Feeding by larval cod in different water-masses on Western Bank, Scotian Shelf

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ABSTRACT

Gut contents were obtained from 1406 cod larvae from 94 stations in seven water masses related to a gyre around Western Bank, Scotian Shelf, 22 November–16 December 1992. Initial samples were from: well-mixed water over the bank crest (CW); a surrounding convergent FRONT; relatively cold, fresh water (CFW) largely east of CW; warmer, salty water (WSW) west of CW and FRONT. After a storm on 3–6 December, samples were from CW and CFW displaced south-east on the bank and, after further winds 11–12 December, from CW displaced north-west off the bank. Zooplankton biomass (300–333 μm mesh, mostly *Calanus* copepodids) did not differ among water masses, but larval concentrations were significantly higher in FRONT than elsewhere. The small-copepod diets of larvae varied among water masses, partly attributable to larval growth during the sampling period. Numbers of prey in guts, and indices of fullness and digestion, varied among water masses. More reliably, after ANCOVAs significant independent variables were: overwhelmingly time of day (maximum prey numbers and fullness at ~19:00) and larval size; water mass; weaker interactions of the above among themselves and with sample depth and date; a very weak negative turbulence-index effect on gut prey numbers in depth-stratified samples. After ANCOVAs, larvae from pre-storm CW had significantly higher prey numbers and fullness than did those from FRONT, WSW, and CFW. Larvae in CFW were significantly fuller when sampled closer to sites of former CW after the storm. Although numbers of prey in larvae advected off the bank in CW decreased significantly, prey averaged larger, so that gut fullness did not decrease. We conclude that larvae were best fed in the 'centre' of the Western Bank gyre, but not greatly affected by subsequent displacement off the bank.

Key words: advection, bank gyres, cod larvae, copepods, feeding success, fronts, turbulence

INTRODUCTION

Several hypotheses attribute variability in fisheries to associations in time and space between fish larvae and their zooplankton prey. Some propose a direct effect: that larval growth and survival, and therefore their recruitment to fisheries, benefit from abundant zooplankton prey, whether through enhanced local productivity or a variety of physical processes (Hjort, 1914; Lasker, 1975; Cushing, 1995). Others argue that the associations reflect the importance of retention in natal areas for ultimate recruitment to regional fish populations (Iles and Sinclair, 1982; Sinclair, 1988). A recent modelling study (Werner *et al.*, 1996) concludes that cod larvae in areas of their high concentration on Georges Bank would benefit simultaneously from retention and enhanced feeding. However, empirical analyses of such associations are still needed, and require careful attention to scales of observations (Taggart and Frank, 1990).

On large scales (order 10–100 km), McLaren and Avendaño (1995) showed that, on and around Western Bank, Scotian Shelf, cod larvae and some zooplankton species were more concentrated over shallower regions of the bank than in surrounding waters. They also showed that larvae were better fed over the bank than in surrounding waters. They attributed higher concentrations on the bank to its associated gyrelike system, which has been recently documented (Bowen *et al.*, 1995; Sanderson, 1995; Griffin and Thompson, 1996). McLaren and Avendaño (1995) also analysed samples taken during December 1992 from several depths at four stations near the crest of the bank. Even in that region of high prey concentrations, consumption of prey items by

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larvae remained related to the abundance of these items in plankton samples, when controlled for depth and larval size. However, McLaren and Avendaño (1995) did not assess feeding by larvae in direct relation to hydrographic features of the gyrelike system around Western Bank. For example, it has been found that fish larvae and their prey may be more abundant at oceanographic fronts than in waters on either side of such fronts (Richardson *et al.*, 1986; Govoni and Grimes, 1992). Some have related this abundance to enhanced growth and improved survival (Taggart *et al.*, 1989; Brandt, 1993), while others (Govoni *et al.*, 1989; Govoni and Grimes, 1992; Kingsford and Suthers, 1996) have attributed it to passive transport and accumulation in frontal regions.

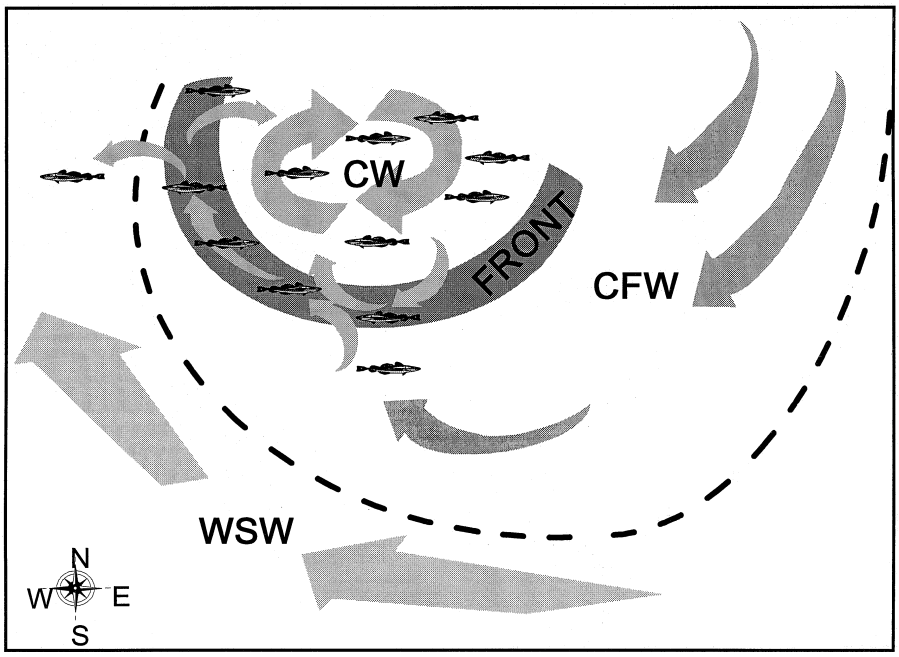
The present study uses data and samples (completely different from those analysed by McLaren and Avendaño, 1995) from a survey by the Ocean Production Enhancement Network (OPEN) during November–December 1992. The overall aim was to follow characteristics of cod larvae by tracking the water masses within which they occurred. The technical aspects of the study, as well as information on the gyrelike system over and around Western Bank, have been described elsewhere (Bowen *et al.*, 1995; Sanderson, 1995; Griffin and Thompson, 1996; Taggart *et al.*, 1996). The general structure of this system in relation to the 60 m isobath (dashed line) is shown schematically on Fig. 1. Here we give a full account of feeding by larvae collected during the survey. This allows us to test the critical hypothesis that feeding success of cod larvae differs among distinguishable water masses, including convergent fronts and waters that were displaced from Western Bank by storms. We are also able to suggest ways in which this hypothesis, and others related to the concentration, retention and nutrition of groundfish larvae in gyrelike systems, may be more critically assessed.

MATERIALS AND METHODS

Field sampling

The data and samples were collected during R/V *Petrel V* Cruise 92–31 (Griffin and Lochmann, 1993) between 22 November and 16 December 1992, over and around Western Bank, the western part of Sable Island Bank, Nova Scotia. Three initial transects, on 23–25 November, totalling 70 stations, were designed to map temperature, salinity, and density fields (CTD at 7 km sample intervals), and the distribution of larval cod using double-oblique tows at $\sim$1 m s^{-1} to 5–10 m from bottom by a 60 cm, 300 μm mesh, metered,

Figure 1. The schematic structure of the apparent gyre and identifiable water masses over Western Bank prior to the storm of 1–3 December 1992 (see text). The well-mixed waters over the shallow crest of the bank (CW) were separated by a convergent FRONT from relatively cold, fresh waters (CFW) that extended from east of CW as a variable 'tongue' between FRONT and warm, salty water (WSW) seaward of the bank.



bongo net sampler. Depth was estimated from angle and length of towing wire. The volumes filtered averaged 150 m^3. This initial survey permitted deployment of the Ocean Probe real-time oceanographic monitoring system (Bowen *et al.*, 1995; Griffin and Thompson, 1996) for tracking the water mass containing high concentrations of cod larvae located initially near the crest of Western Bank.

Subsequently, between 25 November and 3 December, series of oblique samples of zooplankton and larvae were made by (flow-metered, non-closing) bongo nets, and vertically stratified samples by a 1 m^2 EZNET sampler (marketed version by Open Seas Instruments, Musquodoboit Harbour, NS, of BIONESS; Sameoto *et al.*, 1980). The EZNET (ten 333 μm mesh nets with digital flow meters) sampled in a stepped oblique manner, at 5 or 10 m intervals (depending on bottom depth) to within 10 m of bottom. Towing speeds were $\sim$1 m s^{-1}, and each net was opened for 5 min and filtered $\sim$250 m^3. In addition, for fine-scale study of a frontal feature (Taggart *et al.*, 1996; Lochmann *et al.*, 1997), a series of 10 sequential samples was taken on 29 November by the EZNET towed at about $\sim$12.5 m in waters across a defined frontal system.

A severe storm interrupted the survey from 3 to 6 December. After this, a further series of bongo tows and a smaller EZNET series were obtained between 8 and 12 December. Further stormy weather, on 11–12 December, continued to displace water masses northwestward from the crest of Western Bank. This water was sampled off the bank to the north-west on December 14–15.

After recovery, the plankton nets were rinsed to obtain all contents, which were immediately sorted for larvae. Ten larvae, when available, were removed unselectively from each sample for morphometric analysis (Miller *et al.*, 1995) and individually preserved in liquid nitrogen for genetic (Ruzzante *et al.*, 1996; Herbinger *et al.*, 1997) and lipid (Lochmann *et al.*, 1997) analyses. Remaining larvae were preserved in bulk in ethanol, and the zooplankton placed in 4% buffered formaldehyde in seawater.

Classification of stations

Stations and associated samples taken before the early December storm were classified by Taggart *et al.* (1996) and Lochmann *et al.* (1997), using cluster analysis, into four categories with respect to the position of the gyrelike water mass on Western Bank (Figs 1, 2).

1 Stations in the relatively well-mixed waters over the shallows of the bank, of intermediate temperature and salinity, were 'crest water' (CW).

2 Stations within the convergent thermohaline front, sometimes several kilometres wide, between bank crest and surrounding waters, were classed as FRONT stations.

3,4 Stations outside both CW and FRONT were in two distinct water masses. Immediately surrounding CW was a lens of relatively cold, fresher water (CFW), which was sampled largely to the north and west of CW. Further seaward of the crest of the bank was relatively warm, salty, stratified, slope water (WSW) that directly abutted FRONT later in the cruise. Some stations known to be well outside FRONT, but with properties not fully established by CTD profiles, were included in this WSW category.

After the 3–6 December storm, the tracked CW had moved largely south-east of the crest of the bank, following which it was advected rapidly by the storm of 11–12 December off the bank to the north-west (plate 3 in Griffin and Thompson, 1996; Fig. 4 in Taggart *et al.*, 1996). Samples from the post-storm, displaced CW, December 8–15, were thus classifiable (Fig. 2) as on-bank (close to or within the 60 m contour) or off-bank (the cluster outside the 100 m contour to the north-east of the bank). Stations to the east of the on-bank CW continued to be classed as in CFW (also displaced). After the storm of 3–6 December no clearly frontal waters were detectable, and WSW off the bank to the west was not sampled.

Samples from some stations contained no larvae or larvae that were otherwise unavailable (e. g. damaged). In addition, among the above-noted series of samples at 12.5 m across a front on 29 November, five were in FRONT, and five in CW (Fig. 6 in Taggart *et al.*, 1996). All stations that supplied larvae are on Fig. 2. The pre-storm larval sampling pattern (Fig. 2) shows much spatial overlap among the water-mass categories. This is because of considerable movements of water masses during the period, so that stations thus reflect a Lagrangian frame of reference. After the storm of 3–6 December, all samples came from CFW or displaced CW. The sampling pattern makes it clear that the present analysis (unlike the earlier study by McLaren and Avendaño, 1995) of feeding by cod larvae relates to water masses, not to depth contours of Western Bank.

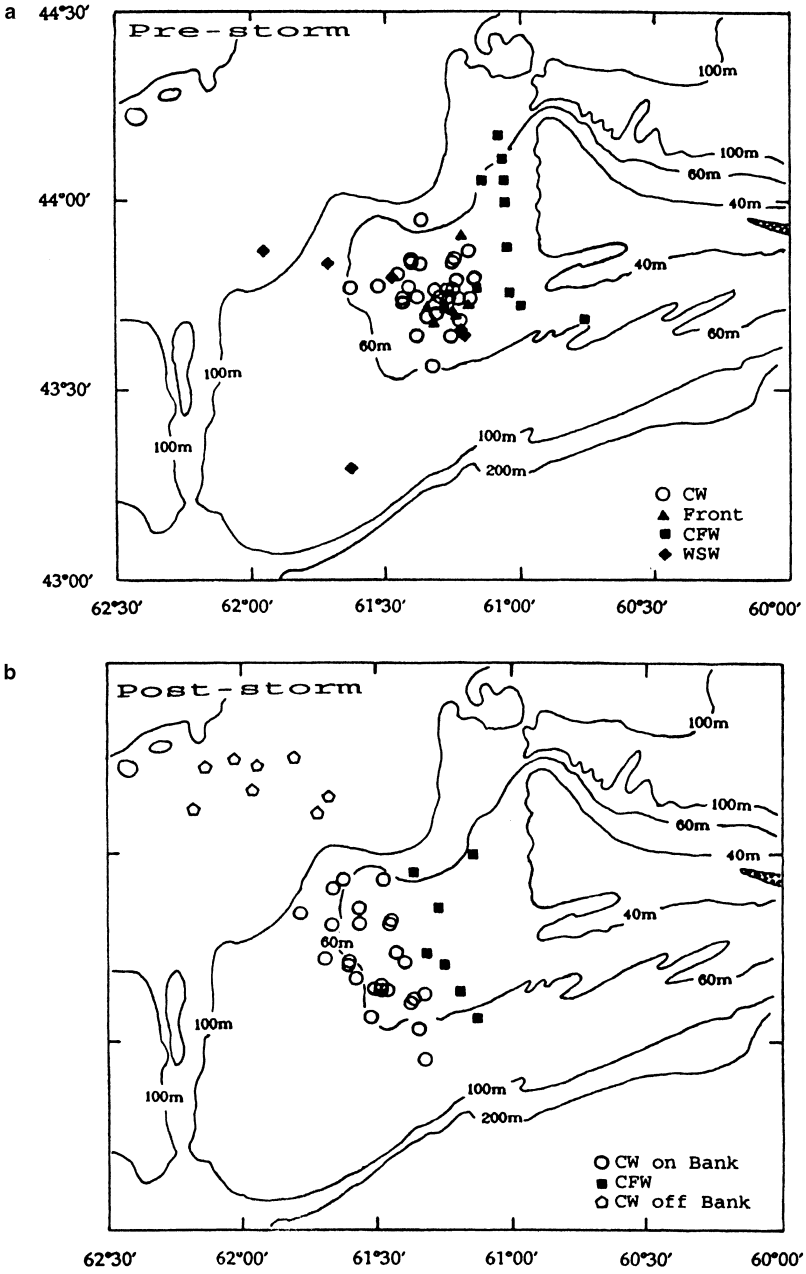
Laboratory procedures

Plankton collections were examined in the laboratory and remaining cod larvae were removed and preserved in 95% ethanol. Each zooplankton sample was then washed, concentrated on 200 μm mesh screen, towel dried, and weighed to the nearest gram to obtain wet biomass per unit volume filtered. For station estimates

of larval numbers and zooplankton biomasses per unit volume filtered, the depth-stratified EZNET estimates were averaged on a volume-weighted basis.

Determination of standard lengths (nearest 0.01 mm) of larvae videotaped on the ship followed Miller *et al.* (1995). A total of 1127 such cod larvae from 63 stations (maximum 10 per sample), originally preserved in liquid nitrogen, were thawed and their stomachs removed and preserved in 4% formaldehyde for gut content analysis. This also avoided distortions of body lipid estimates by lipid from prey in the guts (Lochmann *et al.*, 1996). An additional 279 larvae from 31 stations

Figure 2. Water mass origins (Figure 1, 2) of samples that supplied larvae for analysis of gut contents. (a) Pre-storm samples were taken before interruption of the cruise by a storm on 3–6 December, which displaced CW to the south-west. (b) Post-storm samples were taken between 8 and 15 December, during which another storm, on 11–12 December, displaced CW off the bank to the north-west. Because of such movements of tracked water masses during the cruise, there is much spatial overlap among samples from the different water-mass types.



were removed from ethanol, hydrated for 4 h in distilled water, then measured under a dissecting microscope, before being preserved in 4% formaldehyde. The gut contents of these ethanol-preserved larvae were firmer and more readily analysed than those kept in liquid nitrogen. There is no consensus on the amount of shrinkage of fish larvae in ethanol; estimates range from 0% to 14%, with a median of about 5%. We used a value of 5%, which is said to account for any shrinkage resulting from abrasion of larvae during collection (Theilacker, 1980). Most ethanol-preserved larvae were from stations at the beginning and end of the cruise period, during which time they grew on average about 30% in length (see Results).

Most of the larvae used in this study appeared (per Fossum, 1986) to be beyond stage 5 (4–6 days post-hatch), in which the yolk sac begins to be absorbed. In fact, only a few larvae had a visible remnant of the yolk sac; all seemed morphologically capable of feeding. The gut contents were identified and enumerated to the lowest possible taxon; unidentifiable fragments were not assigned to a separate category. For presentation, copepod taxa were grouped into eggs, nauplius stages 1–3 and 4–6, copepodid stages 1–3 and 4–6 (i.e., 4–adult). Infrequent copepod taxa were grouped as 'other' eggs, nauplii, and copepodids. The only non-copepod taxon of consequence was the pteropod *Limacina helicina* (to which were added a few bivalve larvae of similar size and possibly resistance to digestion). The numbers of identified items in each stomach were combined as one measure of feeding rate of the larva. The fullness of each stomach was also estimated in five subjective categories: empty (1), nearly empty (2), partly full (3), quite full (4) and full (5). The state of digestion of each item was categorized (Tilseth and Ellertsen, 1984): virtually undigested (1); the internal parts separated from the exoskeleton to varying degree (2); and only exoskeleton remains (3). Categories of each prey item were combined as a mean index of digestion for the gut contents of each larva.

Statistical procedures

Mean concentrations of larvae, zooplankton biomasses, and larval feeding variables were compared among water masses using non-parametric Kruskal–Wallis ANOVA because variances were generally non-homogeneous (Bartlett tests). Because other variables can also affect larval feeding, the feeding variables were also treated by stepwise analysis of covariance (ANCOVA) with water masses as categories and other potentially influential variables and their interactions as covariates. Because the 1406 larvae were grouped by stations (all samples), or by net samples (EZNET series), which would lower the effective d.f., we used a quite stringent significance level ($P = 0.05$) for entry or removal of variables in the stepwise analyses.

The three dependent feeding variables for each larva were: (1) number of identifiable prey; (2) index of gut fullness; and (3) mean index of digestion. The independent variables were chosen *a priori* from those available. The water-mass origin of each sample was of primary interest, and was entered as a categorical variable. Sampling date (from 00.00 on the first day of the cruise), time of day (local, AST), and larval lengths were available for every sample. Sample depths and depth-specific zooplankton biomasses were available only for EZNET samples. We also entered an empirical index of depth-specific turbulence using wind speed recorded at the time of sampling: turbulence index = $(\text{wind speed})^3/\text{depth}$ (MacKenzie and Leggett, 1993). We used natural logarithms of larval lengths because gut capacity for numbers of like-sized food items should be allometrically related to length. (This might not be true of gut fullnesses; the transformation slightly increased r^2 values.) Logarithms of zooplankton biomasses were used because these might better express a saturation relationship between food uptake and prey abundance (McLaren and Avendaño, 1995). Sampling times were expressed as deviations from the time of day iteratively estimated (nearest hour) to give minimum residual error (and maximum r^2) in the chosen regressions (McLaren and Avendaño, 1995). No significant improvements of fit came from adding squares of adjusted times, so non-linear time functions (e. g. sine functions) were deemed unnecessary. Because some variables might have been influenced by water-mass properties, depths, and dates of sampling, all potential interactions were included in initial steps of ANCOVAs. We assumed that abundance of larvae could not affect feeding variables; interference competition seems inconceivable at their very low concentrations.

The ANCOVAs were of two classes. Those using all available bongo and EZNET samples included the depth-independent variables of water-mass category, sampling date, time of day, and larval length. ANCOVAs using depth-related variables were possible only with the EZNET samples.

Although potentially important influences on feeding by larval cod were obtained, no ANCOVAs produced r^2 values >0.65, rated as necessary for predictive regressions (Prairie, 1996). Accordingly, we tabulate linear coefficients of main effects only to indicate the directions of influences, and not for prediction. Because the variances of adjusted means were invariably nonhomogeneous, we tested differences

among them using non-parametric multiple comparisons (Zar, 1984). Other statistical matters, such as transformations and distributions of regression residuals, are addressed in the results.

RESULTS

Biological characteristics of water masses categories

Depth-integrated larval concentrations and zooplankton wet biomasses were estimated for 130 EZNET and bongo stations. However, larval stomachs were available from only some of these (Table 1, Fig. 2). There were marked differences in larval concentrations among the 130 stations (Table 2). These differences were attributable mostly to significantly higher concentrations of larvae in FRONT stations compared with all others, although the pre-storm CW also had significantly higher concentrations than did post-storm CW displaced off the bank (Table 2). There were also significant differences among the subset of 94 stations from which larval gut contents were obtained (Kruskal–Wallis (K–W) statistic = 42.059, $P < 0.001$). Among these, FRONT had significantly higher concentrations of larvae than did both WSW and post-storm CW displaced off the bank.

There were no significant differences in zooplankton biomasses among water masses (Table 2). Similarly, there were no significant differences in zooplankton biomasses among water masses using only stations from which larval stomachs were obtained (K–W statistic = 7.660, $P = 0.264$).

McLaren and Avendaño (1995, their Fig. 2) showed that during October and November 1991 and January 1992, waters within the 60 m contour of Western Bank had much higher concentrations of cod larvae and most copepod taxa than did stations outside this contour (but within the upper 75 m). Lower larval concentrations and zooplankton biomasses might result partly from dilution of populations in the deeper water column. However, among stations of the present study within the 60 m depth contour of the bank (i.e. excluding some WSW and CFW stations, and the post-storm CW displaced off the bank, Fig. 2), there remained highly significant differences (K–W statistic = 43.172, $P < 0.001$) among concentrations of larvae, but again not among zooplankton biomasses (K–W statistic = 8.529, $P = 0.129$).

Table 1. Samples from designated water masses of the gyrelike system around Western Bank, Scotian Shelf, used for analyses of stomach contents. The BONGO nets were used to obtain a single, oblique haul at each station. The EZNETs took series of depth-specific samples at each station. A total of 130 stations was used to estimate larval abundances and zooplankton biomasses (Table 2), but only those that supplied larvae for prey analysis are included here. The seven water-mass categories (Figs. 1, 2) are grouped according to a storm on 3–6 December 1992 that led to considerable displacement of tracked water masses: CW, crest water; FRONT, convergent front around CW; CFW, cold, fresh water largely sampled east of CW; WSW, warm, salty water sampled seaward of the CW and CFW.

Gear	Water mass	Stations sampled	Nets sampled	Larvae sampled	Larval lengths (mm) [mean ± SD (range)]
BONGO	Before storm				
	CW	11	11	82	4.46 ± 0.89 (2.85–7.19)
	FRONT	1	1	5	4.50 ± 0.31 (4.15–4.92)
	CFW	11	11	93	4.65 ± 1.28 (2.79–8.97)
	WSW	6	6	45	4.85 ± 2.51 (2.79–18.45)
	After storm				
	CW on bank	19	19	89	5.90 ± 1.97 (3.16–14.88)
	CFW	7	7	65	5.20 ± 1.49 (3.38–8.87)
	CW off bank	8	8	76	5.73 ± 2.30 (2.54–12.39)
EZNET	Before storm				
	CW	20	119	627	4.93 ± 1.24 (2.42–16.70)
	FRONT	5	36	224	4.84 ± 1.10 (2.54–9.69)
	After storm				
	CW on bank	6	36	100	5.30 ± 1.39 (2.95–10.14)
TOTALS		94	257	1406	5.01 ± 1.45 (2.42–18.45)

Table 2. Concentrations of cod larvae and wet zooplankton biomasses at 130 stations in designated water masses of a gyrelike system around Western Bank, Scotian Shelf. The water masses were sampled before and after a storm on 3–6 December 1992 that displaced water masses from the system (CW, crest water over the bank shallows; FRONT, the surrounding, convergent front; CFW, cold, fresh water sampled largely east of the CW; WSW, warmer, salty water seaward of the other categories; see Figs. 1, 2)

	Before storm				After storm		
Variable	CW	FRONT	CFW	WSW	CW on bank	CFW	CW off bank
No. of stations	43	10	15	6	34	14	8
Larvae 100 m^{-3} (SD)	51.8 (32.9)	170.1 (36.6)	22.5 (28.7)	15.6 (17.0)	24.7 (17.9)	21.7 (22.0)	11.8 (5.9)
Zooplankton mg m^{-3} (SD)	224 (112)	302 (125)	164 (131)	212 (160)	226 (142)	220 (133)	244 (77)

Significant differences (at $P < 0.05$) among rank-ordered means of larval densities (Kruskal–Wallace ANOVA, followed by non-parametric multiple comparisons (Zar, 1984). Means that do not differ significantly are underlined. B–S, before storm; A–S, after storm. There were no significant differences among zooplankton biomasses.

Larval concentration	(FRONT)	(B–S CW)	(A–S CW on bank)	(A–S CFW)	(B–S CFW)	(WSW)	(A–S CW off Bank)

Diets

In all, 16082 prey items were identified in stomachs. These were mostly in larvae from CW stations before the storm (Table 1), as that is where sampling effort was concentrated. There were distinct differences among the seven oceanographic categories (*G*-tests, $P < 0.0001$) in both the percentage of larvae feeding on particular items and the percentage representations of taxa in the combined stomachs (Fig. 3). Only the obvious differences are considered here. The copepod *Pseudocalanus* spp. (almost all *P. newmani* per McLaren and Avendaño, 1995) predominated in guts from all seven water-mass categories. Diet was quite similar at CW and FRONT stations sampled before the storm. The larvae from WSW and CFW had conspicuously more *Oithona* and fewer late nauplii of *Centropages*. Stomachs of larvae from WSW lacked the pteropod *Limacina*. Larvae from CW and CFW after the storm had similar prey, except that CFW had relatively more nauplii and fewer later stages of *Pseudocalanus*.

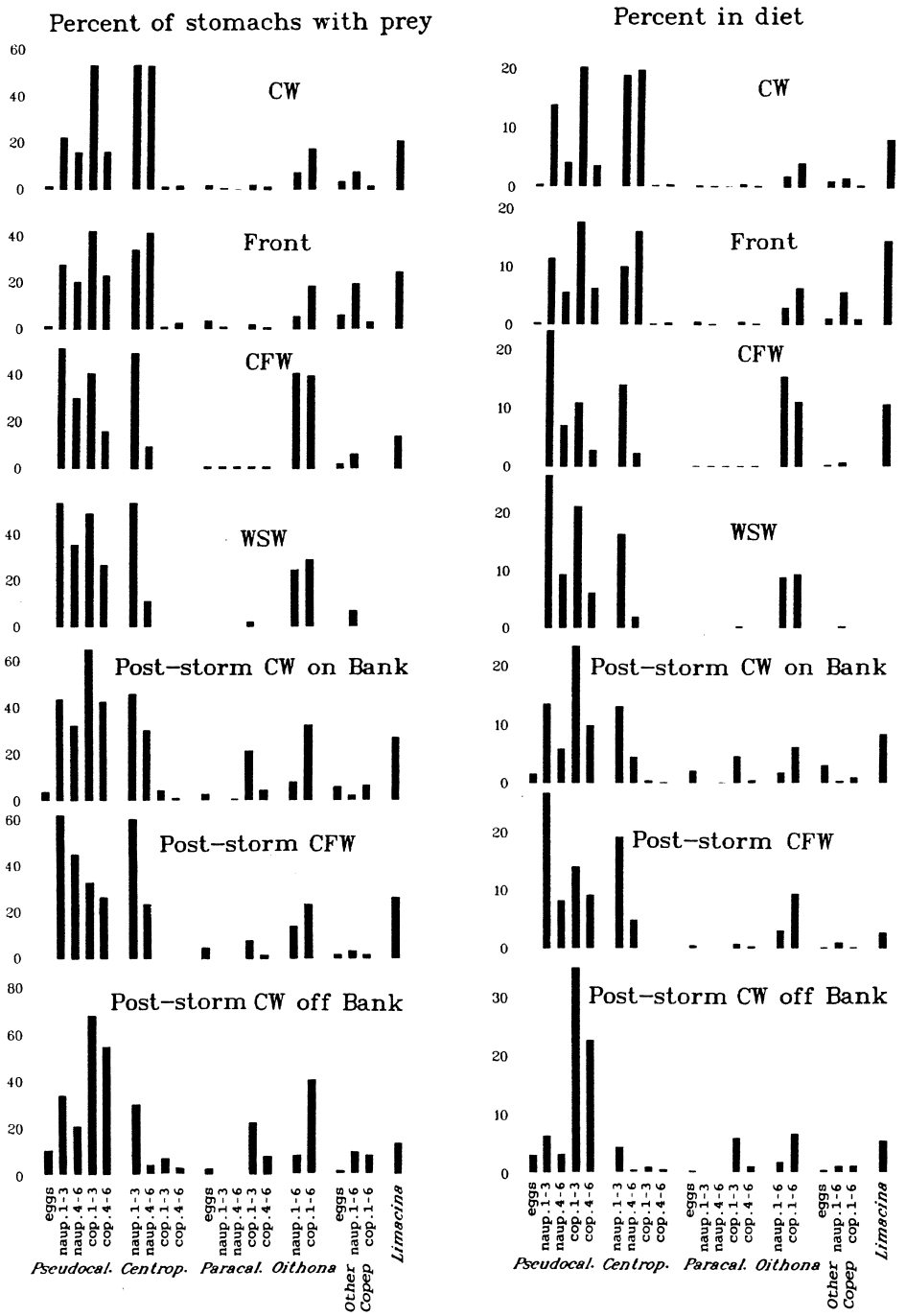
Numbers of prey items

There were significant differences among the mean numbers of prey in larvae from the seven water-mass categories (K–W statistic = 24.872, $P < 0.001$). Larvae from FRONT, together with those from WSW, had significantly fewer prey items than did those from some other water-mass categories, and those from post-storm CFW had significantly more prey (Table 3). However, several variables other than water mass could contribute to feeding by larvae. For example, sizes of larvae differed among water masses (Table 1; K–W statistic = 57.826, $P < 0.001$), and there was a weak, but significant, regression of larval size against sample date ($F_{1,1404} = 68.675$, $P < 0.001$; $r^2 = 0.047$). This implies a mean length increase of about 30% during the sampling period. The slightly larger, older, post-storm animals might have been able to eat more prey. Such data are clearly more appropriately treated by multivariate analysis, taking plausible variables into account.

ANCOVAs of all larvae (bongo and EZNETs combined) yielded highly non-normal residuals. Log transformation (ln[number of prey + 1]) helped, but still produced too many negative outliers (too many empty or near-empty stomachs). Therefore, ANCOVA using ln(number of prey + *n*) was tested for successive integer values of *n*. The ANCOVA with ln(number of prey + 3) produced satisfactorily normal residuals (Lilliefors test, Wilkinson, 1990, $P = 0.295$; $r^2 = 0.400$; 9 negative and 5 positive outliers of 1406 data). This revealed the overwhelming importance of larval size and time of day (Table 4). However, water-mass origins of larvae were also important, and there were significant interactions of larval size, time of day, and sample date with water-mass categories. Whereas larvae from WSW had the lowest numbers of prey items among the original estimates (Table 3), these were among those with most prey when adjusted for larval size and time of day (Table 4). The samples after ANCOVA fell more clearly into two overlapping groups, with those from post-storm CW on the bank occupying an intermediate position (Table 4).

The stepwise ANCOVA using depth-specific EZNET samples eliminated cruise date, sample depth, zooplankton biomass and most interactions. Use of ln

Figure 3. Occurrences of prey items among larvae from different water masses (Figs 1, 2). The numbers of samples and larvae from each water-mass category are in Table 1.



(number of prey + 2) gave satisfactory residuals (Lilliefors test, $P = 0.409$; $r^2 = 0.459$; 7 negative and 2 positive outliers of 951 data points). The analysis (Table 5) again revealed an overwhelming negative influence of time of day, a weaker positive effect of larval size, and a very weak, negative effect of the turbulence index. Water-mass origin was significant, with larvae from pre-storm and post-storm CW together having more prey than did FRONT larvae. Most interactions were non-significant.

Table 3. Differences in mean numbers of prey items and gut fullnesses (see text) among cod larvae from designated water masses of a gyrelike system around Western Bank, Scotian Shelf. The water masses (Figs. 1, 2) were sampled before and after a storm on 3–6 December 1992 that displaced water masses from the system. CW, crest water over the bank shallows; FRONT, surrounding, convergent front; CFW, cold, fresh water sampled largely east of the CW; WSW, warmer, salty water seaward of the other categories.

	Before storm				After storm		
	CW	FRONT	CFW	WSW	CW on bank	CFW	CW off bank
No. of larvae sampled	709	229	93	45	189	65	76
Mean number of prey (SD)	12.37 (9.89)	9.49 (8.37)	10.53 (8.22)	8.75 (6.99)	10.98 (0.09)	12.79 (9.13)	11.11 (9.21)
Mean fullness (SD)	3.88 (1.09)	3.47 (1.37)	3.33 (1.33)	3.02 (1.31)	3.79 (1.03)	3.83 (1.44)	3.92 (1.15)
Mean digestive index (SD)	2.22 (0.40)	2.26 (0.45)	2.45 (0.39)	2.34 (0.44)	1.80 (0.51)	2.02 (0.60)	1.85 (0.51)

Significant differences (at $P < 0.05$) among rank-ordered means (Kruskal–Wallace ANOVA, followed by non-parametric multiple comparisons (Zar, 1984). Means that do not differ significantly are underlined. B–S, before storm; A–S, after storm.

Mean number of prey	(A–S CFW)	(B–S CW)	(A–S CW on bank)	(A–S CW off bank)	(B–S CFW)	(FRONT)	(WSW)
Mean fullness	(A–S CW off bank)	(A–S CFW)	(B–S CW)	(A–S CW on bank)	(FRONT)	(B–S CFW)	(WSW)
Mean digestive index	(B–S CFW)	(B–S WSW)	(FRONT)	(B–S CW)	(A–S CFW)	(A–S CW off bank)	(A–S CW on bank)

Table 4. Determinants of numbers of prey (ln[number + 3]; see text) in larval cod in all bongo and EZNET samples from designated water masses (as shown on Figs. 1, 2, Table 1). The significant differences among adjusted means (non-overlapping vertical bars) are confirmed by non-parametric multiple comparisons. The analysis excludes depths of samples, turbulence indices, and zooplankton wet masses, as these are available only as vertically integrated values for each station from the bongo net samples.

Variable	Coeff.	d.f.	MS	*P*
Constant	1.635	1	11.396	<0.001
Log(larval length)	0.687	1	25.735	<0.001
Time, deviation from 19:00	−0.084	1	18.676	<0.001
Water mass	–	6	2.480	<0.001
(Log[length]) × (water mass)	–	6	1.502	<0.001
Time × (water mass)	–	6	0.862	0.003
(Sample date) × (water mass)	–	6	0.965	0.001
Error		67	0.25662	

Adjusted means of log (number of prey + 3) by water-mass category. Vertical bars indicate means that do not differ significantly (at $P = 0.05$; Kruskal–Wallis rank ANOVA followed by non-parametric multiple comparisons; Zar, 1984).

	Mean		SD	(*n*)
Pre-storm CW	2.560	|	0.517	(709)
Post-storm CFW on bank	2.529	| |	0.536	(65)
Pre-storm WSW	2.521	| |	0.591	(45)
Post-storm CW on bank	2.414	|	0.476	(189)
FRONT	2.334	|	0.538	(229)
Pre-storm CFW	2.317	|	0.690	(93)
Post-storm CW off bank	2.286	|	0.512	(76)

Table 5. Determinants of numbers of prey (log[number + 2]; see text) in larval cod in EZNET samples from designated water masses (as shown on Figs. 1, 2, Table 1) for which depths of samples and associated zooplankton biomasses and turbulence indices are available. Other water-mass categories were not sampled by EZNET.

Variable	Coeff.	d.f.	MS	*P*
Constant	2.230	1	38.493	<0.001
Time, deviation from 19:00	−0.146	1	179.793	<0.001
Log (larval length)	0.455	1	9.547	<0.001
Turbulence index ($wind^3$/depth)	-6.4×10^{-5}	1	1.963	0.009
Water mass	–	2	4.115	<0.000
(Sample date) × (water mass)	–	2	2.396	<0.001
Error		943	0.28698	

Adjusted means of log(number of prey + 2) by water-mass category. Vertical bars indicate means that do not differ (at $P = 0.05$; Kruskal–Wallis rank ANOVA followed by non-parametric multiple comparisons; Zar, 1984).

	Mean		SD	(*n*)
Pre-storm CW	2.436	|	0.517	(627)
Post-storm CW on bank	2.407	| |	0.549	(100)
FRONT	2.146	|	0.548	(224)

Fullness of guts

The indices of gut fullness differed significantly among water masses (K–W statistic = 41.001, $P < 0.001$). These differences were similar to those for number of prey items, with somewhat sharper discriminations between larvae from different water masses (Table 3). Those from WSW averaged less full than those from other water masses, except those from FRONT and before-storm CFW, while those from all other water masses except WSW did not

differ among themselves. Again, it is better to remove effects of other variables.

As with numbers of prey items, iterative step ANCOVA with all samples yielded time of day (again as deviations from 19:00) and larval size as the important main effects, with water mass and its interaction with larval size, time of day, and sample date as significant contributors to the explained variance (Table 6). The regression ($r^2 = 0.328$) was reasonably well behaved, with only 13 of 1406, mostly negative, residual outliers. These outliers, along with clustering around the discrete values of the original fullness index (1–5), produced non-normal distribution of residuals (Lilliefors test, $P < 0.001$). However, no simple transformation normalized the residuals. The adjusted means (Table 6) for various water-mass categories, like the original means (Table 3), show that, before the storm, guts of larvae from CW were significantly fuller than those from the FRONT, WSW, and CFW.

For the EZNET samples, depths and depth-specific zooplankton biomasses and turbulence indices, as well as larval lengths, were eliminated as influences on gut fullness (Table 7). Again, the ANCOVA results ($r^2 = 0.341$) are marred by non-normal residuals (12 outliers, all negative), but the main effect of time of day and its interaction with water mass were clearly paramount.

State of digestion

Digestion was observed to be related to size of prey; smaller prey items were digested first. Also, items closer to the gut wall were often more digested than those in the middle. This variability of digestive states (1, 2 or 3) within guts of individual larvae produced a more or less continuous range of mean digestive indices among larvae. The combined mean digestive indices differed greatly among water masses (Table 3; K–W statistic = 188.863, $P < 0.001$). In the ANCOVA of the whole collection of samples, the main effects were again time of day and larval size (Table 8). Note that the fitted time of day of maximum digestion was 8 h later (03:00 vs. 19:00) than times of maximal number of prey and gut fullness (cf. Table 8, Tables 4–7). Furthermore, the effect of larval size was negative (positive on Tables 4–7). The explanatory power of this regression is, however, low ($r^2 = 0.268$), and the ANCOVA ill-behaved, with somewhat clustered residuals, 27 mostly negative outliers, and no simple means of transforming the dependent variable.

Only larval length had a highly significant main effect on state of digestion in larvae from the EZNET series, although some variance was attributed to depth and four interaction terms (Table 9). The explained variance ($r^2 = 0.216$) was again maximized by ex-

Table 6. Determinants of fullness of guts of larval cod in all bongo and EZNET samples from designated water masses (as shown on Figs. 1, 2, Table 1). The significant differences among adjusted means (non-overlapping vertical bars) are confirmed by non-parametric multiple comparisons. The analysis excludes depths of samples, turbulence indices and zooplankton biomasses, as these are available only as vertically integrated values for each station from the bongo net samples.

Variable	Coeff.	d.f.	MS	*P*
Constant	3.214	1	44.057	<0.001
Time, deviation from 19:00	−0.144	1	54.672	<0.001
Log(larval length)	0.841	1	38.517	<0.001
Water mass	–	6	10.493	<0.001
(Log[length]) × (water mass)	–	6	7.262	<0.001
Time × (water mass)	–	6	2.205	0.036
(Sample date) × (water mass)	–	6	2.404	0.023
Error		1379	0.97728	

Adjusted means of fullness index by water-mass category. Vertical bars indicate means that do not differ (at $P = 0.05$; Kruskal–Wallis rank ANOVA followed by non-parametric multiple comparisons; Zar, 1984).

	Mean		SD	(*n*)
Pre-storm CW	3.899	|	0.925	(709)
Post-storm CFW on bank	3.852	| |	1.032	(65)
Post-storm CW on bank	3.799	| |	0.895	(189)
Post-storm CW off bank	3.671	|	0.964	(76)
FRONT	3.484	|	1.072	(229)
Pre-storm WSW	3.456	| |	1.144	(45)
Pre-storm CFW	3.105	|	1.207	(93)

Table 7. Determinants of fullness of guts of larval cod in EZNET samples from designated water masses (as shown on Figs 1, 2, Table 1) for which depths of samples and associated zooplankton biomasses and turbulence indices are available. Other water-mass categories were not sampled by EZNET.

Variable	Coeff.	d.f.	MS	*P*
Constant	4.799	1	2925.963	<0.001
Time deviation from 19:00	−0.135	1	14.686	<0.001
Time × (water mass)	–	2	19.627	<0.000
(Log[larval length]) × depth	–	1	4.128	0.033
Time × (Sample date)	–	1	4.118	0.033
Error	–	945	0.90385	

Note: there were no significant main effects of the three sampled water masses

Table 8. Determinants of state of digestion of gut contents of larval cod in all bongo and EZNET samples from designated water masses (as shown on Figs 1, 2, Table 1). The significant differences among adjusted means (non-overlapping vertical bars) are confirmed by non-parametric multiple comparisons. The analysis excludes depths of samples, turbulence indices and zooplankton wet masses, as these are available only as vertically integrated values for each station from the bongo net samples.

Variable	Coeff.	d.f.	MS	*P*
Constant	−3.239	1	246.542	<0.001
Time, deviation from 03:00	−0.093	1	10.196	<0.001
Log(larval length)	−0.518	1	21.944	<0.001
Water mass	–	6	1.990	<0.001
Time × (sample date)	–	1	3.228	<0.001
Time × (water mass)	–	6	2.915	<0.001
Error		1390	0.16874	

Adjusted means of digestion index by water-mass category. Vertical bars indicate means that do not differ (at $P = 0.05$; Kruskal–Wallis rank ANOVA followed by non-parametric multiple comparisons; Zar, 1984).

	Mean		SD	(*n*)
Pre-storm CFW	2.405	|	0.374	(93)
Pre-storm WSW	2.309	| |	0.340	(45)
FRONT	2.260	| |	0.452	(229)
Pre-storm CW	2.206	| |	0.372	(709)
Post-storm CFW on bank	2.035	| |	0.500	(65)
Post-storm CW off bank	1.890	|	0.457	(76)
Post-storm CW on bank	1.852	|	0.463	(189)

Table 9. Determinants of state of digestion of gut contents in larval cod from EZNET samples for which depths of samples and associated zooplankton biomasses and turbulence indices are available. Other water-mass categories were not sampled by EZNET.

Variable	Coeff.	d.f.	MS	*P*
Constant	2.843	1	110.896	<0.001
Log(larval length)	−0.487	1	8.493	<0.001
Depth in m	−0.005	1	0.875	0.018
(Log[larval length]) × (water mass)	–	2	2.770	<0.001
(Sample date) × (water mass)	–	2	1.848	<0.001
Time × (water mass)[a]	–	2	0.744	0.009
Depth × (water mass)	–	2	0.621	0.019
Error		940	0.15605	

[a] Time as deviation from 02:00.

pressing times of day as deviations from 02:00, but time only appeared in a weak interaction with water mass. The ANCOVA was again ill-behaved, with 25 mostly negative outliers.

DISCUSSION

All samples from within the 60 m depth contour (Fig. 2) were from regions that supported relatively high concentrations of cod larvae and zooplankton during an earlier survey in late autumn and early winter 1991 (McLaren and Avendaño, 1995). Significantly higher concentrations of larvae at FRONT stations have previously been discussed by Taggart *et al.* (1996). They also found significantly fewer larvae at selected stations in CFW than in pre-storm CW, not here confirmed in wider, non-parametric comparison among water masses (Table 2). Concentration of larvae within convergent fronts is far from unprecedented (Kingsford and Suthers, 1996; Lochmann *et al.*, 1997), although the mechanisms remain incompletely understood. The only other significant difference of larval concentrations among water masses was between CW before the storm and CW displaced off the bank after the storm (Table 2). This reflects the dilution and mortality of larvae when their water mass was swept into deeper waters.

Highest zooplankton biomasses were in FRONT stations, but unlike Lochmann *et al.* (1997) and Taggart *et al.* (1996), we found no significant differences among water masses based on our wider non-parametric comparisons. This is perhaps not surprising as *Calanus finmarchicus* predominated in these coarse-mesh samples, and that species was not relatively more concentrated in samples taken from the bank in earlier surveys (McLaren and Avendaño, 1995). The coarse-mesh samples are inadequate for assessing concentrations of the smaller prey. However, McLaren and Avendaño (1995) showed that numbers of prey consumed by larvae were strongly correlated with concentrations of the same taxa and stages at four stations near the crest of Western Bank, and these prey also predominated in guts of larvae in the present survey (Fig. 3): mostly *Pseudocalanus* nauplii and copepodids and *Centropages* nauplii, along with good numbers of *Limacina* and *Oithona* sp. The complete lack of *Limacina* in larvae from WSW is inexplicable from present knowledge. Otherwise, the sharpest difference in diet seemed to occur in CW swept off the bank after the storm, with diminutions of nauplii and increases of copepodids of both *Pseudocalanus* and *Centropages* (Fig. 3). This could have resulted from more advanced development of copepod cohorts later in the cruise or selection of larger items by the older and slightly larger larvae (Table 1).

The most important aim of this study was to determine if cod larvae were better fed in some parts of the gyre system. There was no indication that the results on numbers of food items and gut fullnesses were distorted by evacuation of guts in nets (Kjørsvik *et al.*, 1991); only three of 1406 larvae were observed to be evacuating the hindgut at the moment of preservation (their midguts were full). On the other hand, the occurrence of many larvae with empty or nearly empty guts in an evidently strong diel feeding rhythm, suggests that feeding by larvae in the net was not important.

The raw data (Table 3) suggest that, in terms of numbers of prey items consumed, larvae in CFW after the early-December storm were significantly better fed than those in FRONT and WSW before the storm. However, more reliable orderings of means after ANCOVA (Tables 4, 5) suggest that larvae in CW before the storm were the best fed, but that they lost this advantage after being swept off the bank (Table 4). It is possible, however, that differences in numbers of prey items, even after removal of other influences, resulted from differences in prey size. Before the storm, larvae from CW consumed not only more, but also relatively larger items, compared with those from CFW and WSW (Fig. 3; relatively more copepodids of *Pseudocalanus*, more older nauplii of *Centropages*, and fewer of the small *Oithona*). However, a noticeable switch to larger items by larvae in CW after it was swept off the bank (Fig. 3; relatively more copepodids of the above genera) could have partly underlain the apparent reduction in numbers consumed (i.e. to the lowest ranking on Table 4). Gut fullness may better reflect the nutritional environment for larvae, as it may be unaffected by prey size.

Although marred by inhomogeneities in residual variances, the very low P values of main effects on gut fullness (Tables 6, 7) and nonparametric assessments of differences among water masses (Table 6) are convincing. The interaction terms may be less trustworthy. By this index of feeding success, larvae in pre-storm CW were best fed, whereas those in other pre-storm water masses, including FRONT, averaged less full (Table 6). This conclusion is empirical support for the conclusion from a modelling study by Werner *et al.* (1996) that regions of highest retention on such banks are also most suitable for larval feeding, even if biomasses of macrozooplankton are not elevated (Table 2). However, it is very important to note that larvae in CW after it was swept by storms off the bank to the north-east did not have significantly

reduced gut fullness (Table 6). Also of interest, larvae in CFW switched from averaging least full before the storm to second fullest afterwards. Note that most stations in post-storm CFW were close to the bank region previously occupied by CW (Fig. 2). There are some indications (Taggart *et al.*, 1996) that, after displacement of CW to the south-west (i.e. post-storm, on-bank CW on Fig. 2), the gyrelike system began to be reestablished around the crest of Western Bank at the time of sampling of post-storm CFW, before CW was swept north-east off the bank by the storm of 11–12 December. Could it be that the seemingly well-fed larvae in post-storm CFW were benefiting from the developing hydrographic regime? Or were they somehow using vertical concentration of prey nearer the crest of Western Bank?

The smaller numbers of prey and lower fullness indices of larvae from FRONT stations (significantly lower than in CW before the storm) do not match expectations that feeding conditions for larval fishes may be enhanced at hydrographic fronts (Taggart *et al.*, 1989, Brandt, 1993). Lochmann *et al.* (1997) found that, for these same larvae, triglycerides (an indication of feeding history) and an index of body condition did not differ at FRONT stations relative to surrounding waters. They concluded that residence in FRONT waters was too ephemeral to enhance lipid or condition. We detected no significant differences among water masses in zooplankton biomasses (Table 2), although the smaller, unsampled size fractions may have been more common at FRONT stations (Fig. 6 in Taggart *et al.*, 1996). However, it is clear that FRONT larvae did not gain short-term enhancement of feeding rates.

Time of day was consistently a major determinant of both numbers of prey in guts and gut fullnesses (Tables 3–7). The apparent peak feeding time (19:00 AST) for both numbers of prey and fullnesses is the same as that obtained for larval cod taken during three cruises a year earlier (McLaren and Avendaño, 1995). Given this strong diel feeding rhythm, no conclusions should be made about larval feeding without standardization or statistical removal of times of sampling. Separation of samples by day and night would be insufficient. Furthermore, the significant interactions between time of day and water mass (Tables 4, 6, 7) or sample date (Table 7) suggest that informative studies should strive for both water-mass homogeneity and temporal resolution.

Larval size is clearly important; larger larvae had more prey and fuller guts (Tables 4–6), although size affected gut fullness only as an interaction with water mass in the depth-specific samples (Table 7). As larger larvae have larger guts and may be more competent at filling their guts, these results are hardly surprising. The practice of separating larval size classes for analysis of gut contents (Lough and Mountain, 1996) is a good one, but statistical removal is more enlightening.

Possible effects of turbulence on feeding success are of considerable current interest (MacKenzie and Leggett, 1993). Although numbers of prey appeared to be related to our simple index of turbulence, the weakly negative effect accounted for only 1% of explained variance, most of which was attributable to time of day and size (Table 5). It is of interest that the more focused study by Lough and Mountain (1996) also found negative relationships between numbers of prey in guts and estimates of turbulent dissipation. Nor, in our data, was there any pattern of residuals indicating more complex effects, for example a dome-shaped response to turbulence (MacKenzie *et al.*, 1994). It is very unlikely, given the trivial effect and its complete absence in the ANCOVA of gut fullnesses (Table 7), that a more complex integration of wind speeds over the previous hours would be informative. Our collections were not designed to seek turbulence effects, which are sensibly sought by more nearly synchronous samples of larvae, and directly measured turbulence and prey concentrations. The possible correlation of wind speeds with time of day (Lough and Mountain, 1996) may require attention. In our study, wind speed was very weakly, although significantly, correlated with times adjusted from 19:00 ($r^2 = 0.010$, $P < 0.001$).

The designated water masses were sampled during different periods of the cruise. Furthermore, larval size was inevitably correlated with sample date. Thus, there were weak interactions with sample date in all analyses (Tables 4–7). These were unlikely to have seriously distorted the substantial main effects, or to have greatly disordered the adjusted means. An ideal sampling regime would either greatly condense or randomize sampling dates among such designated water masses, once they are identified a priori.

There were no significant effects of depth or zooplankton biomasses on numbers of prey or gut fullnesses. As noted above, although there may have be some correlation with smaller zooplankton fractions (Taggart *et al.*, 1996), our coarse-mesh nets would not retain most of the small food items used by the larvae. The zooplankton biomasses may not therefore adequately test the null hypothesis.

The digestive indices are generally uninformative about influences of water mass. As expected, because large amounts of food are less digested, there is a largely reversed order among water masses of mean digestive index compared with numbers of prey and

stomach fullnesses (Tables 3, 8). However, some other results are of interest. The fitted time of day for maximal digestion (Table 8) was 8 h later than the time of maximum amounts of food (Tables 4–7). After this time, presumably, further digestion was not detectable by the simple index, although amounts of digested food in the guts continued to decrease. If cod larvae evacuate their guts on average within about 4 h (Lough and Mountain, 1996), feeding in nature is sharply reduced, but not completely suspended, during much of the 24-h period. The negative effect of larval size on amount of digestion (Tables 8, 9), may indicate that digestion was more protracted or less complete in larvae with larger amounts of food. The weak negative effect of depth (Table 9) and several interactions (Tables 8, 9) are inexplicable; the low r^2 values of the ANCOVAs for digestive index (see Results) make it risky to hypothesize about all but the pronounced main effects.

Several general conclusions are possible.

1 Assessments of feeding by larval fish must consider time of day, larval size, and water-mass origin or character. Also, the widespread use of numbers of prey in guts ('feeding ratio') as an indication of feeding success is also suspect without correction for sizes of prey items; gut fullness is simpler and better.

2 Like McLaren and Avendaño (1995) from spatial distributions on and around Western Bank, and Werner *et al.* (1996) from modelling the Georges Bank system, we conclude from direct sampling of water masses that high concentration/retention in the centre of a gyrelike system (CW) is accompanied by the best feeding conditions for larval cod.

3 Contrary to some expectations, larvae in the surrounding convergent front were significantly less well fed.

4 Larvae initially in the gyre centre largely maintained high gut fullnesses while being advected off the bank. This may have implications for hypotheses about effects of atmospheric forcing on recruitment of larval cod (Cong *et al.*, 1996; Taggart *et al.*, 1996; Lochmann *et al.*, 1997).

5 Analyses of effects of zooplankton biomasses and turbulence on larval feeding must be undertaken with more focused, synchronous sampling.

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