics, Inc., Miami, FL), used to collect fish larvae and zooplankton within depth strata. Typical deployments began with an oblique tow from the surface to the maximum depth (~44 m, nominal 10 m above bottom) followed by a return tow that was divided into strata (a new net for each stratum) according to the fluorescence profile retrieved from the preceding CTD cast. Each tow was ~30 min duration. Five nets were generally employed to fish: (i) the entire water column; (ii) below the fluorescence maximum; (iii) the lower shoulder of the maximum; (iv) within the maximum; and (v) immediately above the maximum to ~5 m below the surface. Each net, during each deployment, nominally filtered 270 m^3 of water (range 100–500 m^3) at a nominal tow speed of 1 m s^{-1}. Plankton from the oblique tow was preserved in 95% (vol : vol) ETOH: freshwater to protect larval otoliths, while plankton from the remaining nets was preserved in 5% (vol : vol) buffered formalin : seawater.

Laboratory analysis

Fish larvae were removed from all plankton samples, identified to species and enumerated. Silver hake (*Merluccius bilinearis*) larvae were measured as total length (TL; ±0.1 mm) under magnification using a video camera and SigmaScan Pro (Ver 5.0.0, SPSS Inc. Chicago, IL). Larvae were assigned to one of three size classes (< 5, 5–9, > 9 mm TL) roughly corresponding to ontogenetic stage. No correction for shrinkage was used. Preliminary analyses showed there was little increase in information content when using more size-classes. Larval fish abundance estimates are expressed as a concentration [number (100 m^3)$^{-1}$].

Zooplankton preserved in formalin from the 64-μm mesh nets were used to enumerate invertebrate eggs, nauplii, copepodids and copepod adults. Six samples were inappropriately preserved and so were not used in further analyses. Copepods were divided into three size classes based on developmental stage and species: early stage copepodids (C1 and C2; small); late stage copepodids (C3–C5; medium); and adult. Cyclopoid copepods (*Oithona similis*) were not included in the analyses because they are extremely small, are in relatively high abundance and are rarely consumed by silver hake (< 2% occurrence by number in > 800 guts from larvae 2.7–35 mm TL; C. Reiss unpublished data), or by other larval fish in the region (McLaren and Avendaño, 1995). Copepod abundance is expressed as a concentration (number m^{-3}).

Feeding success

Larval fish used for gut content analysis were randomly selected from each of the formalin-preserved BIONESS samples in proportion to their concentration among collections (as many as 30 fish per sample) for a total of 615 fish (all collections). On average, 16 fish were examined (range 1–30) per sample. Larval stomach contents were examined under magnification, identified and enumerated according to the method of McLaren and Avendaño (1995). Lengths and widths of individual prey items were determined using a calibrated ocular micrometer. Prey item volume was estimated assuming each item was spherical. We evaluated three measures of feeding success: number of prey items per gut (PIPG, number), average prey length per gut (PLPG, mm) and total prey volume per gut (TPVG, mm^3) for small (< 5 mm TL) larvae using fish collected at 12:00 and 16:00 (local time) on each day during the sampling period. These samples were chosen because the samples were collected almost exactly 24 h apart, and because McLaren *et al.* (1997) showed that gut content was strongly related to the time of day. By choosing two periods during the day, we can use ANCOVA techniques to remove the effect of time of day without concerning ourselves that animals may be satiated and not feeding at the end of the day.

Data analyses

Isopleths of T, S, ρ, N^2, Ri and other measures were constructed using simple linear interpolation (MATLAB ver. 5.1, The Mathworks Inc. Natick, MA). Tidal heave (amplitude of the rising and falling tide), and other internal vertical oscillations of the pycnocline, may be problematic when depth is used to describe the vertical distribution of larval fish and copepods. In our data, the depth of the pycnocline (relative to bottom) oscillated several metres with the tide (see Fig. 3). Thus, for all general analyses we stratified the water column into three zones according to the vertical density field (σ_t) and the Richardson Number (Ri): the upper mixed layer where $\sigma_t < 23.5$; a pycnocline layer where $23.5 < \sigma_t < 24.5$; and a bottom layer where $\sigma_t > 24.5$. Concentrations of larval fish and copepod developmental stages were $\log_e$ transformed to stabilize variances (Sokal and Rohlf, 1981). Kruskal–Wallis (K-W) tests were used to assess differences in abundance estimates among zones [mixed layer ($n = 20$), pycnocline ($n = 6$) and bottom layer ($n = 5$)] by pooling all samples >3.5 m depth within zones over the series for direct comparisons with BIONESS tows. The K-W Z-test was used for multiple comparisons between zonal pairs (Sokal and Rohlf, 1981). More detailed analyses were performed using two-way ANOVA to assess the change in vertical distribution of larval fish and copepods as a function of time-of-day. Larval fish abundance estimates from the BIONESS were re-classified into 7-m thick depth strata from the surface to a maximum of 37.5 m for comparisons with the vertical distribution of copepods collected with the ringnet. Pooling larval fish samples in this manner provided between 3 and 5 samples per depth strata. Two-way ANOVA was also used to examine changes in vertical abundance distributions of fish larvae and copepods over the sampling period. Multiple comparisons were made using Fisher's Least-Significant-Difference (LSD) test.

Regression and correlation analysis was used to assess relations between animal abundance and ε, N^2 and depth. For these analyses, each net stratum was grouped with its corresponding environmental variable as estimated by stratum or by mid-stratum depth. For example, fish larvae or zooplankton concentration estimated using BIONESS or a vertical net within a stratum during a given cycle would be compared with ε, N^2 and Ri as estimated within that stratum during the same cycle. Partial correlations were used to examine the correlations between pairs of variables (i.e. abundance and ε or day) when other variables (N^2) were held constant – similar to regressing the residuals of one relationship against other potential independent variables (Sokal and Rohlf, 1981). Abundance estimates of silver hake larvae were lag-correlated (by up to 6 h, one half a tidal cycle) with environmental variables to determine if relationships strengthened or weakened with increasing or decreasing water column energy as a result of tidal processes.

Model used to predict encounter rate

Depth-specific encounter rate estimates [prey items $(\text{min})^{-1}$] for a 5-mm pause-travel predator were calculated for each day (8 and 9 October) of the sampling period following Kiørboe and Mackenzie (1995). The encounter rate (ER) is defined as:

$$\text{ER} = n\pi r^2 f(2/3r + 1.41\tau\omega) \qquad (1)$$

where: n is the depth-specific total potential prey (small + medium + adult) concentration and r is the reactive distance, taken here as a constant function of body size (for a 5-mm larvae it is 4.3 mm) that defines the radius of the search volume of the larvae (Kiørboe and Mackenzie, 1995). The turbulent velocity (ω; m s^{-1}) is estimated as $\surd\ 3.615\ (\varepsilon * d)^{2/3}$; where ε is the *in situ* depth-specific estimate of rate of dissipation of turbulent kinetic energy from EPSONDE profiles; d (m) is the separation distance, here taken equal to r; f is the pause frequency (0.43 s^{-1}); and τ is the pause duration (2 s). This formulation reduces the variability in the search volume to a function of ε, and reduces the variability in the encounter rate to a function of ε and the depth-specific potential prey concentration. The predictions made using this formulation do not include consumption – only encounter rate is predicted. However, we are not overly concerned as the 'turbulence hypothesis' assumes that the number of prey items consumed is some positive function of the number encountered under observed conditions. Further attempts at separating the effects that ε and prey concentration have on the encounter rate can be difficult if the two components of the model vary inversely (Mackenzie and Leggett, 1991).

RESULTS

Meteorological conditions

A relatively calm period of about 10 h, with hourly average wind speeds between 2 and 3 m s^{-1} preceded the 36-h diel study period (Fig. 2). Winds increased immediately prior to the first sampling cycle and subsequently rose to ~8 m s^{-1} over a 4-h period. Average wind speed remained between 6 and 9 m s^{-1} for the ensuing 20 h and then decreased to between 2 and 4 m s^{-1} for a period of ~8 h and finally rose to ~9 m s^{-1} at the termination of sampling (Fig. 2a). South to south-westerly winds dominated except when the wind veered north-easterly during the last 7 h (Fig. 2b). Hourly average values of wind stress, τ (Fig. 2c), ranged between 0.01 (primarily the end of the series) and 0.13 N m^{-2} (primarily at the beginning of the series). The wind energy flux, E10, followed the wind stress pattern with values ranging from ~ 0–1.2 W m^{-2} (Fig. 2c).

Hydrographic structure

Hydrographic conditions were generally stable throughout the 36-h sampling period (Fig. 3). Temperature, salinity and density (Fig. 3a–c) time-series exhibited similar patterns with depth and the largest gradients showed coherent internal oscillations of ~5 m amplitude. The density stratified zones we imposed above defined the upper mixed layer (σ_t < 23.5) as warm (14.1°C; ±0.10 SD of the mean) and fresh (30.75; ±0.19); the pycnocline (23.5–24.5σ_t) as having typically strong gradients in T, S, and ρ; and the bottom layer (σ_t > 24.5) as relatively cool (9.18°C; ± 0.98) and salty (32.07; ±0.16). As with T, S and σ_t, derived variables such as N^2 and Ri showed predictably similar patterns over the course of the sampling period (Fig. 3d–e) with the regions of highest N^2 and Ri (shaded) coinciding with the pycnocline

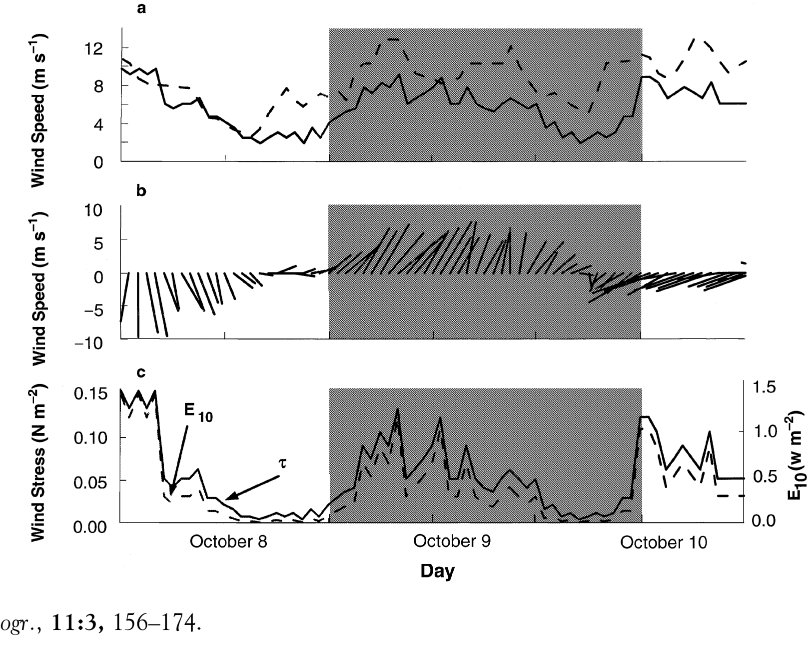
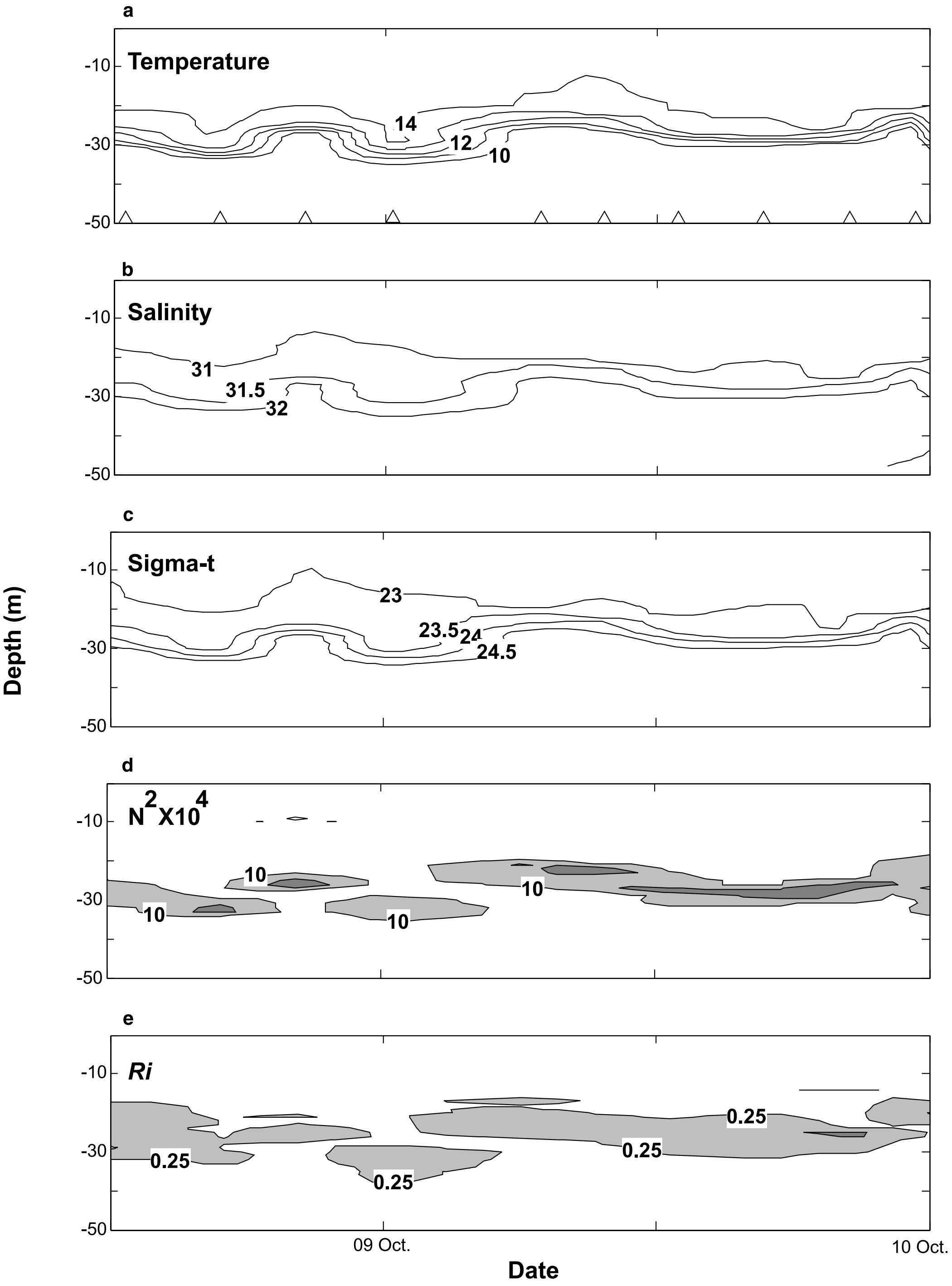


Figure 2. Time series of: (a) hourly average wind speed (m s^{-1}) measured at the meteorological station on Sable Island (solid line) and on board the CCGS *Parizeau* (broken line); (b) wind speed vectors (m s^{-1}; positive values are winds from the south); and (c) surface wind stress (τ; solid line) and wind energy flux ($E_{10} = \tau U_{10}$; W m^{-2}; broken line) computed from the Sable Island hourly average wind data. Shaded background highlights the 36-h sampling period on Western Bank.

Figure 3. Isopleths of: (a) temperature (°C); (b) salinity (psu); (c) density (σ_t); (d) buoyancy frequency (N^2, (rad s^{-1})^2 10^4) derived from EPSONDE profiles; and (e) Richardson number (*Ri*) derived from the EPSONDE density profiles and ADCP velocity profiles all collected during the 36-h sampling period on Western Bank during 08–09 October 1998. The isopycnals represent the limits of the upper mixed layer (< 23.5 σ_t) and the deep layer. (> 24.5 σ_t) zones used in subsequent analyses. Symbols on the bottom axis of panel (a) represent times of EPSONDE casts made during the sampling period. Shaded areas in panels (d) and (e) represent values of N^2 and *Ri* of >10 × 10^4 (rad s^{-1}) and 0.25, respectively.



and oscillating between 20 and 35 m depth. The zone of maximum N^2 and *Ri* was ~5 m thick.

The profiles of ε estimated with EPSONDE were similar over the entire sampling period (Fig. 4a). Epsilon was at a minimum at, or just above, the pycnocline, and was consistently maximal near the surface (perhaps from wind-induced turbulence and wave breaking), and often at depths well below the pycnocline (perhaps because of bottom friction). None of the profiles provided evidence of '*episodic*' turbulent events. At the mid-depth (25–30 m) turbulence minimum, average ε varied between $10^{-8.5}$ and 10^{-7} W kg^{-1}. Within the upper mixed layer, ε ranged across at least two orders of magnitude (10^{-7}–10^{-5} W kg^{-1}). Below the pycnocline (depths matching the deepest BIONESS collections), ε increased from $10^{-7.5}$ to 10^{-6} W kg^{-1}.

We found no meaningful relationship between ε estimated from EPSONDE and the wind-based estimate of turbulence (ε_w) in the upper mixed layer

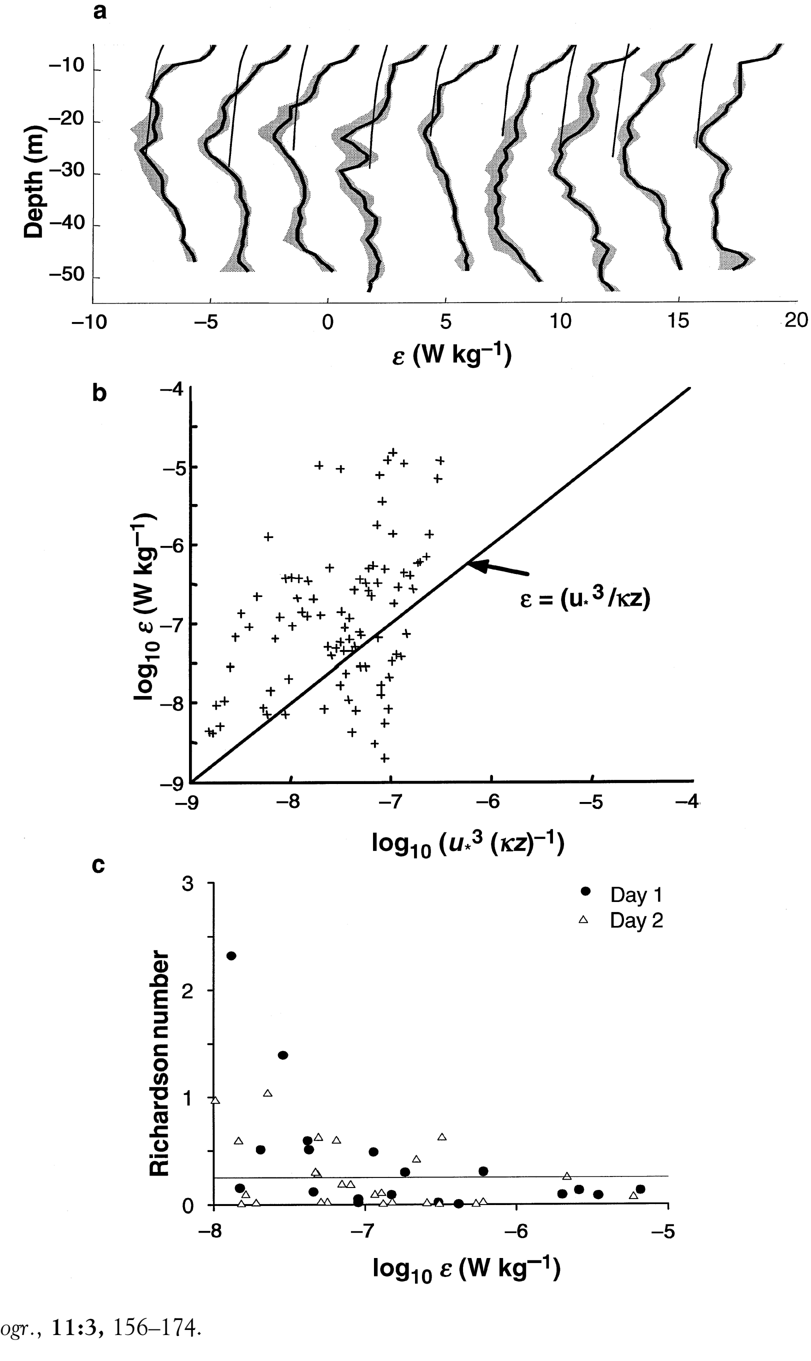


Figure 4. (a) Waterfall representation of the average *in situ* estimates of the rate of dissipation of turbulent kinetic energy, ε (W kg^{-1}; heavy solid line) and bootstrapped 95% confidence limits around the average (stippled) for each of the nine individual EPSONDE and the wind-based estimates of ε_w (u_*^3 $(\kappa z)^{-1}$; thin line) computed using Sable Island wind data for each sampling cycle; individual waterfall profiles and wind based profiles for each sampling cycle are offset by five orders of magnitude for clarity; (b) scattergram of the relationship between the *in situ* estimate of ε and ε_w relative to the 1 : 1 expectation; and (c) scattergram of the relationship between *Ri* number and ε, calculated for the period corresponding to each BIONESS deployment for larvae and zooplankton collections during the 36-h sampling period. The solid line represents a *Ri* of 0.25: values < 0.25 indicate strong potential for mixing.

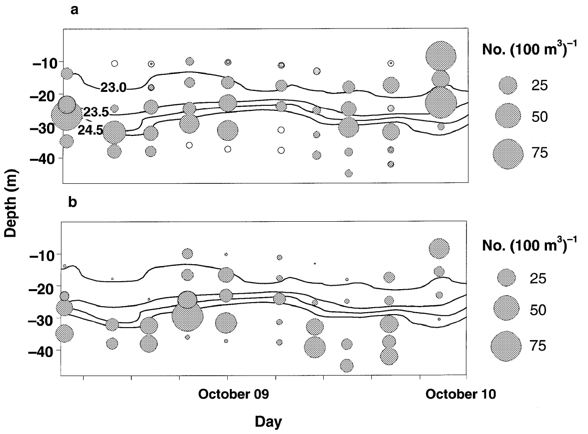
(Fig. 4b). The wind-based estimate of turbulence underestimated *in situ* ε by up to two orders of magnitude. The limitations of the wind-based estimate are clearly seen in the waterfall time-series of ε (Fig. 4a). The wind-based estimates of turbulence always underestimated ε as inferred from EPSONDE in the upper 15 m, and sometimes overestimated ε as inferred from EPSONDE at depth. Similarly, there was little if any relationship between *Ri* number and ε as estimated from EPSONDE (Fig. 4c). For example, at $Ri < 0.25$ (shown as the horizontal line on Fig. 4c), typically indicative of strong mixing potential, ε ranged over three orders of magnitude on both days of the sampling period. At $Ri > 0.25$, ε ranged over at least two orders of magnitude.

Vertical and temporal distributions of silver hake larvae and zooplankton

Greater than 75% of all small (<5 mm TL) silver hake larvae were found within or above the pycnocline when assessed over the entire sampling period. No significant difference in the abundance of small hake larvae was found among the three zones across all collections (Table 1; Fig. 5a). A significant difference among density zones was observed for larger larvae (5–9 mm TL) and multiple comparisons showed that these larvae were more abundant below the pycnocline than either within or above (Table 1, Fig. 5b). The largest silver hake larvae (> 9 mm TL) tended to be more abundant below the pycnocline than within, although there was considerable variability leading to no statistical difference (Table 1).

An analysis of the vertical distribution of silver hake larvae using a two-way ANOVA with time-of-day and depth zone as factors ($n = 3$–5 samples stratum^{-1}) revealed differences between small and large larvae. Small larvae were more abundant at mid depths (between 17 and 25 m). No time-of-day effect and no interaction between time-of-day and depth was observed for small larvae (Table 2), i.e. the vertical distribution did not change between day and night. In contrast, a significant time-of-day and depth interaction was found for the larger larvae (Table 2) indicating a change in the vertical distribution of larger larvae from day to night.

Figure 5. Concentration number (100 m^{-3})$^{-1}$ estimates of: (a) small (< 5 mm TL) and (b) large (5–9 mm) silver hake larvae expressed as expanding symbols (filled circles) during the 36-h sampling period on Western Bank. Each symbol is centred on the average depth of each net stratum and zero-value concentrations are unshaded (i.e. the small open circles in panel a). The 23.0, 23.5, 24.0, and 24.5 isopycnals (σ_t) from the CTD are provided for reference to Fig. 3.



Copepod composition (excluding *Oithona* spp.) was dominated by seven species, of which calanoid genera (*Centropages* sp., *Paracalanus* sp., *Clausocalanus* sp., *Pseudocalanus* sp., *Microcalanus* sp.) were most frequently observed, relative to *Microsetella norvegica* and *Temora longicornis* that occurred only in some samples.

Concentrations of copepod developmental stages did not differ among zones when pooled by water density (Table 1). However, detailed analyses of the vertical distributions, using all five sampling strata ($n = 3$–5 samples stratum^{-1}) and using a two-way ANOVA showed considerable spatio-temporal

Table 1. Kruskal–Wallis (K-W) one-way analysis of variance of physical variables (N^2 and ε), the concentration of silver hake larvae and early (C1–C2) and late (C3–C5) stage copepodids and adult copepods across three zones of water column density (σ_t): upper mixed layer (< 23.5); pycnocline; and bottom layer (> 24.5). N.S. = not significant.

Response	d.f.	*H*	*P*-value	Differences*
Hake (< 5 mm)	2	5.41	0.066	N. S.
Hake (5–9 mm)	2	10.85	0.004	Bottom layer
Hake (> 9 mm)	2	5.87	0.053	N. S.
Early copepodids (C1–C2)	2	0.74	0.691	N. S.
Late copepodids (C3–C5)	2	0.49	0.779	N. S.
Adult copepods	2	0.016	0.992	N. S.

*Results of K-W Z multiple comparisons procedure indicate that at least one of the zones is different at the $\alpha = 0.05$ level.

Table 2. Two-way (depth, time-of-day) analysis of variance of $\log_e$ transformed concentrations of small (< 5 mm TL) and large (5–9 mm TL) silver hake larvae collected during the 36-h sampling series on Western Bank during 8 and 9 October 1998.

	d.f.	Sum of squares	*F*-ratio	Prob. level
< 5 mm TL				
Time-of-day	1	0.10	0.10	0.75
Depth	3	10.29	3.49	< 0.05
Time-of-day × depth	3	6.01	2.04	0.13
Error	22	21.65		
Total (adjusted)	29	38.63		
Total	30			
5–9 mm TL				
Time-of-day	1	6.02	9.03	<0.01
Depth	3	11.9	5.98	<0.005
Time-of-day × depth	3	9.57	4.78	0.010
Error	22	14.6		
Total (Adjusted)	29	45.0		
Total	30			

variation in abundance (Fig. 6; Table 3). Concentrations of early (C1–C2) and late- (C3 to C5) stage copepodids declined over the sampling period (Fig. 6, Table 3). Early stages (C1–C2) were most abundant near the surface (~3.5 m) and between 17 and 25 m. Further, early stage copepodids were an order of magnitude less abundant than late-stage (including adults). No significant date and depth interaction was found for early stage copepodids, indicating that while concentrations declined from one day to the next, their vertical distribution did not change. In contrast, late-stage copepodids exhibited a significant date and depth interaction (Table 3; Fig. 6b), indicating that late-stage copepodids (vertically stratified on day 1) became more vertically homogenous and less concentrated on day 2. Late-stage copepodids were, on average, more abundant at 3 and 17 m than at 10 m. Adult copepods also exhibited a significant change in vertical distribution over the sampling period. However, no day-to-night variation in vertical distribution was found for any species or for any stage, suggesting weak, if any, vertical changes in distribution with time-of-day (two-way ANOVA, depth and time-of-day as factors; $P > 0.2$–0.6 for early, late and adult copepod stages). Significant partial correlations were found between N^2 ($r = 0.43$, $P < 0.01$, $n = 39$), ε ($r = -0.45$, $P < 0.005$, $n = 39$) and the concentration of early stage copepodids after

Figure 6. Average stratum-specific concentrations (thousands m^{-3} ± 2 SE.; $n = 4$ within each stratum) of: (a) early (C1 and C2); and (b) late (C3–C5) copepodids; and (c) adult stage copepods collected on Western Bank on 8 (open circles) and 9 (solid triangles) October 1998.

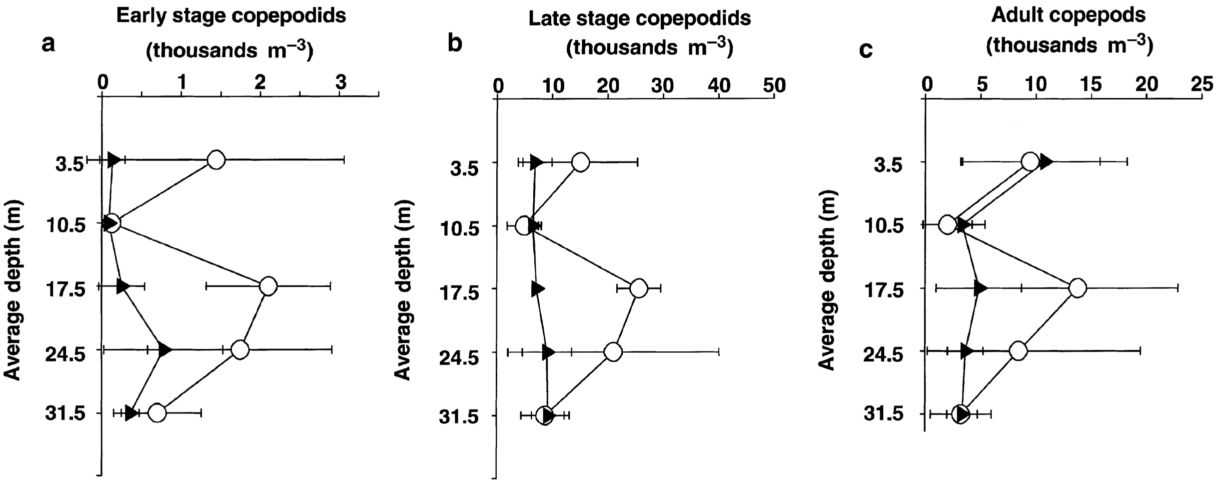


Table 3. Two-way analysis of variance (date, depth) of $\log_e$ transformed concentrations of early (C1–C2), late (C3–C5) and adult copepods collected during the 36-h sampling series on Western Bank during 08 and 09 October 1998.

Source	d.f.	Sum of squares	*F*-ratio	Prob level
C1–C2				
Date	1	14.93	6.96	< 0.002*
Depth	4	47.83	5.57	< 0.02*
Date × depth	4	6.29	0.73	0.57
Error	29	62.24		
Total (Adj.)	38	132.69		
Total	39			
C3–C5				
Date	1	1.57	5.4	< 0.02*
Depth	4	4.06	3.48	< 0.05*
Date × depth	4	3.44	2.95	< 0.05*
Error	29	8.47		
Total (Adj.)	38	17.97		
Total	39			
Adult				
Date	1	0.006	0.01	0.94
Depth	4	13.51	2.86	< 0.05*
Date × depth	4	5.98	1.27	0.30
Error	29	34.23		
Total (Adj.)	38	54.53		
Total	39			

*Term significant at $\alpha = 0.05$.

controlling for the difference in abundance between days. No significant correlations between ε, or N^2 were found for late-stage copepodids or for adult copepods.

Relationship between larval fish abundance, depth, ε, and N^2

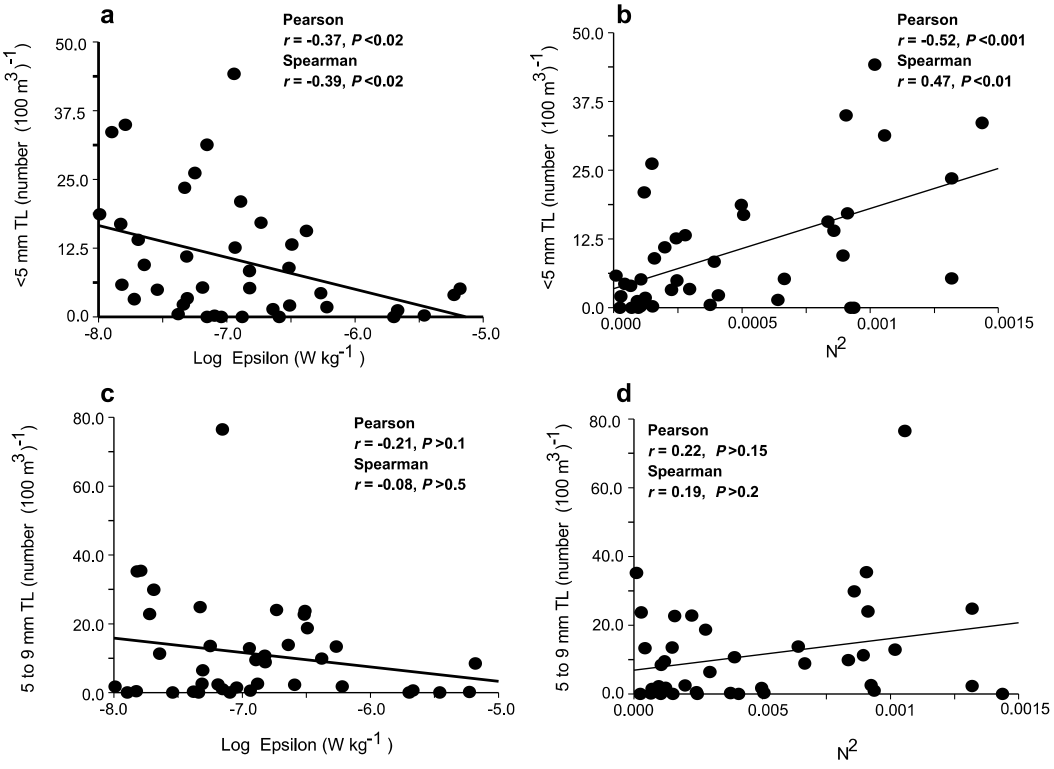
Small silver hake larvae (≤5 mm TL) were negatively associated with ε ($r = -0.38$, $P < 0.02$; Fig. 7a) and positively associated with N^2 ($r = 0.43$, $P < 0.005$; Fig. 7b). N^2 and ε were negatively correlated ($r = -0.43$, $P < 0.01$). The partial correlation of small silver hake with ε, after controlling for N^2, was not significant ($r = -0.21$, $P > 0.18$). In contrast, a significant partial correlation was found between small hake larvae and N^2 after controlling for ε ($r = 0.32$, $P < 0.05$). Despite the significant time-of-day and depth interaction observed for larger silver hake larvae (5–9 mm), indicative of a change in their vertical distribution, these larvae remained significantly correlated with depth ($r = 0.51$, $P < 0.001$), but not with N^2, after controlling for ε (Figs 7c, d). No partial correlations for larger hake larvae were significant after controlling for depth. Further, no improvement in the association between ε and the vertical distribution of small silver hake larvae was found when larval fish abundance was lagged upwards of 6 h (1/2 a tidal cycle) relative to ε ($P > 0.3$).

Model predictions for small (< 5 mm TL) silver hake larvae

The stability of the vertical distribution of small silver hake larvae with time-of-day indicated that we could model the encounter rates between larvae and their potential prey to make predictions about the relative feeding success of larval silver hake under different combinations of water column turbulence, prey concentration and distribution over the sampling period. Depth-specific encounter rate estimates (number min^{-1}) for a 5-mm, pause-travel predator were calculated for each day of the sampling period (8 and 9 October) following Kiørboe and Mackenzie (1995) as described above (Methods).

Significantly different prey encounter rates are predicted among depths and between days (Fig. 8). On the first day of the sampling period, when copepods exhibited a strong subsurface maximum, predicted encounter rates approach two prey items $(\text{min})^{-1}$ at 17.5 m depth, well above the pycnocline. Encounter rates decreased above and below this depth of maximum encounter rate. On the second day there was no significant difference in predicted encounter rate among depths, although

Figure 7. Scattergrams of the relationships between the concentration of small (< 5 mm TL) and large (5–9 mm TL) silver hake larvae and *in situ* estimates of ε (W kg^{-1}; a, c) and N^2 ((rad s^{-1})^2; b, d) as estimated on Western Bank during 8 and 9 October 1998. Pearson and Spearman rank correlation coefficients and significance levels are provided, and a linear least squares fit (solid line) is also shown.

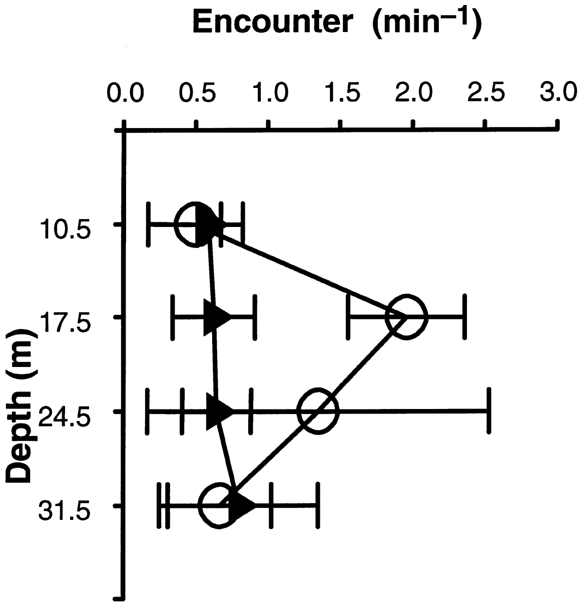


predicted encounters were significantly less frequent [0.5–0.75 prey items (min)$^{-1}$] than on the first day. These results allow us to make several predictions concerning the expected feeding success of small larvae. The first prediction is that feeding success should differ between the 1st and 2nd day as a result large changes in the observed concentrations of potential prey (Fig. 7) and the resulting differences in prey encounter rates (Fig. 8). More specifically, the model predicts that encounter rate, and thus the potential for feeding success (PIPG), should, on the 1st day be the greatest at depth, where turbulence is lowest and where prey concentration is highest. In contrast, there should be no difference in feeding success on the 2nd day at any level of turbulence because encounter rates are not predicted to vary with depth.

Feeding Success

Regression-based approaches did not result in significant relationships between any measure of feeding success and water column turbulence. Therefore, ANCOVAs were used to test the predictions (above) for each measure of feeding success after pooling data into high (> 10^{-7} W kg^{-1}) and low (< 10^{-7} W kg^{-1}) levels of turbulence from samples collected between noon and 16:00. This resulted in between 2 and 3 BIONESS collections and 30 and 60 guts examined at each level of turbulence and day, for a total of 172 guts examined. Factors in each ANCOVA were turbulence level (high and low) and day (8 or 9 October). Time-of-day (12:00 or 16:00) was used as a covariate as indices of feeding success have been shown to increase over the course of the day (e.g. McLaren *et al.*, 1997). Time-of-day was a significant covariate in all analyses (Tables 5–7, $P < 0.001$). No significant day-to-day variability in any of the measures of feeding success was observed after correcting for time-of-day ($P > 0.5$–0.9), contrary to both predictions from the encounter rate model (Fig. 8) and to expectations based on the change in prey concentration between days. The number of PIPG in small silver hake larvae ranged from 0 to 12 items per gut on each day. Larvae collected in the low turbulence environment (< 10^{-7} W kg^{-1}) averaged

Figure 8. Predicted prey encounters min^{-1} ($n = 4$; ± 2 SE) for a 5-mm pause-travel predator for 08 (open symbol) and 09 (filled triangle) October 1998 on Western Bank as estimated using the formula of Kiørboe and Mackenzie (1995) and empirical estimates of depth-specific prey concentration, and *in situ* day- and depth-specific estimates of the rate of dissipation of turbulent kinetic energy.



an adjusted 2.1 PIPG while those from the high turbulence environment (> 10^{-7} W kg^{-1}) averaged 1.6 PIPG (Fig. 9a). In accordance with the lack of day-to-day variability in feeding success, turbulence exerted a negligible effect (Tables 4, $P > 0.05$) on PIPG (Fig. 9a) but suffered from low power (0.43). A significant difference (Tables 5, $P < 0.01$) in the mean length of prey items (PLPG) in the guts of small silver hake larvae was found. The average prey length in guts of small silver hake larvae collected under low and high turbulence conditions averaged 0.36 and 0.47 mm, respectively (Fig. 9b), and was principally driven by the vertical prey distribution on the first sampling date. The total volume of prey items (TPVG) in the guts of small silver hake larvae exhibited the most complicated pattern of the three measures of feeding success (Table 6; Fig. 9c). Whereas neither the level of turbulence nor the sampling date was significantly related to this measure of feeding success, a significant interaction between turbulence and sampling date was observed (Table 6). This is explained by the fact that there was little difference in adjusted total prey volumes at either high or low turbulence levels on the second day of the study (Fig. 9c; open bars). Multiple comparisons, using Fishers LSD showed that TPVG

Table 4. Results of a two-way ANCOVA of water column turbulence and feeding success as measured by the number of prey items per gut (PIPG) of small (< 5 mm TL) silver hake larvae between days and adjusted by the time-of-day of the collection.

Term	d.f.	Mean square	*F*-ratio	Prob level
X (time-of-day)	1	77.85	21.51	< 0.001*
Turbulence	1	11.67	3.23	< 0.074
Day	1	0.47	0.13	0.21
Turbulence × day	1	0.055	0.02	0.901
S	167	3.620		
Total (adjusted)	171			
Total	172			

*Term significant at $\alpha = 0.05$.

Table 5. Results of a two-way ANCOVA of water column turbulence and feeding success as measured by the average length (mm) of prey per gut (PLPG) of small (< 5 mm TL) silver hake larvae between days and adjusted by the time-of-day of the collection.

Term	d.f.	Mean square	*F*-ratio	Prob level
X (time-of-day)	1	0.92	19.45	< 0.001*
Turbulence	1	0.34	6.91	< 0.01*
Day	1	2.4×10^{-4}	0.01	0.94
Turbulence × Day	1	0.04	0.76	0.38
S	132	0.049		
Total (adjusted)	136			
Total	137			

*Term significant at $\alpha = 0.05$.

Table 6. Results of a two-way ANCOVA of water column turbulence and feeding success as measured by the total prey volume (mm^3) per (TVPG) of small (< 5 mm TL) silver hake larvae between days adjusted by the time-of-day of the collection.

Term	d.f.	Mean square	*F*-ratio	Prob level
X (time-of-day)	1	0.03	53.75	< 0.0001*
Turbulence	1	0.001	3.24	0.074
Day	1	0.0002	0.40	0.527
Turbulence × day	1	0.003	5.43	0.02*
S	132	0.0005		
Total (adjusted)	136			
Total	137			

*Term significant at $\alpha = 0.05$.

of small silver hake larvae was greater at high turbulence levels on the first sampling date (Fig. 9c; filled bars) when the prey concentration was vertically structured.

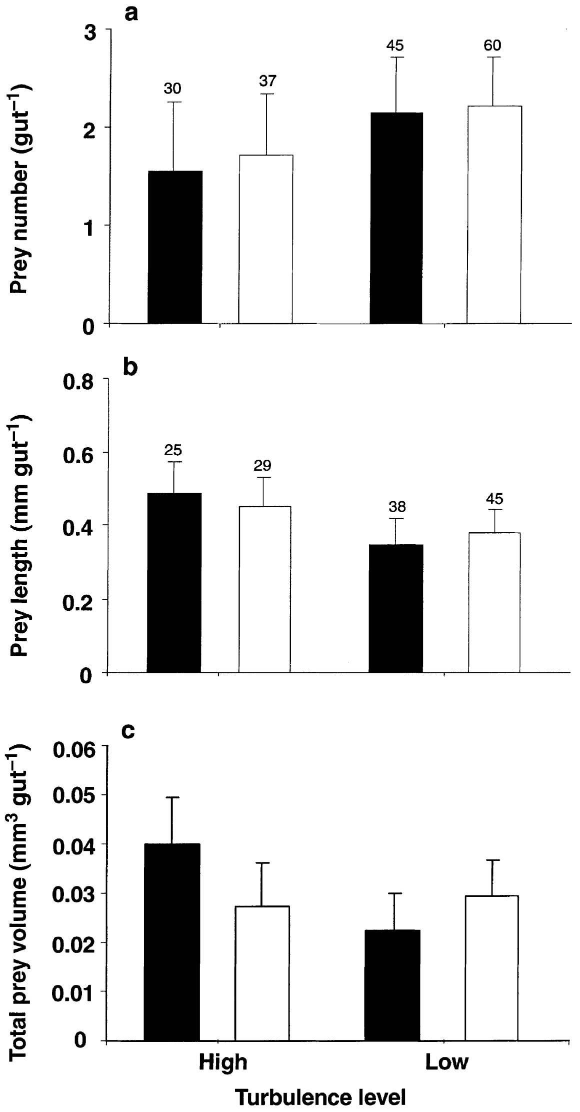
DISCUSSION

Rothschild and Osborn (1988) provided a concept, based on water column turbulence, to link the small scale physical environment that affects individual planktonic animals to the broad scale environment that may contribute to growth and survival effected through a modification of the trophic environment. Despite the limited duration of our study, our results indicate that *in situ* estimates of ε were not particularly powerful in explaining the variation in the vertical distribution of larval fish and their potential prey or, when combined with a prey encounter model, the feeding success of small silver hake larvae between days. Further, neither the Richardson number (*Ri*), nor wind-based indices of water column turbulence were highly correlated with *in situ* estimates of turbulence. The abundance of small silver hake larvae (< 5 mm TL) was negatively correlated with ε and positively correlated with N^2 and remained correlated with N^2 after accounting for the negative association with ε. In contrast, large larvae (> 5 mm TL) were distributed as a function of depth and independently of ε and N^2. It appears that the stratified nature of the water column, rather than ε or time-of-day, most easily explains the vertical distribution of small silver hake larvae during this study. Thus, we cannot reject the hypothesis of no relationship between turbulence and larval fish abundance or size distribution and/or prey concentration.

The predictions from the prey-encounter model of Kiørboe and Mackenzie (1995) were not realized, as there was no significant difference in feeding success between days despite a predicted prey encounter rate that varied by a factor of five. Thus, we cannot reject the null hypothesis that the feeding success of small larvae is independent of encounter rate as predicted using a generally accepted encounter model that employs observed variations in turbulence. Feeding success, as measured by the number PLPG as well as TPVG, varied under different degrees of turbulence and with the vertical structure of the prey concentrations in the water column. These results suggest a rather complicated interaction amongst the vertical distribution of predator, prey and some measure of water column structure (turbulence, stratification, etc.) that may not be easily modelled or parameterized by simple models like those of Mackenzie and Kiørboe (1995).

Many studies have used wind-based indices of turbulence (Sundby and Fossum, 1990; Sundby *et al.*, 1994; McLaren *et al.*, 1997) or *Ri* (Dower *et al.*, 1998) in studying turbulence phenomena, and in doing so make the assumption (explicit or otherwise) that these indices accurately reflect water column turbulence and adequately reflect the turbulence induced encounter probability. Yet, the results of this study indicate that testing the hypothesized relationship between turbulence, larval fish distribution and encounter rate is more difficult than generally assumed. Are the relatively simple indices insufficient in capturing the importance of the dissipation rate to the encounter rate formulations? For example, the wind-based estimates of ε_w invariably underestimated the observed rate of dissipation of turbulent kinetic energy in the upper mixed layer and sometimes overestimated the rate near the pycnocline (Fig. 4). This indicates that in most environments, where small larval fish are invariably associated with the upper mixed layer and the upper pycnocline, or in areas where there is a measurable degree of stratification, the wind-based estimates are of limited predictive value. This is of major consequence as most temperate water columns exhibit (at least) continuous stratification. Further, we found that the relationship between the *Ri* and ε was not strong and that *Ri* was estimated at < 0.25 over a range in ε of two orders of magnitude. This suggests that *Ri* is an inappropriate index for ε, especially when the vertical variation in *Ri* is greater than its temporal variation. Nevertheless, observed values of ε ranged between 10^{-5} and 10^{-8} W kg^{-1} (= m^2 s^{-3} or multiply by 10^4 to get cm^2 s^{-3}, as in Kiørboe and Mackenzie, 1995) and are well within the range where ε is proposed to influence prey encounter (10^{-7} W kg^{-1} or greater for a 5-mm pause-travel predator; Kiørboe and Mackenzie, 1995).

Figure 9. Effects of high (> 10^{-7}) and low (< 10^{-7}) turbulence levels (ε; W kg^{-1}) on the average: (a) number of prey items (PIPG); (b) prey length (PLPG; mm); and (c) total prey volume (TPVG; mm^3) in the guts of small (< 5 mm TL) silver hake larvae collected on 8 (filled bars) and 9 (open bars) October 1998 on Western Bank. Values above bars in (a) and (b) are the numbers of fish examined. Smaller numbers over (b) are the same in (c) and result from empty guts. Error bars are ± 2 SE.



The turbulence-enhanced prey encounter model did not reflect actual feeding success of larval silver hake. The prey encounter model predicted a relatively high prey contact rate on the first day of the sampling period and a relatively low contact rate on the second day. Our examination of three different feeding indices suggests that such models may have limited utility in the field. The observed levels of turbulence over the depth of the water column were 1–2 orders of magnitude greater (10^{-8}–10^{-6} W kg^{-1}) than those predicted to affect feeding success in laboratory experiments (Mackenzie and Kiørboe, 1995; Mackenzie and Kiørboe, 2000). This suggests the relatively high turbulent velocities, even within the pycnocline, may have resulted in the satiation of the feeding response. Munk (1995) found, based on laboratory studies, that satiation in attack rate (attacks min^{-1}) could occur at prey (nauplii) encounter rates of approximately 0.4 min^{-1} at levels of turbulence (~10^{-8} W kg^{-1}) lower than those we observed. Encounter rates that correspond to Munk's (1995) satiation estimates were predicted on the second day of our sampling when overall prey concentrations were lowest (Fig. 8).

Did the limited duration of our study mask any cumulative effects of the lower prey concentrations observed on the second day? The different vertical distributions and concentrations of copepods on the second day indicate that a biologically different water mass was advected through our relatively fixed sampling region. It is unlikely that the change in copepod concentrations reflect vertical mixing of the plankton, as the measured water column turbulence was relatively consistent over time (see Fig. 4). We would predict, based on the encounter model, that small hake larvae collected on the second day should have experienced a feeding history (days) substantially different from larvae collected on the first day of the series (when prey concentrations within that water mass were higher), assuming the larvae were also advected with the water column and its low concentration of prey. We conducted a limited test of this prediction by examining the most recent (5 day) larval growth history using otolith increment area of animals collected during the 1st and 2nd days of sampling, and found no significant difference in recent larval rate growth history between the two presumed water masses (Reiss and Taggart unpublished data). Further, a more thorough analysis of data collected on and around Western Bank by Jeffrey

(2000) showed no differences in growth rates of silver hake larvae among different water masses of varying prey concentration. This was consistent with a similar study, in the same location (Jeffrey and Taggart, 2000). Additionally, no significant differences were found in various condition indices (RNA/DNA, etc.) amongst larvae collected on either day or around our sampling location on Western Bank (P. Grønkjær, personnel communication, Department of Marine Ecology, Institute of Biological Sciences, University of Aarhus, Denmark).

In contrast to the complete lack of significant day to day variability in feeding success by any measure considered, water column turbulence was a contributor to feeding success as estimated using the PLPG and TPVG. This is similar to findings of Dower *et al.* (1998) where, under conditions of higher water column turbulence, fewer but larger prey were ingested. Our results are not entirely inconsistent and suggest that, at high levels of turbulence, smaller prey items are not found in the diet. In such conditions, do the prey become redistributed relative to the larvae (as in the distribution of small copepods from the first to second day), or does prey selection by the larvae change? We have insufficient data to address these questions, although it remains that the day to day prey encounter predictions were not realized.

There are alternative explanations for why the model did not predict the observed feeding success of the larvae. The simplest would be that prey concentrations on Western Bank are not limiting. An important assumption of the turbulence hypothesis is that prey concentration can be limiting. Hence, an energetic benefit can accrue via a turbulence-enhanced prey encounter rate. Water column prey concentrations were comparable to concentrations observed during other studies on Western Bank in autumn (McLaren and Avendaño, 1995) and ranged between ~1000–30 000 m^{-3} (see Fig. 7). These concentrations are also similar to concentrations observed in other locations in stratified environments (Herman *et al.*, 1981, Scotian Shelf; Incze *et al.*, 1990, Shelikof Strait; Turner and Dagg, 1983, mid-Atlantic Bight; Incze *et al.*, 1996, Georges Bank), but are not exceptionally high and no higher than those observed by others who have examined feeding success in relation to indices of water-column turbulence (Sundby and Fossum, 1990; Incze *et al.*, 1996; McLaren *et al.*, 1997).

Another alternative for the inadequate predictions of the most general feeding effect may be a consequence of the prey type consumed by larvae in the field compared with the prey type offered in laboratory studies. While prey size should not (at least as a first approximation) affect the predicted prey encounter rates using the prey encounter model we employed, it may affect realized trophodynamics as larvae will require fewer large items to satisfy their energetic demands. Most laboratory studies have used rather large larvae (> 5 mm TL) and small prey (usually nauplii) assuming that these are the preferred prey items. Our results show small larvae feeding on prey of considerable size (> 0.3 mm TL), and that water column turbulence was considerably higher (1–2 orders of magnitude) than the turbulence levels necessary to satiate the feeding responses in the laboratory. It may be that energetic demands of silver hake are met by selecting larger prey than is typically assumed for similar species of similar developmental stage. Clearly, extrapolation of laboratory studies to predictions in the field is tenuous. Turbulence levels in laboratory studies are orders of magnitude lower than those observed *in situ* and the prey concentrations in the field are typically more variable. For some species (e.g. silver hake), generalities based on contemporary laboratory studies would incorrectly predict the importance of ε on feeding success.

Spatial and temporal scales and sampling assumptions

The first prediction provided by Rothschild and Osborn (1988, p. 472) is that 'predator or prey might modify their vertical or horizontal position in the water column to take advantage of permanent, semi permanent, periodic or episodic turbulence'. To adequately test this and other such predictions it is important to provide, from field studies: (i) evidence that larval fish respond to spatial or temporal variations in ε, presumedly achieved through vertical movement towards some 'optimal level' of turbulence where prey encounter rates would be maximized; and (ii) evidence that the sampling protocols employed can resolve such inferred movements.

Evidence that larvae respond to spatial or temporal variations in ε requires an active (or some would call 'adaptive') movement by the larvae. Adaptive arguments are difficult to test, and there is considerable debate in the literature regarding the adaptive value of vertical migrations (Neilson and Perry, 1990), especially given the variety of patterns in distribution (migration is only inferred) observed for the same species, at the same location at different times (e.g. Sclafani *et al.*, 1993). In the data we examined, turbulence estimates varied by at least an order of magnitude over vertical distances as small as 5 m (generally 7–10 m; Fig. 6). These could be easily traversed by larvae as small as 5 mm swimming at a nominal body length s^{-1}, in as little as 1–2 h to take advantage of turbulence or to maximize prey encounter rate. Yet, small silver hake larvae were consistently most abundant at the ε minimum (25–35 m; Figs 5 and 6), and did not exhibit any diel variation in concentration at depth that might have increased the variability in any relationship. The spatial (< 2–7 m vertically) and temporal (~ 3 h) sampling resolution achieved in this study should have resolved significant changes in the vertical distribution of larvae. Similar arguments have been analytically explored by Franks (2001) based on field observations of the vertical changes in plankton distributions associated with changes in wind forcing and resultant water column mixing. Thus, we conclude that there is no evidence that silver hake larvae we collected maximized their prey encounter rate by redistributing themselves to depths of increased turbulence to increase the size of prey they are observed to have ingested.

Following from above we ask two questions: (i) should the results from laboratory studies be readily extrapolated to the field; and (ii) is the hypothesized relationship between turbulence and larval fish critically important to their early life history? Most laboratory studies of turbulence and encounter rate have focused on fish larvae > 5 mm TL (see Mackenzie and Kiørboe, 1995; Mackenzie and Kiørboe, 2000; and several citations therein). Yet, our results suggest that larval hake (arguably a ‘typical’ gadoid) become independent of their physical environment (ε or N^2) and the associated trophic implications at relatively small sizes (≤ 5 mm TL). Our results are consistent with the most frequently observed distributions of copepods and larval fish, perhaps approaching the status of an ecological law – aggregation at or near pycnoclines (e.g. Herman and Sameoto, 1981; Kendall and Naplin, 1981; Cass-Calay, 1997). It appears from our results that the co-occurrence of larval fish and their potential prey during this study is most easily explained by buoyancy rather than by turbulence, light, etc. as proposed and explored by Sclafani *et al.* (1991) and others.

The results of our study raise many questions regarding the importance of correctly estimating the vertical structure of turbulence, the adequacy of the predictive models, and the vertical structure of both the predator and prey fields. We propose that resolving these complexities and contradictions can only be accomplished by: (a) sampling larval fish and their prey at discrete depths; (b) examining gut content and prey concentration with respect to depth and/or density; and (c) testing the hypothesis that gut content is directly related to the proportion of prey within each depth stratum. Only if gut content is found to differ significantly among depths, and after correcting for prey concentration, can we begin to test the hypothesis that turbulence (as expressed through encounter rate) is a better predictor of fish feeding success than simply prey concentration and distribution, or any other intercorrelated variables (e.g. light level or temperature). Finally, laboratory studies that focus on smaller larvae (< 5 mm), address variation in prey size (e.g. Dower *et al.*, 1998), and use turbulence levels that reflect those observed *in situ* in the field may provide greater clarity in hypothesis testing. If our observations on the vertical distribution of predator and potential prey can be generalized to other species, then more refined spatio-temporal field sampling along with direct estimates of turbulence would be necessary before concluding that turbulence provides a ‘link’ between large-scale oceanographic phenomena (e.g. wind forcing) and microscale events (e.g. feeding success) and thence to larval survival and juvenile recruitment.

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