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Canada

Sea scallop larvae *Placopecten magellanicus* in the Georges Bank region: distribution, abundance and condition

by

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To Linda, Roddy, Marc and Peter

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Abstract

The vertical and horizontal distribution of sea scallop larvae *Placopecten magellanicus* was studied. Scallop larvae can undertake diel vertical migrations in some parts of their range but since the migration is diel and of small amplitude (< 10 m), the effect on horizontal dispersal is probably small. The vertical distribution of larvae on Georges Bank was closely associated with the density structure of the water column. In well mixed waters larvae were distributed evenly with depth, while in stratified waters larvae were aggregated above or within the pycnocline. Larvae did not aggregate in relation to food as measured by chlorophyll < 15 μm. Subsurface aggregations of larvae may be related to lower turbulence near the pycnocline.

The horizontal distribution of sea scallop larvae on the northeast part of Georges Bank and the adjacent waters is described for the late summer and fall periods from 1985 to 1988. Larvae are generally retained on this part of Georges Bank, probably by physical processes. On the Northern Flank, larval abundance was not related to any frontal feature. Abundance declined near the bank edge (200 m isobath), where the cross-frontal component of the residual current was directed on-bank. Larval abundance on the Northern Flank was more patchy when on-bank temperature stratification was high, a situation which coincided with winds from the north.

On Georges Bank, changes in the position and size structure of some high density larval patches indicate that some scallop larvae do move in the direction of the residual circulation, and that exchange among the fished aggregations (Northeast Peak, Southeast Part and South Channel) is probable. Georges Bank may be a single recruitment unit for sea scallops.

A condition index for bivalve larvae based on lipid stained by Oil Red O (ORO lipid) was tested on both hatchery-reared and sea-caught larvae of the sea scallop. ORO lipid in hatchery-reared larvae decreased with increasing periods of starvation. Georges Bank larvae had stain artifacts, perhaps related to at-sea staining procedures. ORO lipid was successfully quantified in 224 large (> 230 μm in length) larvae from Georges Bank. These measurements suggest that for large larvae: (i) starvation is rare; (ii) lipid levels are comparable to those of well-fed larvae; and (iii) condition may at times be more a function of physical stratification than of food concentration.

A coarse estimate of the annual production of late stage larvae (120-1500 m^{-2}) on Georges Bank suggests that considerable mortality is associated with metamorphosis, settlement, and the early juvenile period.

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General Introduction

The sea scallop *Placopecten magellanicus* occurs in the coastal and shelf waters of the Northwest Atlantic from the Strait of Belle Isle south to Virginia (Posgay 1979), but is sufficiently concentrated for commercial fishing in only a few locations (Fig. 1). The Georges Bank population is the world's largest natural aggregation of scallops and is characterized by irregular recruitment (Caddy 1989).

Like many benthic marine invertebrates, individual sea scallops annually produce millions of eggs which develop into planktotrophic larvae. The planktonic period of sea scallops lasts at least 4 weeks and probably less than 7 weeks (Culliney 1974, Tremblay 1988). Sea scallops from different aggregations are most likely to intermingle via planktonic dispersal (temporal changes in horizontal distribution due to advection and mixing processes), because after settlement movement appears to be limited. Small scallops, with shell height (SH) of ca 10 mm, may spend up to 75% of their time attached by byssus threads (Caddy 1972). With increasing size scallops spend less time attached (Caddy 1972), but swimming by juvenile and adult scallops appears to be primarily for avoidance (Caddy 1968), and large scallops (SH > 100 mm) swim less (Caddy 1968, Gould 1971). Tagging studies of scallops greater than 60 mm SH indicate annual movements of less than a 5-10 kilometers by most individuals, with little evidence for directed migration (Baird 1954, Posgay 1981, Melvin et al. 1985). On Georges Bank mid-sized scallops (60-89 mm SH) move more than other sizes (Melvin et al. 1985), perhaps because mid-sized scallops have greater hydrodynamic efficiency (Dadswell and Weihs 1990). Scallops less than 60 mm SH have seldomly been tagged, but it is doubtful that they migrate between the major scallop aggregations (Fig. 1).

The extent to which the sea scallop aggregations in Fig. 1 are self-sustaining is unresolved. Some suggest that no aggregations of scallops can be self-sustaining except

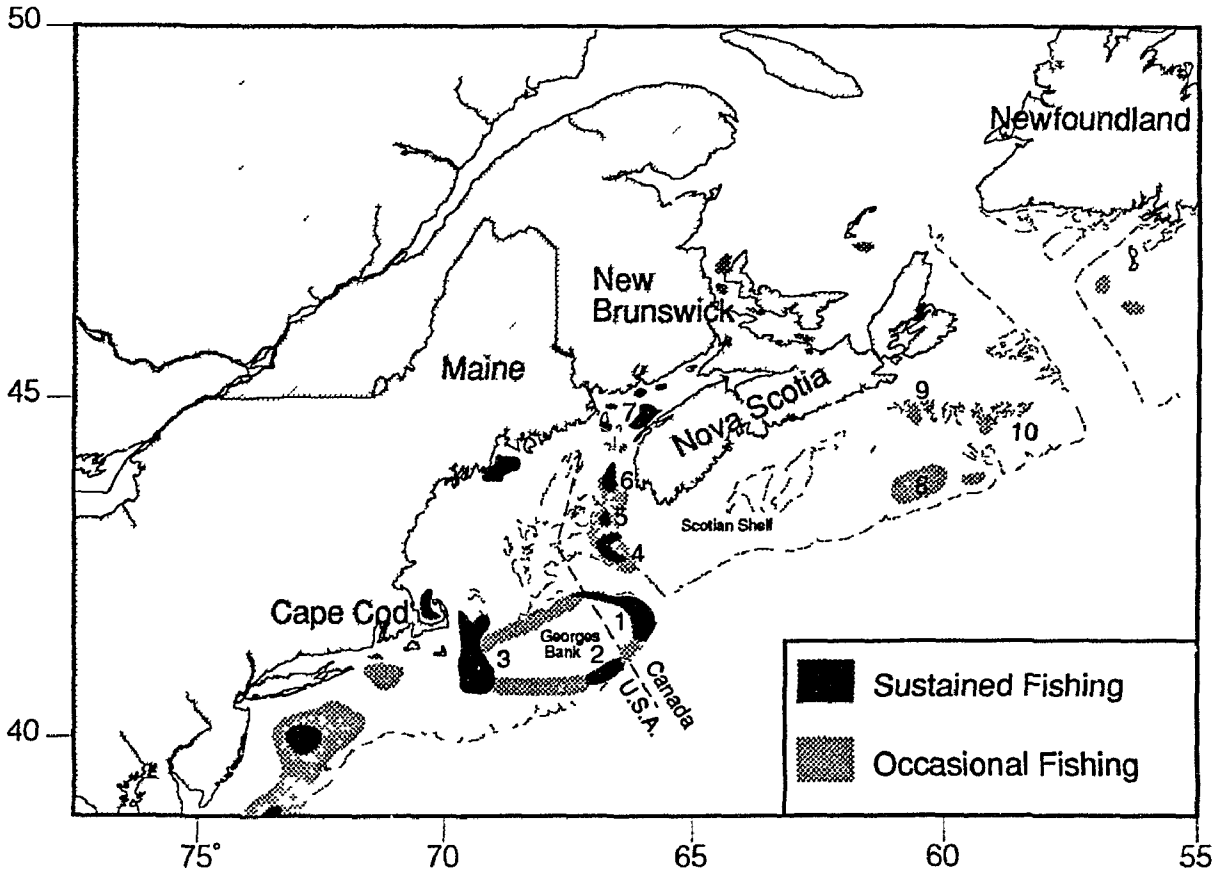

Figure 1. Major fishing aggregations for sea scallops in the Georges Bank and Scotian Shelf areas (modified from Sinclair et al. 1985 and Robert et al. 1989a). Long dashed line across Georges Bank is boundary between Canadian and U. S. sides. Fishing areas are as follows. 1: Northern Flank and Northeast Peak; 2: Southeast Part; 3: South Channel; 4: Browns Bank; 5: German Bank; 6: Lurcher Shoals; 7: Bay of Fundy; 8: Sable Island Bank area; 9: Middle Grounds; 10: Banquereau Bank.

for Georges Bank, and that scallop larvae must be transported long distances (Posgay 1979). Differences among aggregations with respect to the growth rate of individuals (Robert et al. 1985, Serchuk et al. 1979), spawning time (Dickie 1955, Sinclair et al. 1985), and morphometrics (E. Kenchington, Dept. of Fisheries and Oceans, Halifax, N. S., unpublished data) are consistent with the view that the different aggregations are to some extent independent, as is the persistence over time of some scallop aggregations in relatively fixed locations (Sinclair et al. 1985). The distribution of sea scallop larvae in the Bay of Fundy suggests that recruitment in the outer part is locally derived (Tremblay and Sinclair 1988).

Electrophoresis indicates that there is little genetic differentiation among sea scallop aggregations at the level of isoenzymes (Gartner-Kepkay and Zouros, unpublished MS), but this finding is neutral with respect to the question of whether the aggregations are self-sustaining. Stocks can be electrophoretically indistinguishable yet adapted to their respective environments (Ihssen et al. 1981). In addition, genetic homogeneity can result from the exchange of relatively few larvae among aggregations.

The concept that the larval period of benthic invertebrates is an adaptation for dispersal is commonly held (Hedgecock 1986), but in the short term (10's-100's of generations) larval dispersal may be disadvantageous because individuals land in areas with unfavourable conditions (Strathmann 1980, Palmer and Strathmann 1981, Strathmann et al. 1981), or become 'vagrants', unable to locate potential mates (Sinclair 1988, Sinclair and Iles 1989). Substantial genetic differentiation in species with larvae which have a high dispersal capacity (Burton and Feldman 1982, Burton 1983, Hedgecock 1986), is contrary to the concept that longer planktonic periods result in greater dispersal and population mixing. This genetic differentiation suggests that planktonic dispersal is more restricted than is commonly supposed, or that genetic differences arise after settlement through natural selection. Dispersal during the

planktonic period may be more restricted if larvae undertake certain types of vertical movements (see below).

This thesis investigates the factors affecting dispersal of sea scallop larvae, and whether the aggregations on and around Georges Bank (Fig. 1) are likely to exchange larvae. Chapters 1 and 2 are concerned with the vertical distribution of larvae and the implications for horizontal dispersal. Chapters 3 and 4 are studies of horizontal distribution on different spatial scales. Chapter 5 assesses the potential application of a condition index to assess food limitation of sea scallop larvae. Other studies of the identification of planktonic sea scallop larvae (Tremblay et al. 1987), and of the distribution of larvae in the Bay of Fundy (Tremblay and Sinclair 1988) are referenced in the thesis but are not part of it.

Planktonic larvae have little direct control over their horizontal position, but they can swim vertically. Since there are often vertical changes in current speed and direction (vertical shear), the currents to which larvae are exposed will depend upon the range of depths they occupy. Vertical migrations by larvae can thus result in a pattern of dispersal that cannot be predicted from physical processes alone. In estuaries, the potential role of behavior in the retention of larvae has long been recognized, and has been demonstrated for some species (for reviews see Mann 1986a [bivalves], Sulkin 1984 [crabs], Norcross and Shaw 1984 [fish]).

Many of the sea scallop aggregations in Fig. 1 are associated with areas with strong tidal circulation (Sinclair et al. 1985). Sinclair et al. (1985) suggested that sea scallop larvae might 'use' the tidal circulation by vertically migrating to limit the extent of larval dispersal. This idea was earlier put forward to explain the retention of herring larvae which are found in some of the same locations as sea scallops (Iles and Sinclair 1982, Sinclair and Iles 1985). Chapter 1 is an examination of the evidence for vertical migration of sea scallop larvae based on depth stratified sampling for 50 h near Grand

Manan, N.B. A diel vertical migration can occur, but is of small amplitude. A similar version of this chapter is published (Tremblay and Sinclair 1990a).

Additional variables which may affect the vertical distribution of planktonic larvae include the physical characteristics of the water column, and the vertical distribution of larval food. In the Bay of Fundy larvae were found to be distributed over the whole water column in well mixed waters, but aggregated above the thermocline in water columns with some density stratification (Tremblay and Sinclair 1988). Chapter 2 establishes the conditions associated with subsurface aggregations of larvae on Georges Bank, shows that the larval aggregations do not coincide with increased concentrations of chlorophyll $a < 15$ µm , and assesses the potential role of depth regulation via swimming of sea scallop larvae on Georges Bank. A similar version of this chapter is published (Tremblay and Sinclair 1990b).

Many studies of the broadscale distribution of plankton on Georges Bank indicate that exchange with the surrounding area is limited, and that most larvae or zooplankton which originate on the bank are retained there (haddock larvae: Smith and Morse 1985, Hurley and Campana 1989; chaetognaths: Clarke et al. 1943; herring larvae: Boyar et al. 1973, Schnack and Stobo 1973, Bumpus 1976, Iles and Sinclair 1982; cod larvae: Hurley and Campana 1989, Lough and Bolz 1989; and copepods: Davis 1984). Other studies suggest that extensive losses of larvae from Georges Bank do occur, or that the residual circulation does not fully explain the pattern of larval distribution (Walford 1938, Colton and Temple 1961, Harding et al. 1982, Colton and Anderson 1983).

Active vertical swimming may enhance the retention of some Georges Bank fish larvae and zooplankton (Iles and Sinclair 1982, Lough and Bolz 1989, Lough and Trites 1989). The swimming ability of sea scallop larvae is less than many of the planktonic larvae and zooplankters which have been the subject of broadscale distribution studies on Georges Bank. If behavior is important for retention, it might be expected that the

retention of sea scallop larvae on Georges Bank would be less than for more mobile larvae and zooplankton. In Chapter 3 the pattern of sea scallop larval dispersal on and around Georges Bank is inferred from three sources of information: larval distribution and abundance during plankton surveys, the potential locations of larval origin (fished aggregations as an index of spawning biomass), and the residual circulation. The inferred dispersal pattern, and the abundance of late stage larvae, are discussed in relation to scallop population structure and recruitment. A similar version of Chapter 3 will be submitted to the Canadian Journal of Fisheries and Aquatic Sciences.

The tidally induced frontal zones where sea scallops occur in the Gulf of Maine region are characterized by strong gradients in physical and biological variables that may play an important role in the ecology of planktonic larvae of continental shelf species. Physical processes at the front may affect the distribution of sea scallop larvae directly, or gradients in physical or biological features associated with the front (e.g. temperature, food) may affect larval growth and survival. Chapter 4 assesses how the abundance of sea scallop larvae relates to the frontal zone on the Northern Flank of Georges Bank during October.

Mortality during the larval period of sea scallops must be very high, but as in other marine larvae, the mortality rate and the factors influencing it are difficult to determine. Starvation, predation, and dispersal to adverse locations have all been implicated. Laboratory studies of a condition index for bivalve larvae based on a lipid-specific stain (Oil Red O) have raised the possibility that food limitation of marine bivalve larvae can be studied (Gallager and Mann 1981, Gallager et al. 1986, Gallager and Mann 1986a). In Chapter 5 I describe my laboratory studies of the effects of food regime and temperature on the Oil Red O condition index, and field studies of the application of the index to sea-caught larvae.

Chapter 1

Diel vertical migration of sea scallop larvae *Placopecten magellanicus* in a shallow embayment.

1.1 Introduction

The distribution of marine planktonic larvae is largely a function of the direction and strength of the currents in which they are carried, coupled with the location of larval origin. As models of the physical circulation improve, there is a need to better understand what role larval behavior plays in determining their vertical distribution. Whether the larvae undertake active vertical migrations must be known, since modelling studies show that this can alter the pattern of planktonic dispersal from that expected from physical processes alone (Kamykowski 1976, Rothlisberg 1982, Rothlisberg et al. 1983, Lough and Trites 1989).

Vertical migration by some species of bivalve larvae may be significant despite their small size (< 300 μm) and low vertical swimming speeds (generally < 2.0 mm sec^{-1} -- Mileikovsky 1973, Cragg 1980, Mann and Wolf 1983). Active migration of late stage oyster larvae in relation to tidal circulation within some estuaries has been reported (Nelson and Perkins 1931, Carriker 1951, Kunkle 1958), although there are other interpretations of these data which do not involve larval behavior (Korringa 1952, de Wolf 1973, Andrews 1983). Diel vertical migration of some coastal bivalve larvae (Quayle 1952, 1959, Verwey 1966, Harding et al. 1986), and offshore bivalve larvae (Scrope-Howe and Jones 1986) is suggested by the occurrence of the larvae in shallower depths at night.

Pectinid larvae in mesocosms migrate to shallower waters at night (Kaartvedt et al. 1987, Silva and O'Dor 1988) but there are no published field studies to corroborate these

findings. The present chapter is an investigation of whether sea scallop larvae vertically migrate in a shallow embayment in the outer Bay of Fundy.

1.2 Methods

1.2.1 Sampling

Scallop larvae were collected for 50 h from 3 to 5 October 1985 from a ship anchored within an embayment of Grand Manan Island at the mouth of the Bay of Fundy (Fig. 1.1). The site was chosen because of its weak tidal currents in comparison with other locations in the Bay of Fundy, a feature which made depth stratified sampling via pump possible. Bottom depth at the site ranged between 20 and 24 m depending on the tide. Sampling took place every 2 h, for a total of 26 profiles.

The pump system used for sampling scallop larvae consists of a FLYGT model 2051 electric pump, 6 cm suction hose and a SIGNET in-line flowmeter and readout. The pump intake was attached to a hydrographic wire and moved vertically through a depth interval of 5-9 m for 6-10 min until a sample of 2-3.5 m^3 (mean: 2.7) was obtained. Four depth intervals were sampled every 2 h: 0.5-5 m, 5.5-10 m, 10.5-15 m, and from 15.5 m to within 0.5-1 m of the bottom. For the last profile only, samples were obtained at 2 m intervals to a depth of 24 m.

On deck, the pump outflow was directed first through a coarse mesh net (333 μm) to remove larger particles, and then through a fine mesh net (85 μm) for sample collection. Samples were preserved in 4% formalin buffered with sodium borate. Sea scallop larvae and other heavier components of the plankton samples were physically separated from the lighter components using a colloidal silica (Tremblay et al. 1987). All sea scallop larvae in the samples were then identified and counted using a dissecting microscope. After transferring the larvae from the counting dish to a welled slide, the lengths of the larvae were measured to the nearest 6 μm using an inverted microscope.

Once every 2 h, in between larval profiles, an Aanderaa RCM4S current meter was lowered through the water column to measure current speed and direction, temperature, and conductivity. Measurements were made at 2 m intervals to a depth of 18-22 m depending on the water depth. Unless otherwise noted, current speed refers to the average from the surface to 18 or 20 m. Tidal height was obtained from tide tables for Saint John, N. B., prepared by the Canadian Hydrographic Service.

1.2.2 Data Analyses

To reflect the mean depth of sea scallop larvae for any given profile, the centre of mass (ZCM) was calculated as in Fortier and Leggett (1982):

$$ZCM = \sum_{i=1}^{n} p_i \, z_i$$

where p_i is the proportion of the total number of larvae caught within the i th depth interval, and z_i is the mid-depth of the i th interval. The centre of the deepest interval was taken as 18 m. As a measure of larval aggregation, the coefficient of variation (CV) of the concentration of larvae over the 4 depth intervals was used. A high CV indicates strong aggregation of larvae while a low CV indicates that the larvae are more evenly distributed over the water column.

The structure of the water column during each physical profile over the 50 h was characterized by the depth of the pycnocline and by the level of density stratification. Pycnocline depth (P) was estimated as the centre of the 6 m interval where the change in sigma-t was maximum. An index of the density stratification of the water column (S) from the surface to 18-20 m was calculated as:

$$S = \Delta\text{Sigma-t}/\Delta Z$$

where Z is depth.

All data were analyzed using SYSTAT version 3.1 (Wilkinson 1987).

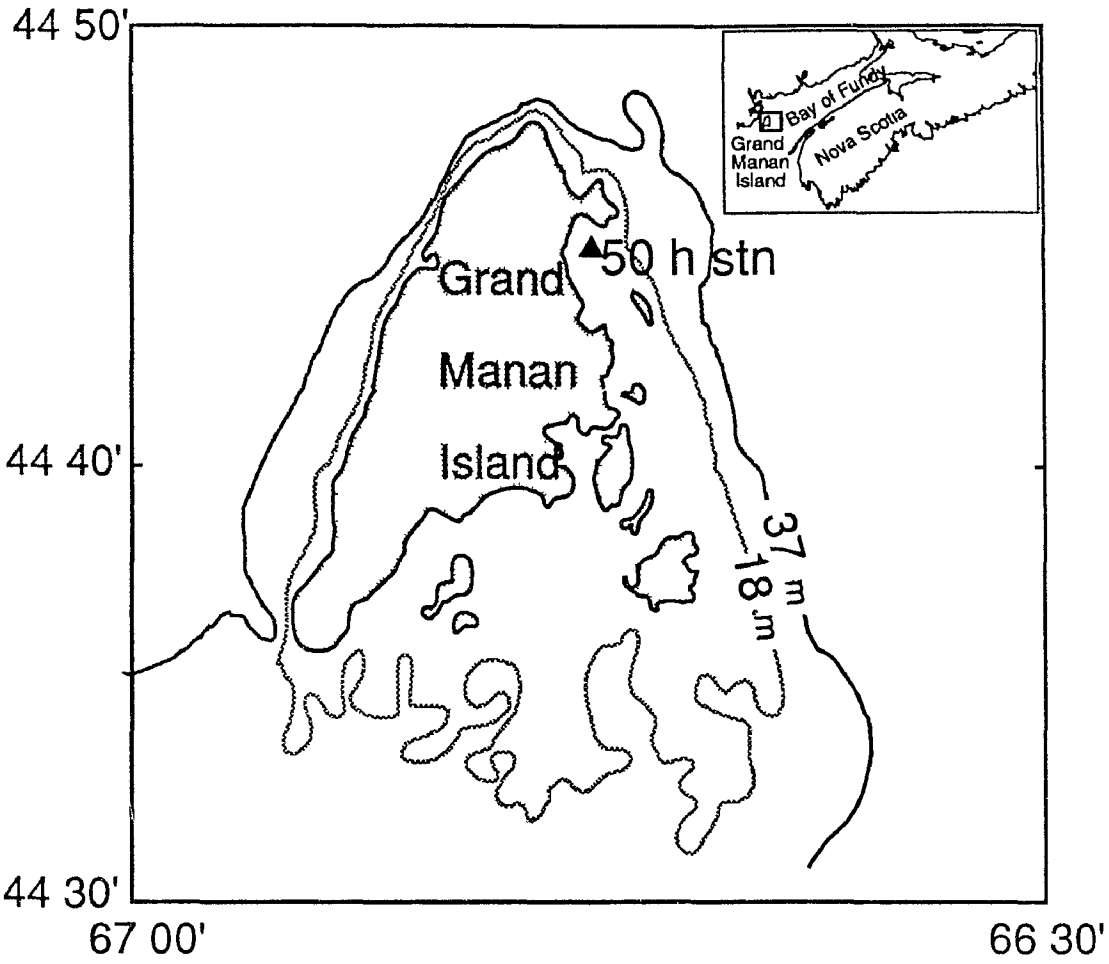

Figure 1.1. Grand Manan Island and location of 50 h anchor station.

1.3 Results

Vertical differences in temperature in the water column were small, with mean temperatures over the sampling period of 11.8 °C at the surface and 11.3 °C at 22 m (Fig. 1.2a). Density structure was primarily a function of the temperature structure, and the water column was weakly stratified with a poorly defined pycnocline (Fig. 1.2b). Mean current speeds were fairly uniform with depth, ranging between 6 and 12 cm sec^{-1} (Fig. 1.2c). The higher speed at 2 m was due both to wind and some pumping by the ship which was unrelated to the study.

Sea scallop larvae were usually most concentrated in the upper 10 m, with sharply reduced densities below 15 m (Fig. 1.3). Strong aggregations within the upper 5 m were limited to night profiles, while aggregations below 10 m were limited to day profiles (Fig. 1.3). A rise in the larval centre of mass (ZCM) occurred between 1930 and 2130 h on both days, and a lowering of the ZCM occurred between 0730 and 0930 h (Fig. 1.4a). Over the 50 h of sampling, the ZCM was shallower during the night than the day, and occurred within a narrower depth interval (Figs. 1.3, 1.4a, Table 1.1).

Although current speed and density stratification (S) were more variable during the day, there were no significant day-night differences in these physical variables to parallel the differences in the ZCM (Table 1.1). The ZCM was not correlated with density stratification, current speed, or pycnocline depth (Figs. 1.4a, c, d, Table 1.2), and did not fluctuate in relation to tide height (Fig. 1.4b). Some large changes in the ZCM did correspond to abrupt changes in the physical regime (e.g. S between profiles 1 and 2 in Fig. 1.4c) but such correspondences were inconsistent.

The depth-averaged concentration of sea scallop larvae (n m^{-3}) trended downward over the 50 h (Fig. 1.4e), but more striking were the sinusoidal fluctuations. Comparison with the ZCM series (Fig. 1.4a) suggests that the fluctuations in larval concentration occurred with a shorter period. The two series are short (n=26) for time series analysis,

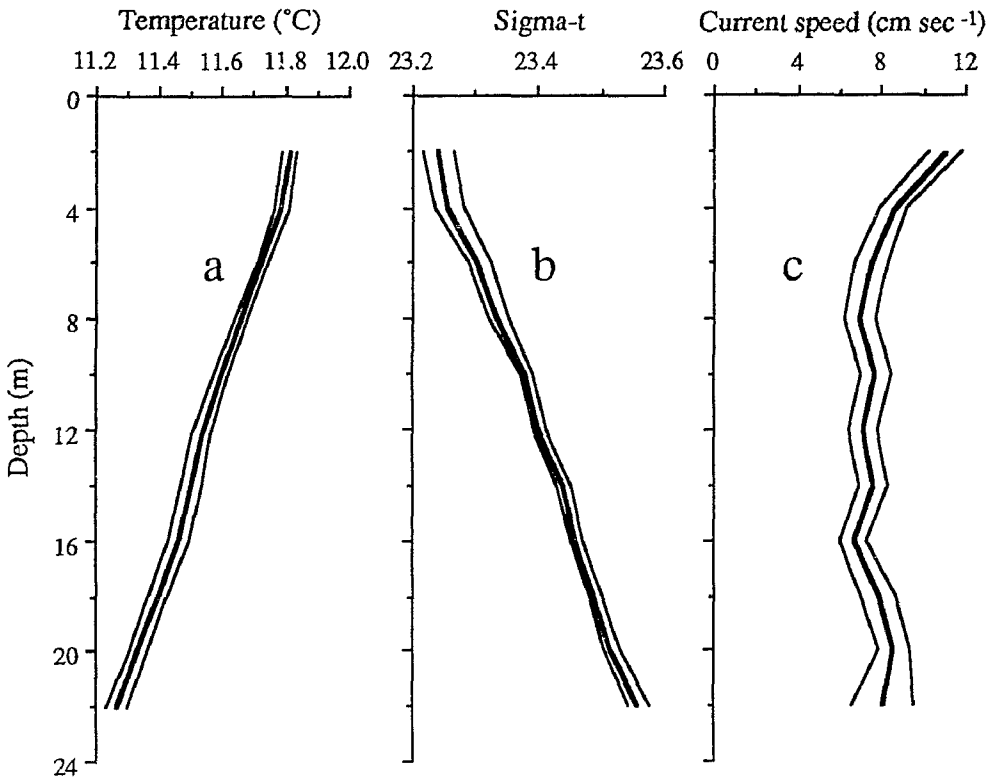

Figure 1.2. Composite profiles of (a):temperature, (b):sigma-t , and (c): current speed at the anchor station. Bold line is the mean of all profiles completed over the 50 h. Lighter lines show plus or minus one standard error. Based on 26 profiles for temperature and 25 for current speed and sigma-t.

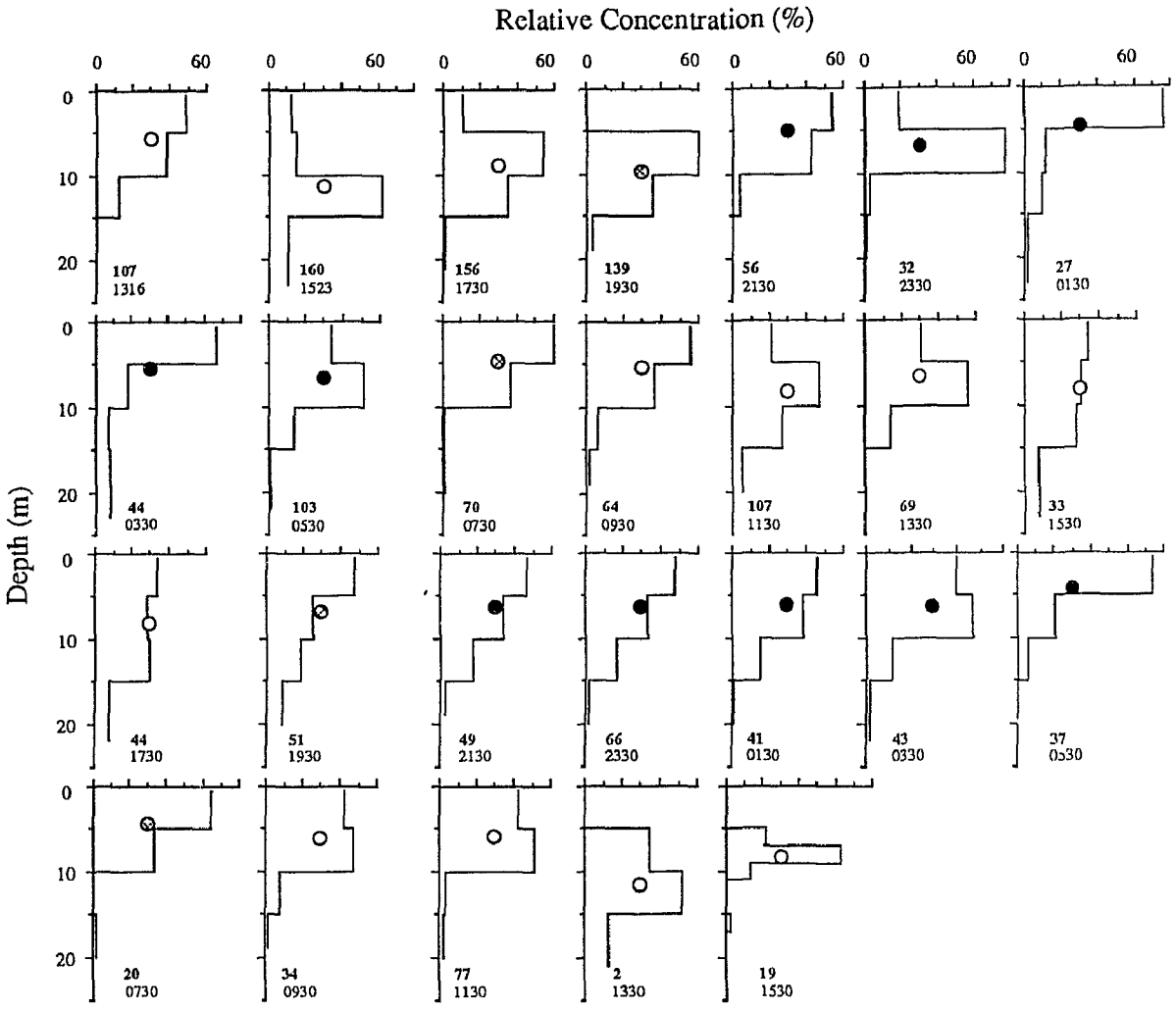

Figure 1.3. Vertical distribution of sea scallop larvae for individual profiles expressed as relative concentration within each depth interval. Plotted values are the percentage of the larval n m^{-3} summed over all 4 depth intervals. Circles show ZCM and are patterned according to light conditions: open indicates day, closed indicates night, and cross-hatched indicates dawn or dusk. At bottom of each profile is time of day (bottom number) and larval n m^{-3} summed over all depth intervals (top number). The top number multiplied by 2.7 approximates the actual number of larvae caught in the profile (since the mean volume sampled per interval was 2.7 m^3).

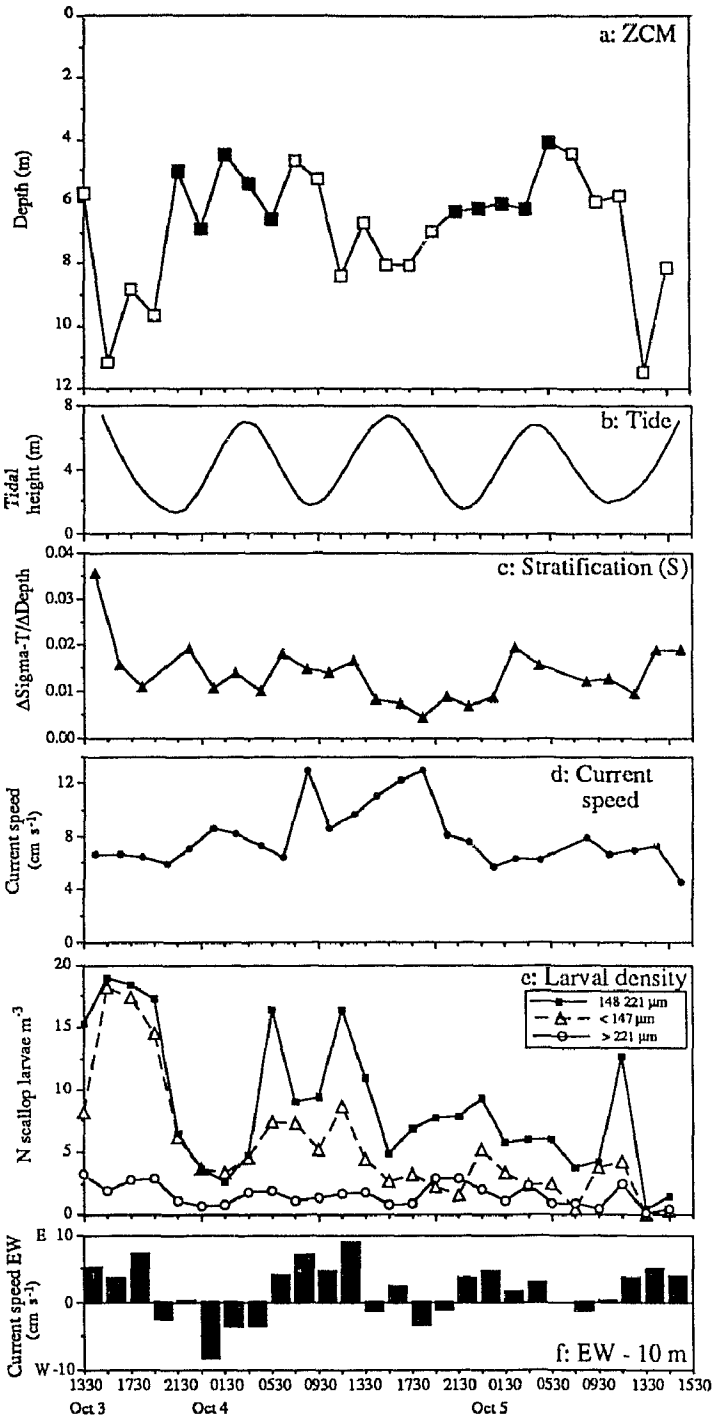

Figure 1.4. Larval sea scallop distribution and physical variables versus time for the 50 h anchor station. (a): Larval centre of mass (ZCM) patterned according to light conditions (see Fig. 3 caption); (b): tidal height from tide tables (Saint John, N.B.); (c): index of density stratification (S); (d): depth-averaged current speed; (e): depth-averaged concentration of 3 size groups of sea scallop larvae; (f): current speed at 10 m, east-west component.

Table 1.1. Day-night differences in the depth of the larval centre of mass (ZCM), stratification index (S), and current speed. Profiles corresponding to day-night groups are indicated in Fig. 3. Day-night differences were significant only for the ZCM (Mann-Whitney comparison, $p < 0.05$).

	Day			Night		
	mean	min	max	mean	min	max
Larval ZCM	7.8	5.7	11.5	5.7	4.1	6.8
Current speed	8.3	4.6	13.0	7.0	5.7	8.6
Stratification index (S)	0.014	0.004	0.036	0.014	0.007	0.020

Table 1.2. Spearman rank correlation coefficients for vertical distribution of sea scallop larvae versus physical variables. N = 24-26. Coefficients which are significant (5% level, Sokal and Rohlf 1969) are indicated with an asterix. N m^{-3}: concentration of larvae; ZCM: larval centre of mass; CV: coefficient of variation; P: depth of pycnocline; S: stratification index; Curr: depth-averaged current speed; NS 4: current speed at 4 m, north-south component; NS 10: current speed at 10 m, north-south component; EW 4: current speed at 4 m, east-west component; EW 10: current speed at 10 m, east-west component.

	ZCM	CV	P	S	Curr	NS 4	NS 10	EW 4	EW10
N m^{-3}	0.22	-0.21	-0.14	0.04	-0.13	0.18	0.06	-0.15	0.40*
ZCM	-	-0.36	-0.04	-0.08	-0.15	-0.19	0.05	-0.13	0.17
CV	-	-	-0.31	0.25	-0.11	0.14	0.02	-0.30	-0.27
P		-	-	-0.50*	-0.15	-0.15	0.14	-0.01	-0.05
S	-		-	-	-0.44*	0.02	-0.18	-0.52*	-0.39
Curr	-		-	-	-	-0.35	-0.05	0.75*	-0.19
NS 4	-	-	-	-	-	-	0.01	-0.15	-0.12
NS 10	-	-	-	-	-	-	-	-0.05	-0.17
EW 4	-	-	-	-	-	-	-	-	-0.33

but the patterns in the autocorrelations substantiate this interpretation. After removing the linear trend in the mean larval concentration series, peak negative correlations occurred at lags of 6-10 h , and peak positive correlations occurred at lags of 16-18 h (Fig. 1.5a). In the ZCM series, the peak negative correlations occurred at lags of 8-14 h and peak positive correlations at lags of 22-26 h (Fig. 1.5b). Individual correlations were not significant except for those at lags of 1 (2 h).

To determine if the changes in current speed were related to fluctuations in mean larval concentration, correlations were run between the latter variable and (i) depth-averaged current and (ii) the east-west and north-south components of the current at depths which bracket the larval ZCM (Table 1.2). The only significant correlation was that between larval concentration and the east-west component of the current at 10 m. Larval concentration was highest when currents at 10 m were eastward, i.e. out of the embayment (Fig. 1.4f). The correlation was higher in the first half of the series, with the Spearman correlation coefficient increasing from 0.40 (Table 1.2) to 0.62 when only the first 24 h was used.

Larvae tended to be more dispersed (CVs less than 50%) when the stratification index (S) was at its lowest (Fig. 1.6). Above these low levels of S there was considerable scatter in the relationship (Fig. 1.6), and the correlation between larval aggregation and stratification was positive but not significant (Table 1.2).

A wide size range of sea scallop larvae was present in the water column over the entire 50 hours of sampling (Fig. 1.7) but there was no evidence for size specific depth distribution. Visual examination of changes in the length frequency distribution with depth indicated no consistent pattern, and the ranked ZCMs of larvae of different size groups did not differ in a systematic fashion over the 50 h (Table 1.3).

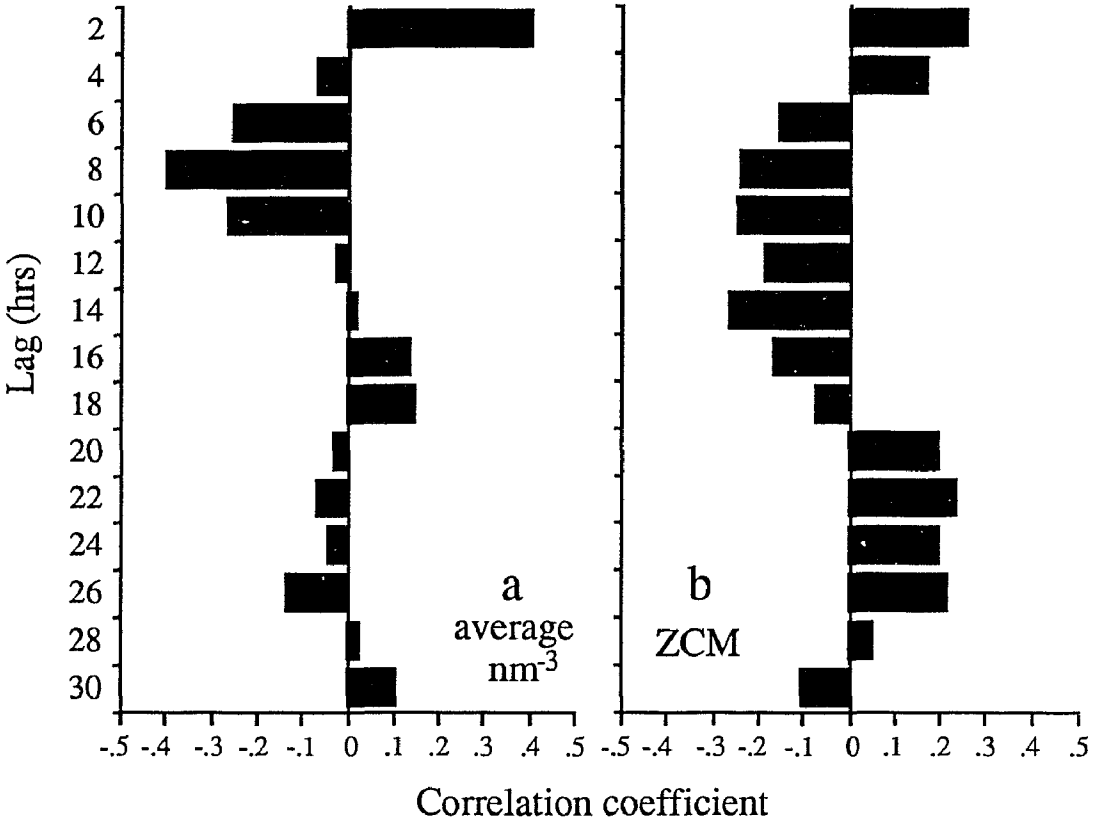

Figure 1.5. Autocorrelation analyses of (a) the depth-averaged concentration of sea scallop larvae , and (b) the larval centre of mass (ZCM). N = 26 for both series. Shown is the Pearson correlation coefficient for lags in the series ranging from 1 to 15 (2 to 30 h since sampling occurred every 2 h). Except for lags of 1, all coefficients were less than 2 standard errors.

Table 1.3. Day-night values for the larval centre of mass (ZCM) within different length groups. The ZCMs of different size groups (within day or night periods) were not significantly different at p = 0.05 (Kruskal-Wallis test).

	Day			Night		
Length (μm)	Mean	Min	Max	Mean	Min	Max
< 147	7.2	4.3	10.6	5.5	3.3	7.2
148-221	8.0	5.6	11.5	5.7	4.1	6.8
> 221	7.4	3.2	12.5	5.2	2.5	7.9

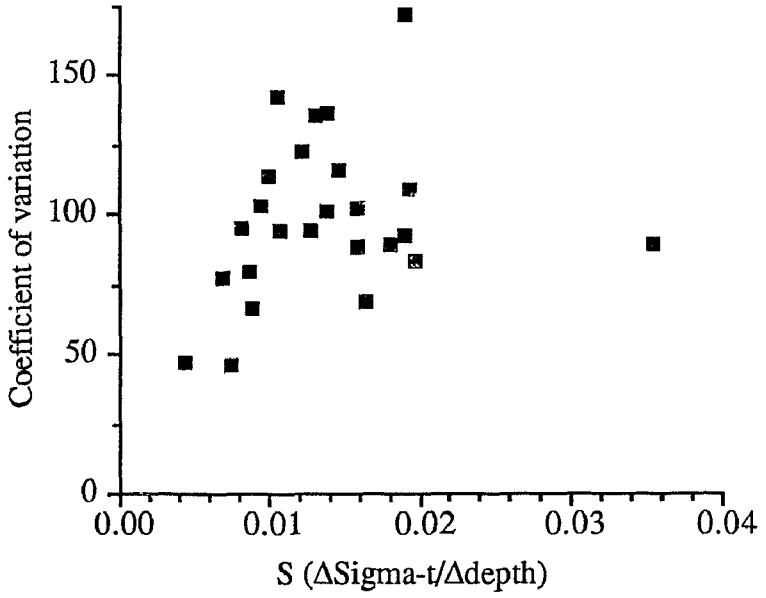

Figure 1.6. Aggregation of sea scallop larvae (coefficient of variation: CV) versus index of water column stratification (S).

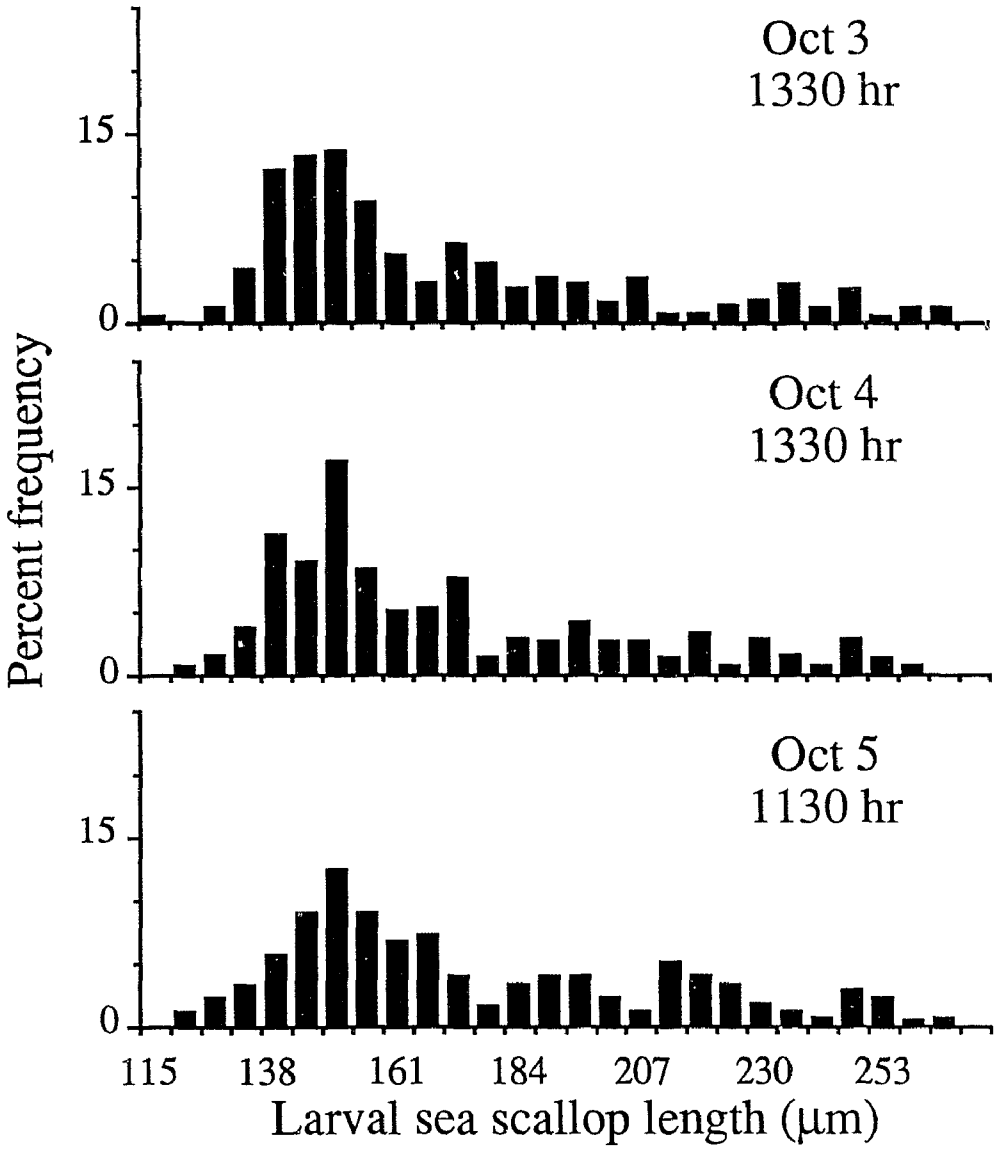

Figure 1.7. Length frequency of sea scallop larvae, averaged over all depths, at start, middle, and end of sampling.

1.4 Discussion

A physical mechanism put forward by de Wolf (1973) to explain short term variation in the density of barnacle larvae is based on changes in current speed over a tidal cycle and the effect on bottom dwelling larvae. By this argument, larvae are on or close to the bottom when current speeds are low, and are mixed upwards into the water column as current speeds increase. If this were the case in the present study, the depth-averaged concentration of sea scallop larvae would be expected to be positively correlated with current speed, and negatively correlated with the larval centre of mass (ZCM). This was not the case (Table 1.2), and larval concentration fluctuated with a shorter period than did the ZCM (Figs. 4a,e, 5). A negative correlation between larval concentration and the ZCM would also be expected if sea scallop larvae were actively dropping out of the water column to rest on the bottom as has been observed in mesocosm studies (R. O'Dor, Dalhousie University). In the present study it appears that fluctuations in the mean concentration of sea scallop larvae were driven by factors different than those affecting the mean depth (ZCM) of sea scallop larvae.

The strong tides in the Bay of Fundy were probably a factor in the changes in mean larval concentration, and it appears that a patch (or patches) of sea scallop larvae was advected back and forth past the anchor station. The positive correlation between larval concentration and the east-west current at 10 m substantiates this interpretation, as does the autocorrelation analysis of the larval concentration. Although none of the individual correlations were significant in the autocorrelation series, the pattern of correlations was not random (Fig. 1.5), and peak negative correlations were observed at lags of 6 to 10 h , which would be expected if changes in the tidal current underlied the changes in mean larval concentration.

The length frequency of larvae was fairly consistent over the 50 h (Fig. 1.7), indicating either that the same patch of larvae was sampled, or that larvae arriving from

contiguous areas had the same length frequency. Adult sea scallops are present throughout the area, and the origin of the larvae found at the 50 h station is therefore unknown. Based on length frequency, sea scallop larvae collected at the anchor station cannot be distinguished from those collected in the outer Bay of Fundy (Tremblay and Sinclair 1988: Fig. 13). It is assumed here that larvae in contiguous areas have a similar pattern of vertical migration, and that the observed fluctuations in the larval centre of mass (ZCM) would be observed if a single patch of larvae were sampled.

The deeper ZCM of sea scallop larvae during the day compared to that of the night (Table 1.1) indicates that a diel vertical migration occurred. The alternative explanation, that the diel changes in the ZCM were caused by corresponding physical changes in the water column, is not tenable because there were no significant day-night differences in stratification (S) or current speed (Table 1.1), and no significant correlation between the ZCM and any of the physical variables (Table 1.2).

The apparent amplitude of the vertical migration was small (Table 1.1). Depth-stratified sampling may underestimate the amplitude of migration if individual larvae are migrating at different times (Pearre 1979), but the bimodal distributions typical of such migratory asynchrony were not apparent in the present study (Fig. 1.3). Depth-stratified sampling may also underestimate the amplitude of migration if the width of the sampling strata (5 m in the present study) is substantially greater than the true width of the larval aggregations. Finer scale sampling is required to resolve this question. A small amplitude vertical migration of scallop larvae into shallower waters at night is consistent with observations under controlled conditions. In a 10 m mesocosm, sea scallop larvae moved from a mean depth of 6.9 m during the day to 3.7 m at night (Silva and O'Dor 1988), and *Pecten maximus* larvae also occur shallower at night in experimental water columns (Kaartvedt et al. 1987). Field studies of other species of bivalve larvae (Quayle 1952,

1959) and total bivalve larvae (Harding et al. 1986, Scrope-Howe and Jones 1986) have also found this pattern.

Larval behaviour underlies both the formation of aggregations and the vertical migration observed in this study. Because the swimming behavior of scallop larvae is to some extent size specific (Cragg 1980, Silva and O'Dor 1988) it might be expected that some depth stratification by size would be observed in nature. For example larvae capable of metamorphosis (ca 230-290 μm - Culliney 1974) would be expected to be close to the bottom, searching for appropriate settlement locations. This study and those in the Bay of Fundy and on Georges Bank (Tremblay and Sinclair 1988, Chapter 2) have found little evidence for stratification by size. It may be that this is a real phenomenon and that turbulence in these tidally energetic areas is usually too great for size specific swimming behaviors to manifest themselves. Alternatively the depth intervals sampled are too coarse, or the sampler is unable to get close enough to the bottom to sample late stage larvae.

The patterns of diel vertical migration, and hypotheses regarding its adaptive value, have been extensively reviewed (e.g. Russell 1927, Cushing 1951, McLaren 1963, Banse 1964, Longhurst 1976). These hypotheses may be characterized as involving one of the following features: (i) the avoidance of predation, (ii) increased ability to locate food, (iii) the use of vertical shear for transport or retention, (iv) demographic or energetic advantages, and (v) avoidance of competition. Vertical migration must confer different selective advantages for different species. To evaluate the advantage of vertical migration to sea scallop larvae, more needs to be known about their predators, the distribution of their preferred food, and the physical circulation where they are studied. This paper shows that a small amplitude vertical migration of sea scallop larvae can occur in some areas, and that the effect of this migration should be considered in models of larval transport.

1.5 Summary

The vertical distribution of sea scallop larvae was studied while anchored for 50 h at a shallow location (< 25 m) off Grand Manan Island in the outer Bay of Fundy. Changes in the depth-averaged concentration of larvae (n m^{-3}) were unrelated to changes in the centre of mass (ZCM) of larvae, and appear to reflect the movement of a patch (or patches) of larvae back and forth past the anchor station. A small amplitude diel vertical migration, comparable to observations under controlled conditions, was indicated by changes in the ZCM. During the day the ZCM ranged from 5.2 to 11.5 m, while at night the ZCM was shallower and less variable (4.1 to 6.8 m). The concentration of all size groups was greatly reduced within 1-8 m of the bottom, and evidence for vertical stratification by size was lacking.

Chapter 2

Sea scallop larvae *Placopecten magellanicus* on Georges Bank: Vertical distribution in relation to water column stratification and food.

2.1 Introduction

How marine planktonic larvae are vertically distributed in the water column is fundamental to understanding their dispersal patterns, but studies of the vertical distribution of single species of bivalve larvae on continental shelves are rare (Mann 1985, 1986a, Tremblay and Sinclair 1988), perhaps because of problems with identification and logistics. Our knowledge of the vertical distribution of bivalve larvae in nature is restricted mainly to estuarine and nearshore species (e.g. Nelson and Perkins 1931, Carriker 1951, Korringa 1952, Quayle 1952, 1959, Kunkle 1958, Verwey 1966, Wood and Hargis 1971, Drinnan and Stallworthy 1979, Boicourt 1982, Seliger et al. 1982, Andrews 1983, Harding et al. 1986, Mann 1988a) which inhabit environments very different from that of the continental shelf.

Since bivalve larvae have a specific gravity of about 1.3 (Mann 1986a) the fact that they are planktonic indicates either strong physical mixing, or active swimming. Active swimming implies the possibility of vertical migration and depth regulation, defined here as the maintenance of a depth range where preferred temperatures, food, or other conditions are met. Depth regulation by bivalve larvae on continental shelves may be less prevalent than in estuarine larvae, which live in environments characterized by sharp vertical gradients in temperature and salinity. Several laboratory studies suggest that bivalve larvae which inhabit deeper environments are less pressure sensitive, and thus less likely to depth regulate (Cragg 1980, Mann 1986a, 1988a). Nevertheless depth regulation by bivalve larvae found on continental shelves is indicated by diel differences in depth (Scrope-Howe and Jones 1986), and by finding larvae in nature at depths

predicted from laboratory study of temperature preference (Mann 1986b). Lack of depth regulation by bivalve larvae is suggested where larvae are well mixed over the water column (Scrope-Howe and Jones 1986), and where larvae are not found at depths corresponding to their preferred temperature (Mann 1986b).

The conditions of transition from active depth regulator to passive particle are poorly defined for the larvae of *Arctica islandica* (Mann 1986b), and the same can be said for sea scallop larvae *Placopecten magellanicus*, the subject of the present study. Active depth regulation is indicated by diel vertical migration (Chapter 1), but limits to this ability are suggested by distribution over the whole water column in areas of the Bay of Fundy where there is no thermocline (Tremblay and Sinclair 1988). In areas with a thermocline sea scallop larvae are aggregated below the surface, at depths of 5 to 20 m, but the factors influencing the subsurface aggregation of larvae are not well understood (Tremblay and Sinclair 1988).

Bivalve larvae are aggregated in the region of the subsurface chlorophyll maximum at night at some locations in the Irish Sea (Scrope-Howe and Jones 1986). Other zooplankton groups aggregate in relation to subsurface chlorophyll maxima (or the closely associated production maxima), depending upon species, life stage and oceanographic regime (Anderson et al. 1972, Hargreaves 1981, Longhurst and Herman 1981, Ortner et al. 1981, Bird 1983, Southward and Barrett 1983, Sameoto 1984, Townsend et al. 1984, Scrope-Howe and Jones 1986). Sea scallop larvae occur in the Gulf of Maine and Georges Bank area, where subsurface chlorophyll maxima are present under certain conditions (Hargreaves 1981, Sameoto 1984, Townsend et al. 1984, O'Reilly et al. 1987).

Size fractionated chlorophyll should be better than bulk chlorophyll as an indicator of food for sea scallop larvae, since this species and other bivalve larvae grow on a diet of small phytoplankters (< 10 μm) in hatcheries (Loosanoff and Davis 1963, Culliney

1974, Walne 1974, Bayne 1983, Carriker 1986). To what extent bivalve larvae in nature can utilize other food sources has not been critically assessed (Mann 1988b) but in controlled environments they can utilize dissolved organic matter (Rice et al. 1980, Manahan and Crisp 1982, Marshall and Lee 1990), and other invertebrate larvae can feed on bacteria (Rivkin et al. 1986). Ongoing studies of the feeding of sea scallop larvae on Georges Bank indicate that sea scallop larvae actively graze on phytoplankton less than 30 μm in size (D. V. S. Rao, Bedford Institute of Oceanography, unpublished data).

The present study builds upon the findings of Chapter 1, and vertical distribution studies in the Bay of Fundy (Tremblay and Sinclair 1988). The relationships among the vertical distribution of sea scallop larvae, their food, and physical variables are investigated for Georges Bank. The specific objectives are to establish the conditions associated with subsurface aggregations, to determine if there is an association between sea scallop larvae and their food, and to assess the potential role of active depth regulation via swimming in sea scallop larvae.

2.2 Methods

2.2.1 Sample collection

Georges Bank was sampled in 1986 and 1987 during October, when sea scallop larvae are at or near their peak abundance. A total of 8 stations were occupied in different regions of the bank (Fig. 2.1), after first establishing the presence of sea scallop larvae. Three stations (M1, M2, M3) were occupied in the central, shallow (< 50 m) part of the bank, which is characterized by vertically well mixed waters (Flagg 1987), 4 stations (S1, S2a, S2b, S3) were occupied in the deeper (60-90 m) waters of the Northeast Peak, which have some density stratification, and 1 station (F1) was

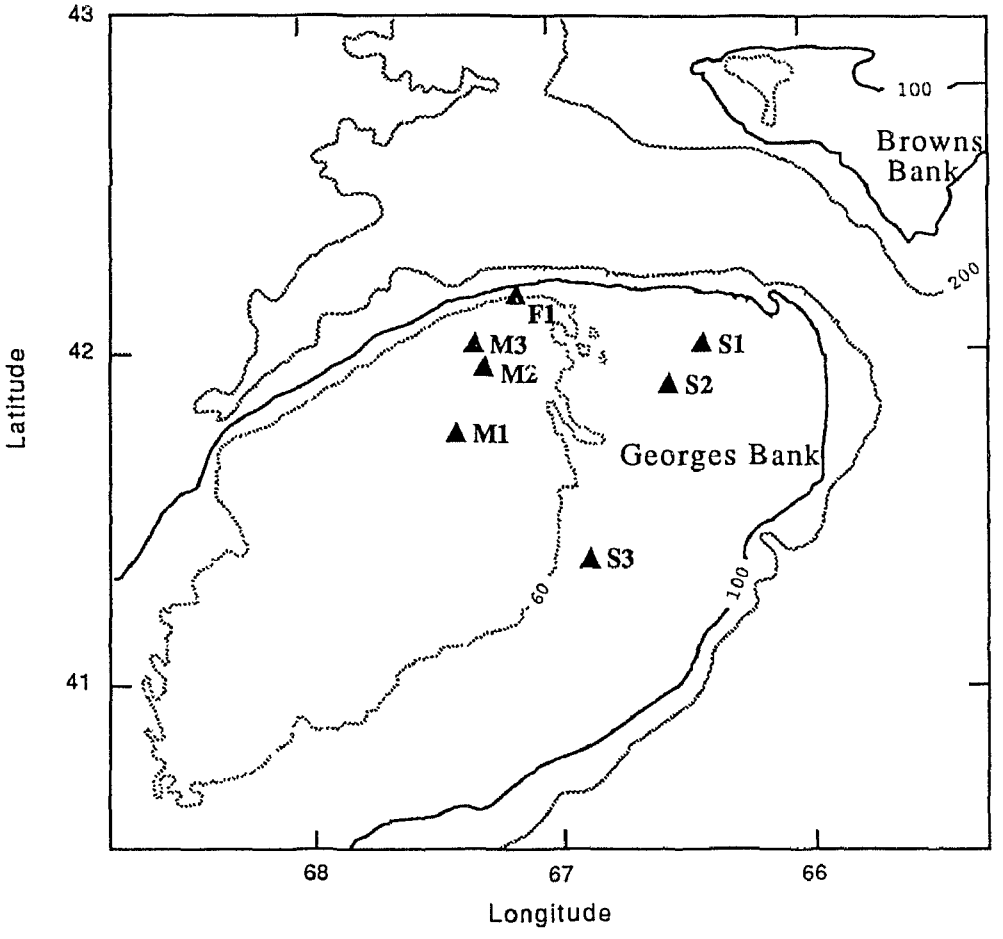

Figure 2.1. Locations of drift sampling on Georges Bank during 1986 and 1987. 'S' indicates stratified station, 'M' a mixed station, and 'F' a frontal station. Location S2 was occupied twice (stations S2a and S2b in text). Isobaths are in meters.

occupied on the Northern Flank, a frontal region where the water column alternates between strong and weak stratification (Fig. 2.1).

Certain constraints exist when sampling with a pump in a tidally energetic area such as Georges Bank. Anchoring is not an option where currents are strong because the large surface area of the hose prevents it from reaching the deeper sampling intervals. For most profiles sampling was carried out while drifting with the ship engine off, periodically returning to the starting location. Profiles took an average of 74 minutes to complete (standard deviation: 16.6).

2.2.2 Pump system

The pump system used for sampling scallop larvae consisted of an electric centrifugal pump (FLYGT model 2051) capable of delivering 250-400 l min^{-1}, 2.5 cm suction hose, and an in-line paddlewheel flowsensor and readout (SIGNET). The pump intake, attached to a hydrographic wire, was moved up and down within each depth interval until a sample of 2-3 m^3 was obtained. In 1986 the depth of the pump intake was controlled with an electronic meter block and inclinometer, while in 1987 the depth of the pump intake was controlled from a CTD readout (see below). The usual width of the depth intervals was 10 m. Intervals less than 10 m were sometimes sampled in the region of the pycnocline, or when conditions prevented deeper sampling. Interval widths greater than 10 m were used to sample below 50-60 m, to a maximum depth of 80 m. Part of the bottom 10 m of the water column was always sampled in water columns with depths less than 50 m, but not in water columns greater than 60 m.

On deck, the pump outflow was directed first through a coarse mesh net (333 μm) to remove larger particles, and then through an 85 μm mesh net for sample collection. Larval samples were preserved in 4% formalin buffered with sodium borate. Methods for processing the samples and identifying larval sea scallops are described in Tremblay et al. (1987). Total counts were done on approximately 75% of the samples; where

larvae numbered greater than approximately 300, the sample was split with a Motoda splitter such that a total of at least 200 larvae were counted. Subsampling variability contributed only a small fraction of the total variance in larval abundance estimates (see Appendix 1 for details).

2.2.3 Physical measurements

To characterize the water column structure, temperature and salinity were measured with a Guildline CTD in 1986 and an Applied Microsystems CTD in 1987. In 1986 physical profiling was independent of the pump profiles, while in 1987 the CTD was mounted with the pump intake within a protective steel frame allowing real time monitoring of temperature and salinity. The intake pipe extended approximately 80 cm away from the frame and was directed into the current with a large fin on the opposite side of the frame, similar to that shown in Harris et al. (1986).

2.2.4 Measurements of chlorophyll *a* and particles

Chlorophyll *a* from the < 15 μm size fraction of seawater was used as an indicator of the the quantity of living phytoplankton available as food for sea scallop larvae. As an indicator of potential food items not containing chlorophyll *a*, the concentration of particles between 2.5 and 16 μm was measured.

Seawater samples for chlorophyll *a* were obtained simultaneous to the larval scallop collections in 1987. During the sampling of each depth interval, a garden hose line off the main pump outflow was directed through a 160 μm screen and into 10 l carboys. Duplicate subsamples for up to four size fractions were then withdrawn: < 160, < 30, < 15 and 3-15 μm. The < 160 μm fraction came straight from the carboy, while the < 30 μm and < 15 μm fractions were obtained after passing the seawater through 30 μm and 15 μm screens. From each of these size fractions, an aliquot of 200-500 ml was passed through a Whatman GF/F filter (effective retention 0.7 μm). The 3-15 μm size fraction was obtained by passing the < 15 μm size fraction through a 3

μm Nuclepore® filter. Chlorophyll *a* determinations were made by the fluorometric method of Holm-Hansen et al. (1965), after treating the filters with $MgCO_3$, and extracting the chlorophyll *a* from the filters in acetone for at least 12 h at 0°C.

The concentration of particles with equivalent spherical diameters from 2.5 to 16.0 μm was determined from the < 160 μm size fraction of sea water for some profiles using a Coulter Counter Model TA2. The 70 μm aperture used with the Coulter Counter quantified particles with sizes from 1.0 to 32.0 μm, but the lowest 4 channels (1.0, 1.3, 1.6, 2.0 μm) gave unreliable readings.

2.2.5 Data Analyses

To reflect the mean depth of sea scallop larvae and of chlorophyll *a* for any given profile, the centre of mass (ZCM) was calculated as follows (after Fortier and Leggett 1982):

$$ZCM = \sum_{i=1}^{n} p_i \, z_i$$

where p_i is the proportion of the total number of larvae caught within the *i* th depth interval, and z_i is the mid-depth of the *i* th interval. Depth intervals below 50 m were not included in the calculations, because sampling often did not include depths greater than 50 m. Where the depth intervals were not of equal width, wider intervals were given more weight in the calculation of the ZCM, a practice also followed in calculations of water column averages.

Indices of the depth of the pycnocline (P) and the extent of density stratification (S) were calculated as follows. P was taken as the centre of the 10 m interval where the change in sigma-t was maximum. S was calculated as:

$$S = \Delta\text{sigma-t} / \Delta z$$

where Δz = the difference between 1 m and the greatest depth sampled or 50 m, and Δsigma-t is the difference in sigma-t over the interval Δz.

2.3 Results

2.3.1 Water column structure

The 2-6 profiles within each 'station' occurred over several 10's of km^2, because of ship drift during sampling (Fig. 2.2). Total distance drifted was related both to the currents in the area, and whether or not the ship returned to the starting location after each profile was completed. Wind changed little between profiles (Table 2.1), and cannot explain the regular changes in drift direction during the 12-24 h of sampling at any one station. Although between profile differences in location were sometimes substantial, the changes in water column structure and bottom depth during profiling were minimal. Initial and composite profiles of temperature and density were usually very similar (Figs. 2.3-2.8), and bottom depths did not vary by more than +/- 5 m during 36 of the 41 profiles.

Density stratification was well developed only at the frontal station (F1), where substantial differences in pycnocline depth between profiles were observed (Fig. 2.5). At the other stratified stations (Figs. 2.3, 2.6, 2.8, 2.9) the pycnocline was absent or only weakly developed and the temperature difference between the surface and 50 m was often < 3 °C. Physical profiles at the mixed stations (Figs. 2.4, 2.7, 2.10) were homogenous except for single profiles at each of M2 and M3 (Figs. 2.4, 2.7) which were done in slightly stratified waters due to the ship drifting out of the well mixed area.

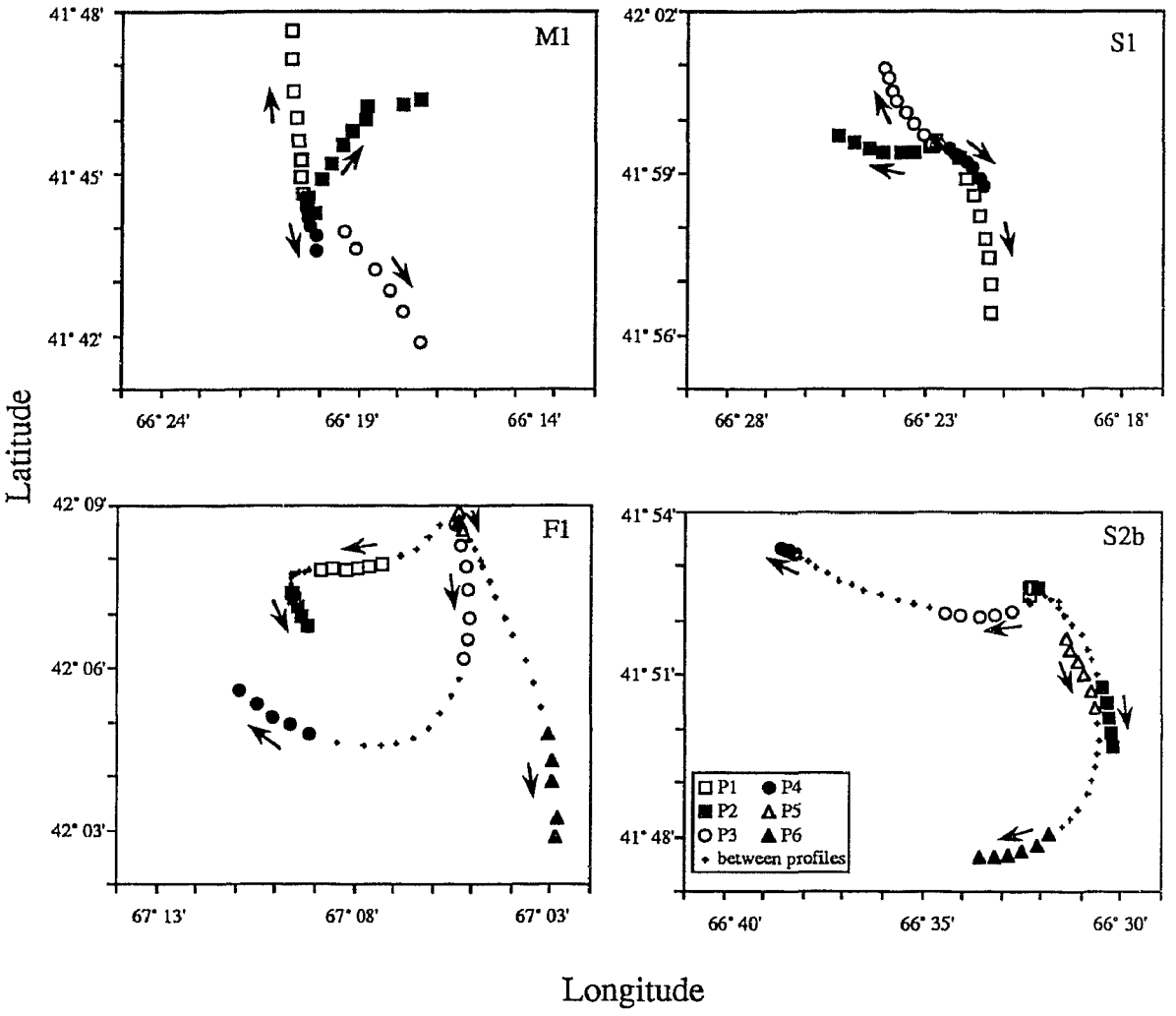

Figure 2.2. Drift track while sampling 2 stations in 1986 (M1 and S1) and 2 stations in 1987 (F1 and S2b). Time separating symbols is 15 minutes. In 1986 the ship returned to the plotted station location for the start of each profile. In 1987 2 profiles were done before returning to the original location. Non-pumping periods are indicated for 1987 tracks. The time of the profiles can be obtained from Figs. 2.5, 2.6, 2.9 and 2.10.

Table 2.1. Wind speed and direction during sampling of stations M1 and S1.

Station	Profile	Speed (km hr^{-1}) Mean (S.d)	Direction (°) Mean (S.d)
M1	1	28.8 (0.0)	214 (8.8)
	2	21.6 (4.4)	224 (2.3)
	3	20.4 (3.4)	243 (19.1)
	4	19.2 (0.0)	296 (61.6)
S1	1	38.4 (0.0)	90 (0.0)
	2	35.7 (4.7)	90 (0.0)
	3	28.8 (0.0)	96 (9.8)
	4	28.8 (0.0)	120 (0.0)

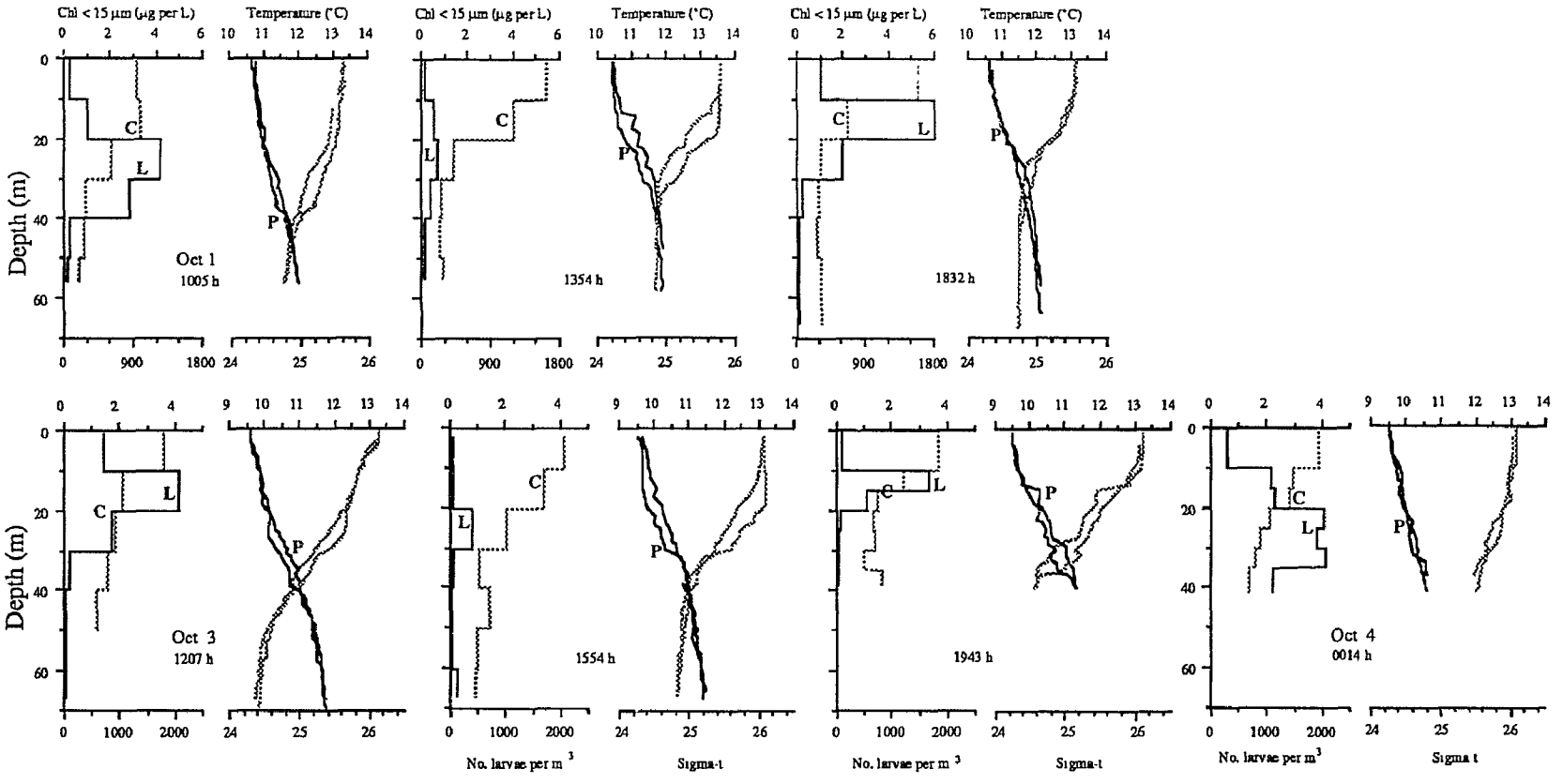

Figure 2.3. Profiles of the concentration of sea scallop larvae and chlorophyll *a* < 15 µm, and temperature and density generated during drift sampling of station S2a (Oct. 1, and Oct. 3-4, 1987). Depicted in the left panels is the larval concentration (solid line) and the chlorophyll concentration (dotted line). Depicted in the right panels is density (solid line) and temperature (dotted line). **L** is larval centre of mass, **C** is chlorophyll *a* centre of mass, and **P** is calculated position of pycnocline. The two traces of temperature and density for each profile represent initial and composite conditions. **P** is calculated for composite conditions. Time is Atlantic Daylight Savings Time.

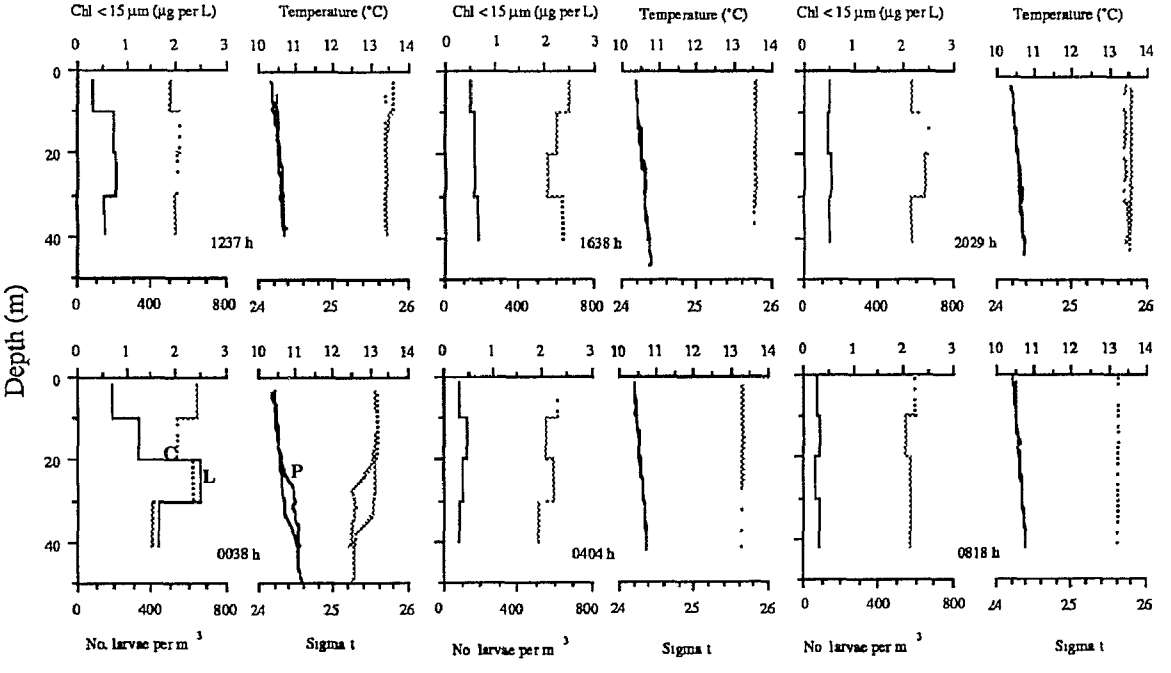

Figure 2.4. Profiles of sea scallop larvae, chlorophyll *a* < 15 µm, temperature and density generated during drift sampling of station M2 (Oct. 6-7, 1987). See Fig. 2.3 caption.

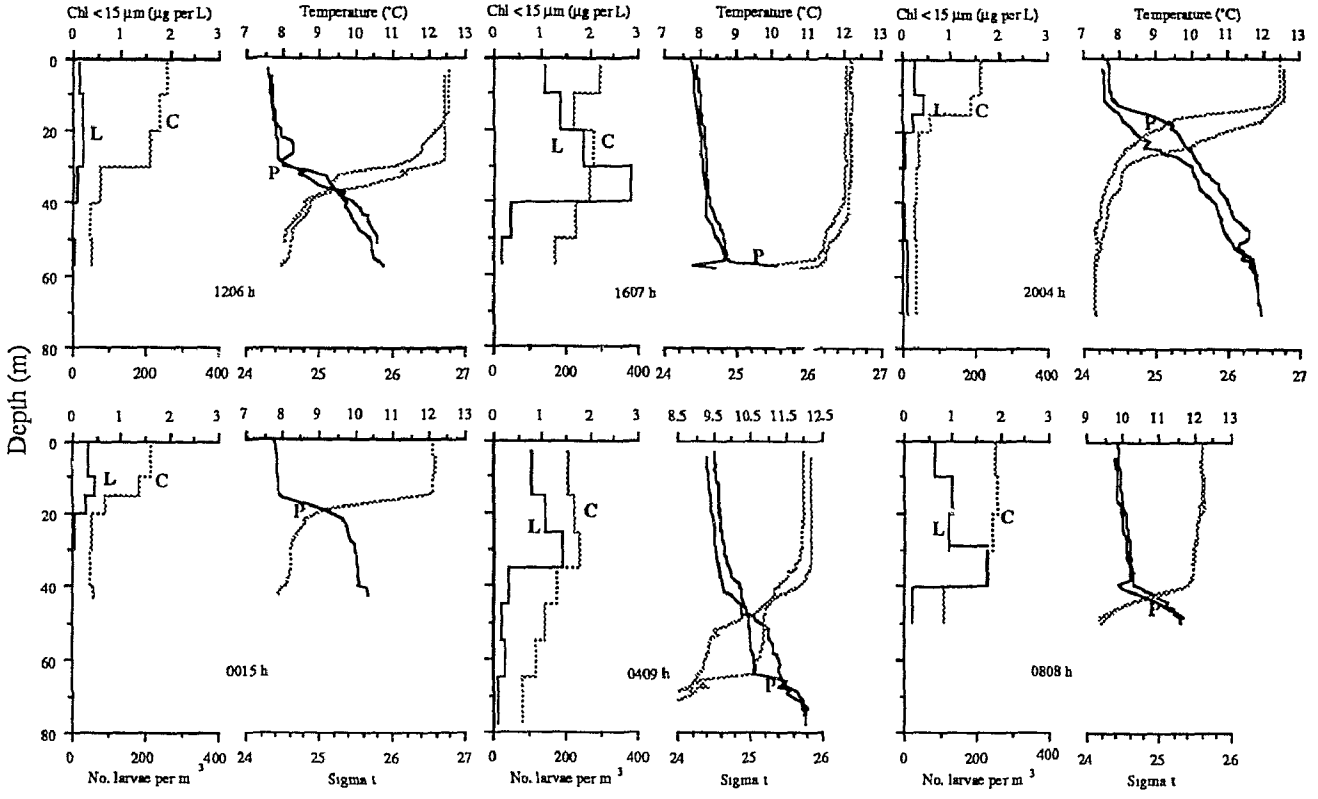

Figure 2.5. Profiles of sea scallop larvae, chlorophyll *a* < 15 µm, temperature and density generated during drift sampling of station F1 (Oct. 12-13, 1987). Composite physical conditions are unavailable for the 0015 h profile. See Fig. 2.3 caption.

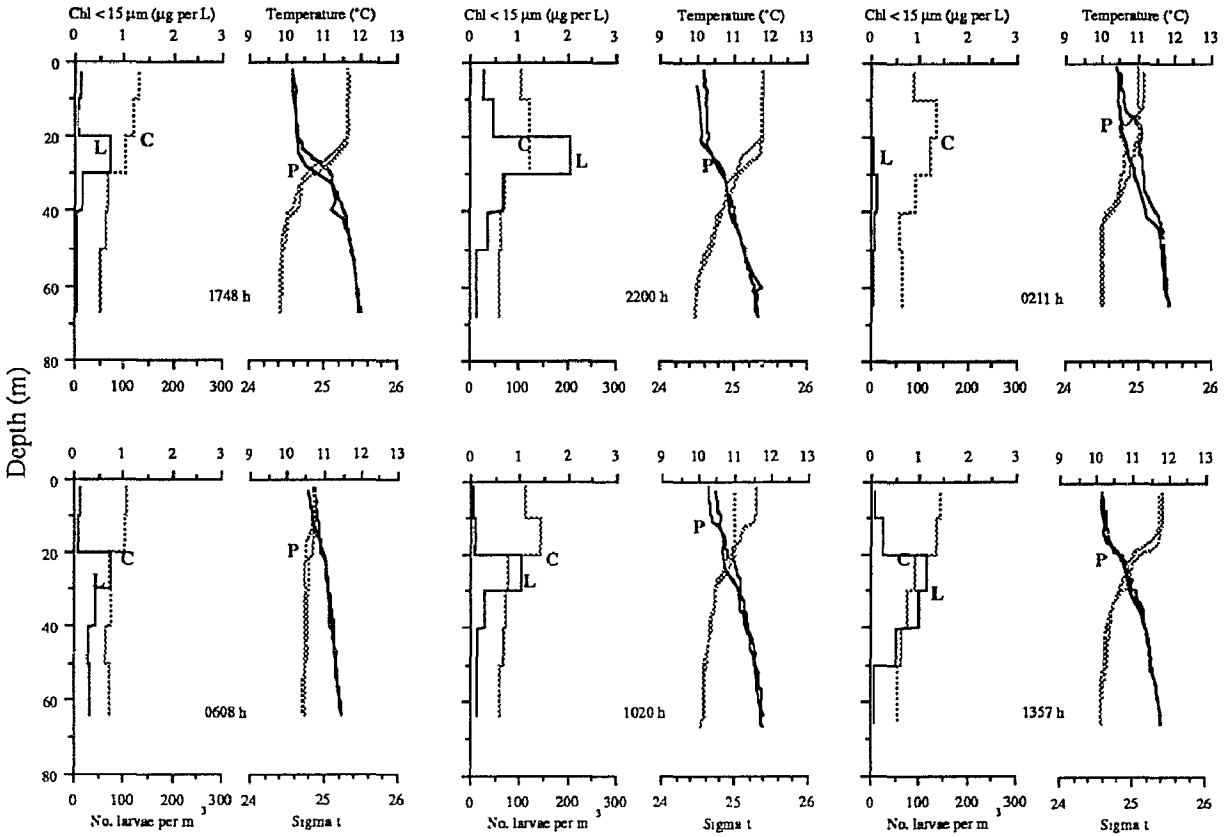

Figure 2.6. Profiles of sea scallop larvae, chlorophyll *a* < 15 µm, temperature and density generated during drift sampling of station S2b (Oct. 14-15, 1987). See Fig. 2.3 caption.

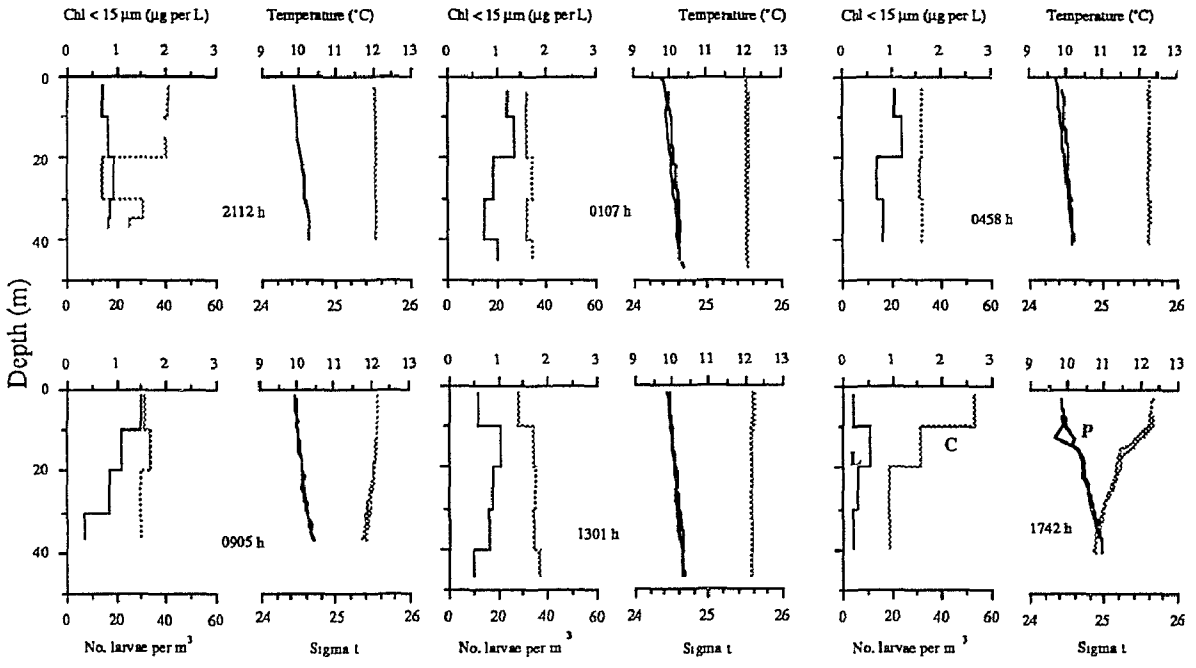

Figure 2.7. Profiles of sea scallop larvae, chlorophyll *a* < 15 µm, temperature and density generated during drift sampling of station M3 (Oct. 15-16, 1987). See Fig. 2.3 caption.

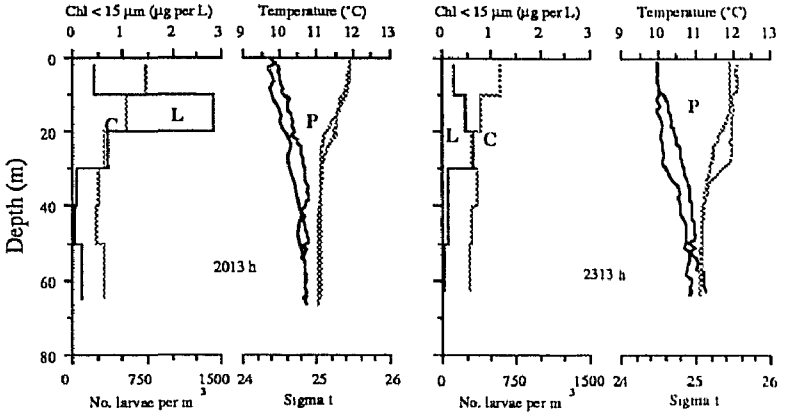

Figure 2.8. Profiles of sea scallop larvae, chlorophyll *a* < 15 µm, temperature and density generated during drift sampling of station S3 (Oct. 17-18, 1987). See Fig. 2.3 caption.

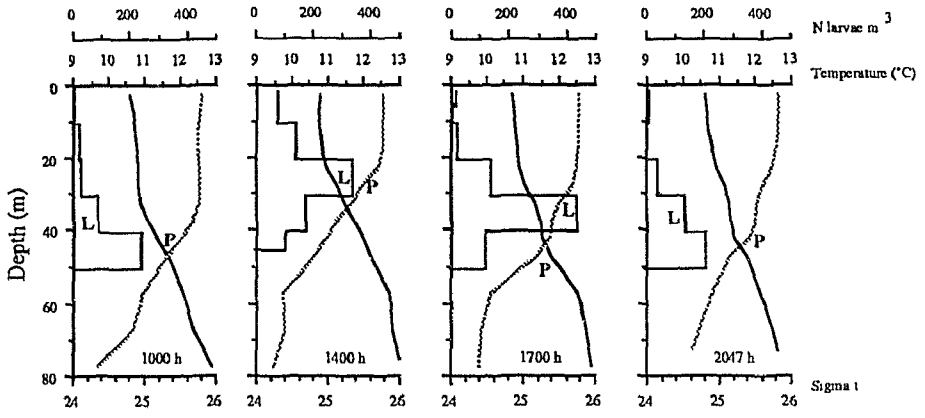

Figure 2.9. Profiles of the concentration of sea scallop larvae, temperature and density generated during drift sampling of station S1 (Oct. 11, 1986). Solid stepped line is larval concentration, other solid line is density, dotted line is temperature.

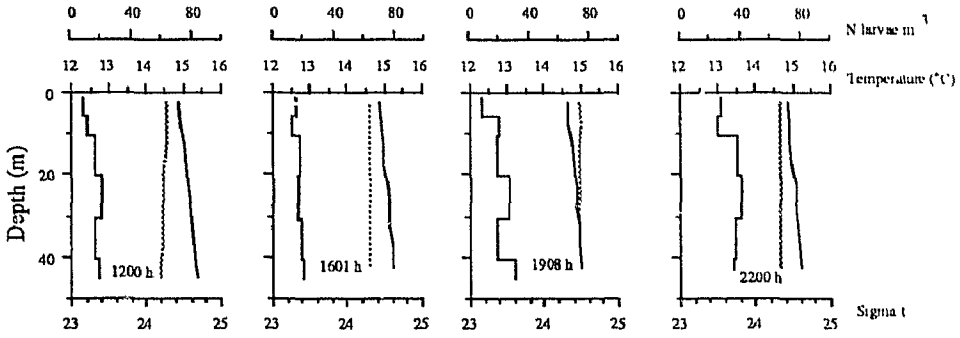

Figure 2.10. Profiles of the concentration of sea scallop larvae, temperature and density generated during drift sampling of station M1 (Oct. 10, 1986). See Fig. 2.9 caption.

2.3.2 Chlorophyll *a* and particle profiles

The concentration of chlorophyll *a* < 15 μm comprised 61-88 % of the total chlorophyll *a* (Table 2.2). Together with particle concentration, chlorophyll *a* < 15 μm generally declined during October of 1987 (Table 2.2, Fig. 2.11) with the steepest declines occurring at the weakly stratified stations (Figs. 2.3, 2.5, 2.6, 2.8, 2.11).

The concentration of chlorophyll *a* < 15 μm and the concentration of particles showed similar trends with depth (Fig. 2.11). Where the water column was well mixed, chlorophyll *a* and particles were generally evenly distributed over the whole water column (Figs. 2.4, 2.7, 2.11), while at stations with some stratification, these variables were usually most concentrated in the upper 10 m, decreasing with depth (Figs. 2.3, 2.5, 2.6, 2.8, 2.11). Ignoring profiles in mixed waters, only 5 of the 21 profiles had subsurface increases in chlorophyll *a* < 15 μm, and most of these increases were marginal (Figs. 2.3, 2.5, 2.6). Subsurface increases in particle concentration were also small (Fig. 2.11).

2.3.3 Density, aggregation and the ZCM of sea scallop larvae

Depth-averaged concentrations of sea scallop larvae at the stratified stations were generally greater and more variable than at the mixed stations (Table 2.2). The mean concentration of larvae ranged from 16 m^{-3} at station M3 to 520 m^{-3} at station S2a, while the coefficient of variation (CV) among profiles ranged from 33% at M3 to 94% at station F1 (Table 2.2).

Sea scallop larvae were aggregated within subsurface depth intervals at stratified stations (Figs. 2.3, 2.5, 2.6, 2.8, 2.9), and well mixed over the water column where stratification was low (Figs. 2.4, 2.7, 2.10). An index of the extent of aggregation for any given profile is the CV of the larval concentration over the different depth intervals (i.e. a high aggregation generates a high CV). This index increased with density stratification (S), and above S values of about 0.007, larvae were aggregated at

Table 2.2. Concentrations of sea scallop larvae (n m^{-3}) and chlorophyll *a* < 15 μm (μg l^{-1}) averaged over the upper 50 m or to the maximum sampling depth. N is the number of profiles upon which means are based. CV is the coefficient of variation among profiles. PCT is the concentration of chlorophyll < 15 μm as a percentage of the total chlorophyll *a* from all size fractions (based on one profile done at each station except for S2a which is based on 3 profiles).

Station	Date	N profiles	Larvae	CV (larvae)	Chl	PCT
M1	10/10/86	4	19.6	38.7	-	-
S1	11/10/86	4	120.8	37.5	-	-
S2a	1-4/10/87	7	519.5	75.8	2.20	63
M2	6/10/87	6	171.2	69.1	2.15	75
F1	12/10/87	6	78.8	93.6	1.27	88
S2b	14/10/87	6	19.6	53.9	0.95	84
M3	15/10/87	6	16.1	32.5	1.57	70
S3	18/10/87	2	285.7	61.2	0.80	61

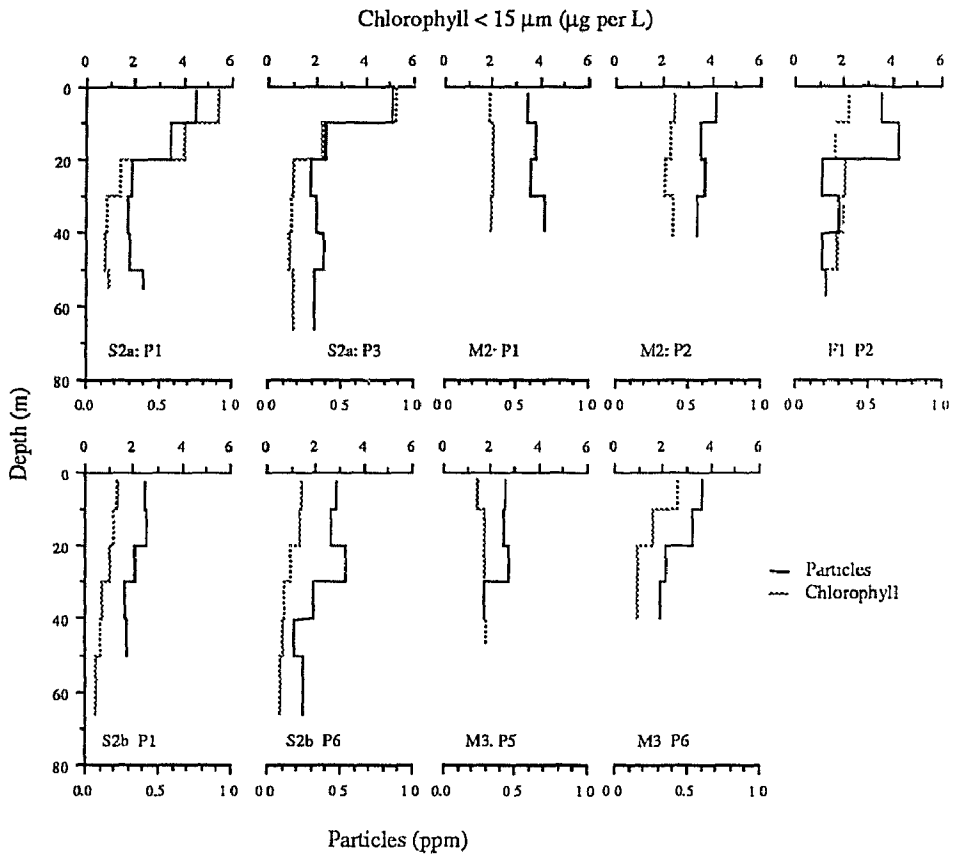

Figure 2.11. Profiles of the concentration of particles 2.5-16.0 µm, and chlorophyll *a* < 15 µm. At bottom of each profile is station code and profile number (P#).

subsurface depths (Fig. 2.12). Chlorophyll *a* < 15 μm showed the same increased aggregation with stratification but was less aggregated than sea scallop larvae for any given value of S (Fig. 2.12) perhaps reflecting the lower mobility of the phytoplankton.

The ZCM of sea scallop larvae is meaningful only when the aggregation of larvae is substantial, defined here as when the CV is greater than 50%. This eliminates most of the profiles from the mixed stations (Fig. 2.12). In the remaining 28 profiles, the larval ZCM ranged from 11 to 38 m and was above or within 2 m of the pycnocline in 21 profiles. The larval ZCM was usually below both the depth interval where chlorophyll *a* < 15 μm was most concentrated, and the corresponding chlorophyll ZCM (Figs. 2.3-2.8). In only one profile was there a coincidence between a subsurface increase in chlorophyll *a* < 15 μm and the larval ZCM (Fig. 2.5). This was at the frontal station (F1), where the pycnocline was particularly strong, and the larval ZCM and the chlorophyll *a* ZCM covaried with the depth of the pycnocline (Fig. 2.5, Table 2.3). Where the pycnocline was shallow, sea scallop larvae were compressed into the region above it and the underlying cold water mass (Fig. 2.5). For two of the other three stratified stations, the larval ZCM was positively related to the depth of the pycnocline, but the chlorophyll *a* ZCM was not clearly related to either the larval ZCM or the pycnocline depth (Table 2.3). Station S2b was anomalous in that the ZCM was below the calculated pycnocline depth in 4 of 6 profiles, perhaps due to the lower stratification at this station (Fig. 2.6, Table 2.3).

Temperature at the larval ZCM was 10.4-12.8 °C (mean: 11.9, s.d.: 0.70) and 75% of the larvae for any profile were usually within +/- 2 °C of the ZCM (Fig. 2.13). Larvae were found in the lowest temperatures at stations S2b and S3, where temperatures above the weak pycnocline were lower than other stations (Figs. 2.6, 2.8, 2.13).

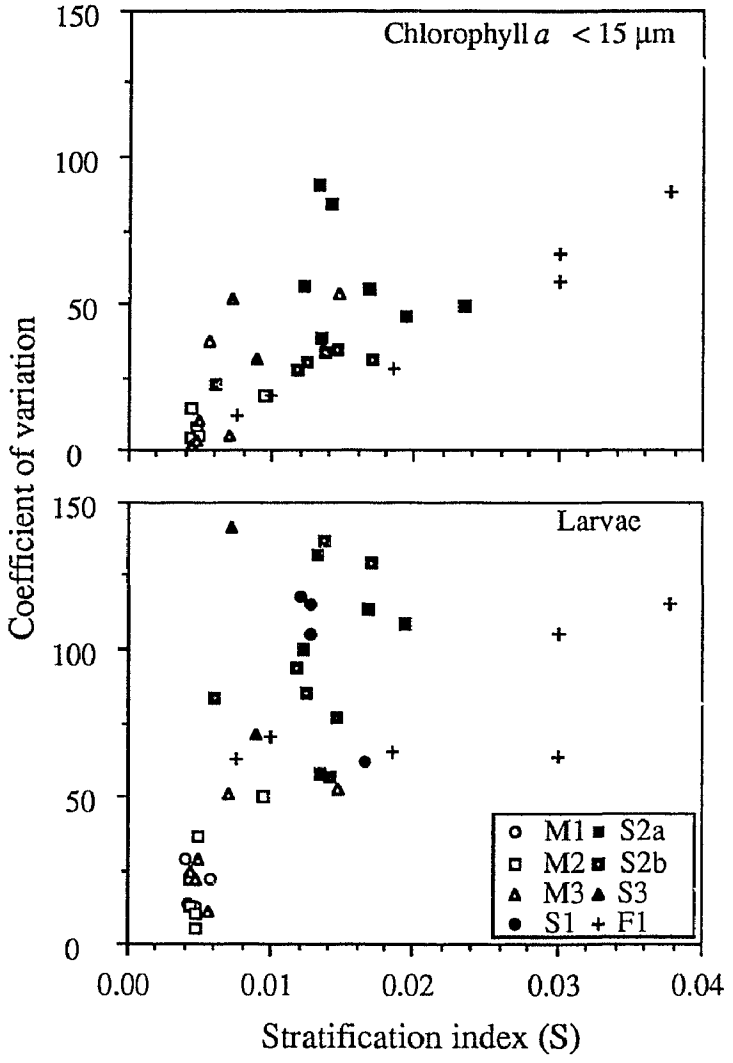

Figure 2.12. Coefficient of variation versus stratification index (S) for chlorophyll *a* < 15 µm and sea scallop larvae. Points from different stations are keyed by symbol (one point for each profile within a station).

Table 2.3. Pearson correlation coefficients among ZCMs of sea scallop larvae and chlorophyll *a* < 15 μm, and the depth of the pycnocline. Only stations where larval aggregation is an important feature are included (see text). S is stratification index, LZCM is larval centre of mass, CZCM is chlorophyll *a* < 15 μm centre of mass, and P is pycnocline depth. N (number of profiles) ranged from 4 to 7. Significant correlations (from Sokal and Rohlf 1969) are indicated as follows: *: $p < 0.05$; ** $p < 0.01$.

Station	S	LZCM & P	LZCM & CZCM	CZCM & P
S1	0.014	0.71	-	-
S2a	0.016	0.67	0.00	0.35
F1	0.022	0.86*	0.97**	0.00
S2b	0.013	-0.81*	0.39	0.04

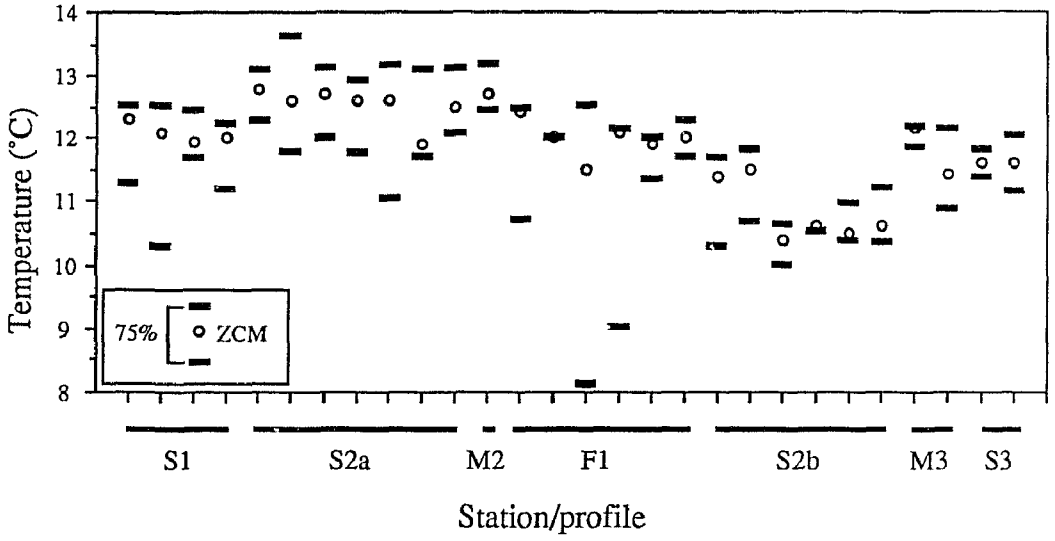

Figure 2.13. Temperature at ZCM and range over which most larvae were found. Range corresponds to temperatures at depths equidistant from ZCM, between which 75% of larvae found.

2.3.4 Diel differences in the ZCM and differences in larval length with depth.

There were no consistent day-night differences in the ZCM of larvae to suggest diel vertical migration. This was the case whether the data were examined within station (Figs. 2.3, 2.5, 2.6, 2.10) or over all stations (Fig. 2.14, Table 2.4). Where the pycnocline was strong, variation in the pycnocline depth had more effect on the ZCM than did the diel light cycle. Size dependent differences in vertical distribution were undetectable or unsystematic. The ZCMs of different sized larvae were not significantly different (Table 2.4), and a comparison of the length distribution of larvae at different depth intervals showed small differences at station S2, and no significant differences at station M1 (Table 2.5).

2.4 Discussion

2.4.1 Ship drift and effect on profiles of larval concentration

The drift of the ship during sampling was largely a function of the lunar semidiurnal tidal current on Georges Bank. On the Northeast Peak, this current swings in a clockwise direction though an ellipse every 12.4 hours. The ellipse is oriented northwest-southeast and has a major axis length of 12-15 km (Lough and Trites 1989). The direction and distances drifted by the ship (Fig. 2.2) were close to that predicted from tide tables and tidal current speeds. Fortunately changes in water column structure during profiling were generally small, indicating that the ship drifted within relatively homogenous water masses. The ship was probably not an effective drogue of patches of sea scallop larvae however, since currents decrease with depth (Butman et al. 1982, 1987, Lough and Trites 1989, Fig. 3.4) and the ZCM of sea scallop larvae was usually 10-30 m below the ship. This current shear may explain some of the patchiness indicated by the variance in larval concentration between profiles, and the fact that the

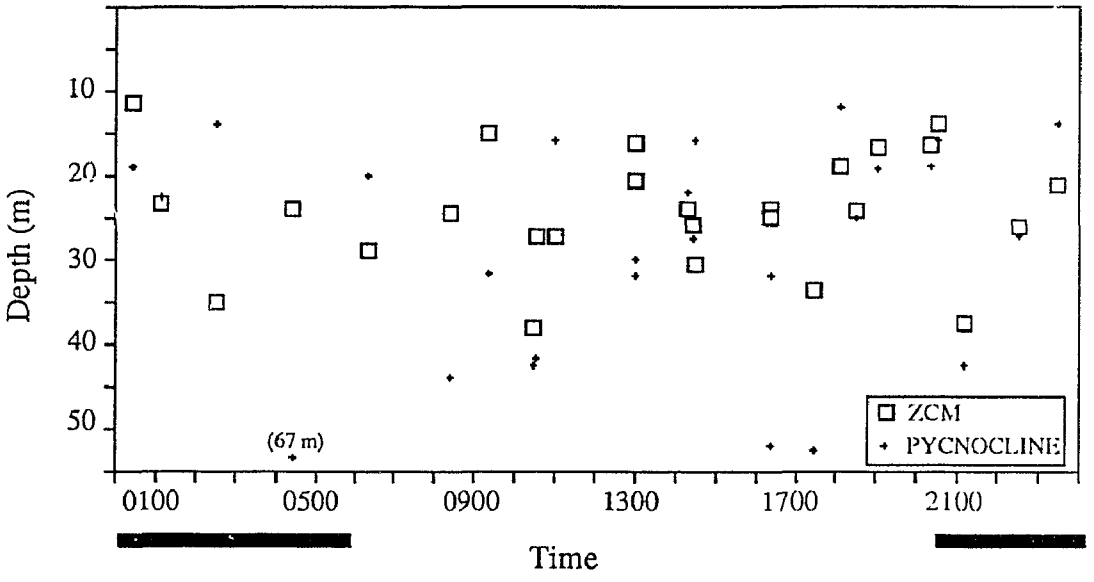

Figure 2.14. ZCM of sea scallop larvae versus time of day for all profiles where larval aggregation important. Black bar delimits profiles done during darkness. Also depicted is location of pycnocline.

Table 2.4. ZCMs (m) of larvae within different size classes summarized for profiles completed during daylight (0800-1830) and darkness (2100-0500). Not included were profiles done where the CV of larval concentration (over all depth intervals) was < 50%, and profiles done near dawn or dusk. N is number of profiles. Analysis of variance indicated that neither size class nor time of day had a significant effect on the ZCM ($p > 0.4$)

		Length (μm)		
Time of day	N	< 133	133-201	> 201
daylight	15	23.9	24.9	24.8
darkness	7	25.5	23.7	22.7

Table 2.5. Mean lengths of sea scallop larvae within different depth intervals for stratified (S1) and mixed (M1) stations in 1986. For comparison of lengths at different depths within stations, a Kruskal-Wallis analysis of variance by ranks was performed. Depth intervals with length distributions which are significantly different (Mann-Whitney comparisons, $p < 0.05$) are indicated by different superscripted letters adjacent to the means. Mean number of larvae measured per depth interval was 98 for S1 (s.d: 48.1) and 60 for M1 (s.d: 23.8). P is profile.

	Stratified				Mixed			
Depth (m)	P1	P2	P3	P4	P1	P2	P3	P4
0-5	157^{a}	155^{ab}	156	152^{ab}	138	141	141	141
6-10	160^{a}	152^{a}	165	153^{ab}	134	146	136	139
11-20	162^{a}	158 ^{bc}	157	157^{ab}	136	139	137	140
21-30	162^{a}	162 ^{c}	159	150^{a}	144	142	139	138
31-40	170 ^{b}	160 ^{c}	158	158 ^{b}	146	144	137	137
41-50	159^{a}	161 ^{c}	160	151^{a}	139	138	139	139

CV of the average concentration of larvae was lower at the mixed stations (Table 2.2), where current shear is expected to be low.

2.4.2 Subsurface aggregations of scallop larvae: the importance of water column density structure

The presence or absence of a subsurface aggregation of sea scallop larvae on Georges Bank is predictable from the density structure. Below an S value of about 0.007, sea scallop larvae were distributed evenly over the whole water column, and can probably be considered passive particles. Above S values of 0.007, sea scallop larvae were aggregated at subsurface depths, in most cases above or within the pycnocline.

A specific objective of this study was to determine if sea scallop larvae aggregate in relation to increased concentrations of food. It is apparent that sea scallop larvae on Georges Bank do not aggregate in relation to the concentrations of chlorophyll *a* < 15 μm or particles 2.5-16.0 μm. Subsurface increases in the concentration of chlorophyll *a* < 15 μm or particles were not a prominent feature, with most profiles showing the greatest concentration of phytoplankton and particles in the upper 10 m, above the depth where sea scallop larvae were most concentrated. Even where a subsurface chlorophyll *a* maximum was present, the larval ZCM was below it in all but one profile. Although our sampling resolution (5-10 m) was not sufficient to detect small spikes in chlorophyll *a* less than 5 m in width, it was sufficient to detect subsurface chlorophyll maxima typical of the Gulf of Maine region. In this area chlorophyll *a* concentrations within subsurface maxima are typically 2-5 times the background levels, and are 10-15 m in width (Sameoto 1984, Townsend et al. 1984).

A number of factors can give rise to the formation of subsurface chlorophyll *a* maxima (Cullen and Eppley 1981, Cullen 1982) but a sufficiently developed pycnocline may be required for their formation in the Gulf of Maine area (Townsend et al. 1984) and in other tidally dominated seas (Pingree et al. 1976). On Georges Bank the month of

October is a period of transition to the more vertically mixed waters of late autumn and winter, and subsurface chlorophyll maxima are not a regular feature (Sameoto 1984, O'Reilly et al. 1987). September is more consistently stratified and subsurface chlorophyll maxima are more prevalent (O'Reilly et al. 1987).

Our measurements of chlorophyll *a* (Table 2.2) are somewhat higher than those done previously on Georges Bank at this time of year. Water column averages of chlorophyll *a* in the nanoplankton (< 20 μm) during October averaged over 6 years are approximately 0.6 μg l^{-1} in the weakly stratified area, and 0.9 μg l^{-1} in the well mixed area (O'Reilly et al. 1987). The high concentrations of chlorophyll *a* observed at station S2a in early October (Table 2.2, Fig. 2.3) must represent a temporary, perhaps anomalous situation. The close relationship between particles and chlorophyll *a* for these profiles (Fig. 2.11) suggests that the particle field was dominated by living phytoplankters.

Given that sea scallop larvae feed on phytoplankters less than 10-15 μm, the percentage of the total phytoplankton within this size range may be a factor in its availability to sea scallop larvae. The percentage of chlorophyll *a* which is contained in the nanoplankton (< 20 μm) has been used to distinguish areas of Georges Bank (O'Reilly et al. 1987). During October, the central mixed region generally has the lowest percentage (30-50%) while the stratified region at the edge of Georges Bank has the highest percentage of nanoplankton (O'Reilly et al. 1987). The 8 profiles for which total chlorophyll *a* was measured together with the < 15 μm fraction in the present study only partially substantiate this generalization. The most stratified station (F1), had the highest percentage nanoplankton (88%), but the mixed station did not have the lowest percentage (Table 2.2).

Profiles of production by food organisms consumed by sea scallop larvae may differ from the profiles of food concentration (Figs. 2.3-2.8, 2.11). Picoplankton (< 3

μm), which may be a significant source of food for sea scallop larvae, comprises a greater fraction of the total primary production at subsurface depths than at the surface, due to more efficient utilization of low light intensities and green light than by larger phytoplankters (Glover et al. 1985, Waterbury et al. 1986). Further study is required to determine the importance of picoplankton to the nutrition of sea scallop larvae, and whether there is an increase in picoplankton production in subsurface layers where sea scallop larvae aggregate.

The location of the pycnocline is an important feature in determining the vertical distribution of sea scallop larvae on Georges Bank. Where it is well developed, it coincides with the lower limit of occurrence of larvae (Fig. 2.5), and fluctuations in pycnocline depth are associated with fluctuations in the larval ZCM. The depth of the pycnocline on the Northern Flank of Georges Bank varies with location and tidal stage (see Fig. 12 of Lough and Trites 1989) and the differences in pycnocline depth between profiles at station F1 could have resulted from ship drift, changes in the tidal current, or a combination thereof. Whether individual sea scallop larvae actually undergo the shifts in vertical position suggested by the changes in the ZCM between profiles at station F1 (Fig. 2.5) cannot be determined from the present study.

Short-term variation in the ZCM of sea scallop larvae may be affected by the action of internal waves, which propagate onto the Northern Flank with the tidal current (J. Loder, Bedford Institute of Oceanography, pers. comm.). Tidally driven internal waves can cause vertical oscillations of the pycnocline of up to 30 m for 1-2 hours of every tidal cycle off the coast of Maine (Haury et al. 1983) and zooplankton and phytoplankton can be transported with such oscillations (Haury 1976, Haury et al. 1978, Hargreaves 1981, Haury et al. 1983, Le Fevre 1986). In the present study, internal waves were not a dominant feature during profiling (Figs. 2.3-2.8), although internal waves may have passed during profiles 3 and 5 at station F1 (Fig. 2.5). The ship was at its most

ship was at its most northerly extent during these profiles, and the tidal current was flowing onto the bank (Fig. 2.2), conditions which suggest the presence of internal waves.

2.4.3 The role of larval swimming behavior in determining vertical distribution

Evidence that swimming behavior of sea scallop larvae was important in regulating their vertical distribution was absent from the present study. In the mixed parts of Georges Bank, the swimming ability of scallop larvae appears to be overwhelmed by vertical mixing and the horizontal movement of larvae should be a function of the depth averaged residual current. Estimates of vertical mixing rates in the mixed parts of Georges Bank indicate a passive particle will be redistributed over a 50 m depth interval in 2-5 h (Loder et al. 1988), or at a rate of 9-25 m h^{-1}. By comparison, a scallop larva might swim upwards at 5 m h^{-1} (at 1.3 mm s^{-1}) and downwards at 6 m h^{-1} (at 1.7 mm s^{-1}) if it maintained the speeds observed in a 10 m tank over much shorter periods (Silva and O'Dor 1988). Swimming in one direction for extended periods is unlikely since larvae tend to alternate between rising and sinking (Silva and O'Dor 1988).

In areas with density stratification, the role of behavior is less certain, but short term changes in the depth of the pycnocline will likely overwhelm directed movement by sea scallop larvae. The lack of a diel difference in the larval ZCM, and the fact that differences in larval size with depth were not systematic supports this view. Scallop larvae can vertically migrate (Chapter 1) presumably as a reaction to light (Kaartvedt et al. 1987, Silva and O'Dor 1988), but their pressure response is less than that of estuarine species (Cragg 1980, Mann and Wolf 1983). Small differences in depth distribution (< 5-10 m) over time or with size would not have been detected with the sampling resolution of the present study, but changes of this magnitude are likely to be secondary to short term changes in water column structure.

The temperature range (10-13.5°C) over which sea scallop larvae were usually found coincides with the temperatures found in the upper mixed layer, and whether temperature, or some other stimulus caused the larvae to swim above the pycnocline cannot be discerned from the present study. Sea scallop larvae are successfully grown in hatcheries at temperatures of 12-15 °C, but more systematic study is required to establish their optimum temperature (Tremblay 1988).

Although larval swimming behavior may not be significant in determining short term variations in vertical distribution, the formation of subsurface aggregations above or within the pycnocline may well result from an interaction between behavior and water column turbulence. In the laboratory, sea scallop larvae often swarm, and if this tendency is present in nature, the subsurface aggregations may reflect such swarms. Low turbulence may be necessary for the low swimming speeds of larvae to be effective in forming swarms, and turbulence is expected to decline in the region of the pycnocline (Sundby 1989). Estimates of vertical mixing rates for the weakly stratified part of Georges Bank are less certain than for the mixed area, but suggest a passive particle will be redistributed over 50 m in 4-20 h (Loder et al. 1988), or at a rate of 2-13 m h^{-1}. This rate is closer to the potential swimming speeds of sea scallop larvae.

Other bivalve larvae are also associated with the pycnocline (or thermocline) but the associations have been explained either in terms of temperature or food. Mann (1986b) argued that the restriction of *Arctica islandica* larvae to depths of 20-40 m during September was due to active avoidance of warm surface water, but since these larvae were most aggregated in the region of the thermocline at that time, an association with decreased turbulence cannot be ruled out. Similarly Scrope-Howe and Jones (1986) found that bivalve larvae were associated with a subsurface chlorophyll *a* maximum, but since this was associated with the thermocline, decreased turbulence may have been important in the formation of the larval aggregations. To test the hypothesis

that subsurface aggregations of bivalve larvae occur where turbulence is low, profiles of the velocity of turbulence (Rothschild and Osborn 1988) are necessary. Swimming speeds of bivalve larvae can then be compared with the turbulent velocity profiles to assess whether active swimming plays a role in the formation of the subsurface aggregations.

Active movement by sea scallop larvae must play a small role in depth regulation relative to larger, more mobile zooplankters. Swimming speeds of sea scallop larvae (< 1.7 mm s^{-1}; Silva and O'Dor 1988) are on the low side of the planktonic groups examined to date on Georges Bank. Small herring larvae for example (ca 10 mm length) can cruise at 10 mm s^{-1}, and have maximum speeds of 30 mm s^{-1} (Blaxter, 1965). Using similar sampling resolution at the same time of year, several studies show that some zooplankters undertake extensive diel vertical migrations, or have size dependent vertical distributions. These include some larval fish, chaetognaths, and some copepods (Lough 1976, Sameoto 1984, Lough and Trites 1989). Other zooplankters are similar to sea scallop larvae in that they do not show diel differences in depth on Georges Bank at this time of year (Turner and Dagg 1983, Sameoto 1984).

In areas where vertical shear is important, the horizontal movement of planktonic organisms will be affected by (i) the mean position of the plankters in the water column and (ii) the amplitude and the period of vertical migration which occurs. Although previous authors have suggested that scallop larvae in nature are near the surface (Posgay 1979, Cragg 1980), this is clearly not the case for Georges Bank or the Bay of Fundy (Tremblay and Sinclair 1988), and therefore surface currents alone will be inadequate for predicting horizontal movement of sea scallop larvae.

Modelling the horizontal movement of plankton via currents is more complex if the plankter vertically migrates, because of the interaction between vertical current shear and the vertical migration (Wroblewski 1982, Rothlisberg et al. 1983, Lough and Trites

migrating (up to 60 m daily) adult chaetognaths on Georges Bank is much different than that predicted for non-migrating drifters (Lough and Trites 1989). For periods greater than two weeks the situation is different because the daily 50 minute shift in the tidal current has an averaging effect, and the horizontal displacement of chaetognaths was reduced by only 30% over non-migrators. To be effective in either retarding or enhancing horizontal movement over several weeks, vertical migrations must be on a tidal frequency rather than a diel frequency (Lough and Trites 1989). Sea scallop larvae may undertake a small amplitude vertical migration (< 10 m) on Georges Bank, but the frequency of the migration is most likely to be diel (Chapter 1). Therefore modelling the horizontal movement of sea scallop larvae from circulation models of Georges Bank should be simpler than for larger plankters which undertake extensive vertical migrations.

2.5 Summary

The vertical distribution of sea scallop larvae was studied from pump samples in mixed, stratified, and frontal areas of Georges Bank. The extent of larval aggregation was positively related to the degree of water column stratification. In mixed areas larvae were distributed evenly over the 40-50 m water column, while in stratified waters larvae showed subsurface peaks in concentration above the pycnocline. Where the pycnocline was well developed, differences in the larval centre of mass (ZCM) were associated with differences in the position of the pycnocline. Food for sea scallop larvae was measured as the concentration of chlorophyll *a* < 15 μm and particles 2.5-16 μm. In stratified areas food was usually greatest within the upper 10 m. Sea scallop larvae were most concentrated below 10 m and did not aggregate in relation to food concentration.

The capacity of sea scallop larvae for depth regulation on Georges Bank appears limited, since (i) larvae were distributed evenly over the water column in well mixed

waters, (ii) there were no diel differences in the ZCM, and (iii) size dependent differences in vertical distribution were weak and inconsistent. Swimming behaviour of sea scallop larvae, coupled with vertical changes in turbulence may explain the subsurface aggregations of scallop larvae near the pycnocline.

Chapter 3

The broadscale distribution and abundance of sea scallop larvae *Placopecten magellanicus* in the Georges Bank region

3.1 Introduction

The extent to which sea scallop larvae are transported from one adult scallop aggregation to another in the Georges Bank region (Fig. 3.1) is important to our understanding of population structure and recruitment processes in sea scallops. The extent of larval dispersal in sea scallops also bears upon the larger question of whether planktotrophic larvae dramatically increase gene flow among separate benthic aggregations as has long been assumed (Thorson 1946), or whether the gene flow resulting from larval dispersal is less than expected (Burton and Feldman 1982, Hedgecock 1986, Sinclair 1988).

At present the extent of mixing among the aggregations of sea scallops on Georges Bank and the surrounding area is not well understood (Sinclair et al. 1985). Nor are the relationships among Georges Bank aggregations, which since 1984 have spanned the management jurisdictions of Canada and the United States. Since movement by scallops on the bottom is thought to be minimal and undirected (Baird 1954, Posgay 1981, Melvin et al. 1985), exchange among scallop aggregations most likely occurs during the planktonic larval phase. Events during the larval period may be important to recruitment to fishable sizes (Dickie 1955, Caddy 1979, 1989), but definitive studies are lacking.

In the present chapter, I infer the extent of sea scallop larval dispersal in the Georges Bank region from three sources of information: larval distribution during plankton surveys, the potential locations of larval origin (fished aggregations as an index of spawning biomass), and the residual circulation. The term dispersal is used here to imply

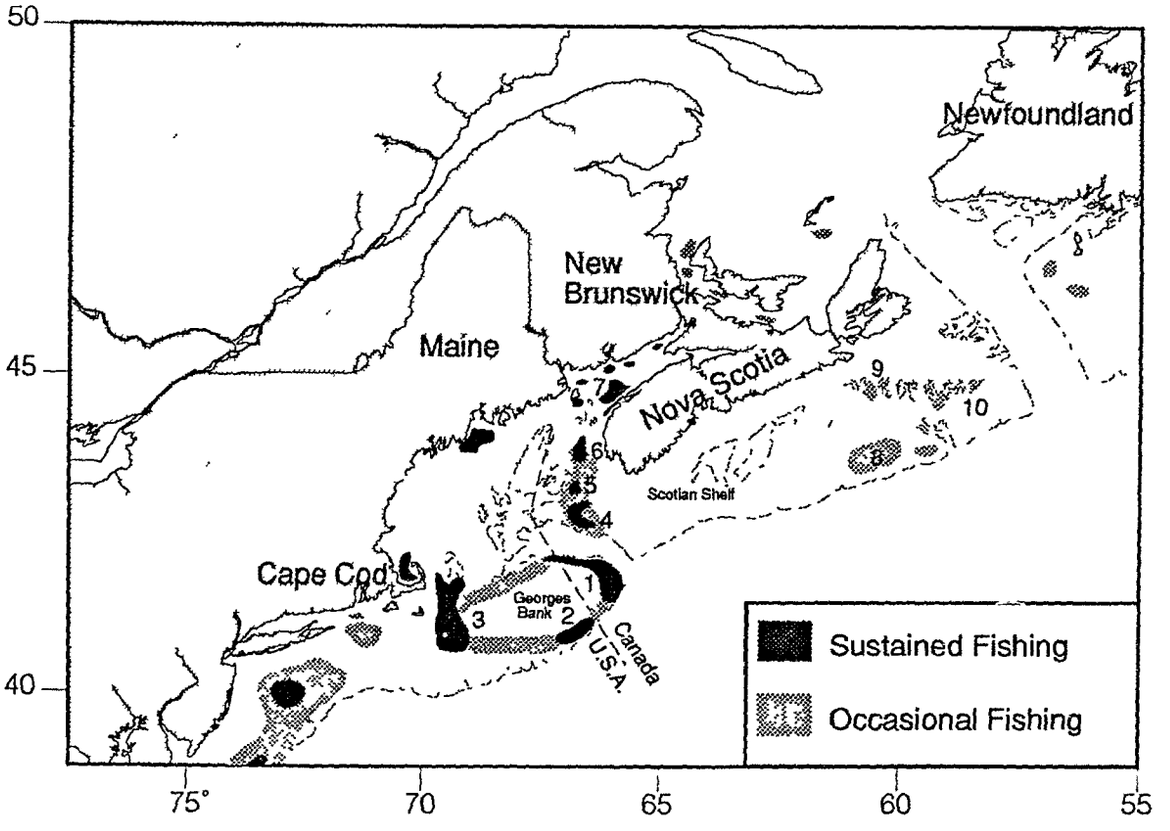

Figure 3.1. Major fishing aggregations for sea scallops in the Georges Bank and Scotian Shelf areas (modified from Sinclair et al. 1985 and Robert et al. 1989a). Long dashed line across Georges Bank is boundary between Canadian and U. S. sides. Fishing areas are as follows. 1: Northern Flank and Northeast Peak; 2: Southeast Part; 3: South Channel; 4: Browns Bank; 5: German Bank; 6: Lurcher Shoals; 7: Bay of Fundy; 8: Sable Island Bank area; 9: Middle Grounds; 10: Banquereau Bank.

temporal changes in the horizontal distribution of larvae, brought about by both advection and mixing processes.

Many studies of the broadscale distribution of plankton on Georges Bank indicate that exchange with the surrounding area is limited, and that a substantial portion of the larvae or zooplankton which originate on the bank are retained there (haddock larvae: Smith and Morse 1985, Hurley and Campana 1989; chaetognaths: Clarke et al. 1943, Lough and Trites 1989; herring larvae: Boyar et al. 1973, Schnack and Stobo 1973, Bumpus 1976, Iles and Sinclair 1982; cod larvae: Hurley and Campana 1989; and copepods: Davis 1984). Several of these studies also show temporal shifts in the distribution of plankters in the direction of the Georges Bank gyre, and an increase in the percentage of older plankters downstream from spawning locations.

In contrast to the above, some studies suggest that extensive losses of larvae from Georges Bank do occur, or that the residual circulation does not fully explain the pattern of larval distribution. Based on plankton surveys, Walford (1938) concluded that in 1931 haddock eggs and larvae were retained on Georges Bank, but that in 1932 extensive losses occurred to the north and south of the bank. Colton and Temple (1961) inferred from drifter studies and the spawning distribution of haddock and herring that in most years large losses of eggs and larvae occur due to an eastern drift off the southern side of Georges Bank, but they were unable to substantiate that larval drift actually occurs. Later drifter studies (Colton and Anderson 1983) again suggested extensive losses of larvae from the south side of the bank, but no relationships were found between drifter direction and larval abundance or mortality. Lobster larvae have also been hypothesized to be exported from Georges Bank. Based on surface currents, water temperature, landings trends and the distribution of large females and late stage larvae, Harding et al. (1983) reasoned that lobster larvae from the Northeast Peak of Georg Bank seeded the large lobster stocks along the southern coast of Nova Scotia and the inner Gulf of Maine.

The discrepancy between drifter trajectories and the distribution of fish larvae in Colton and Anderson (1983) may be related to non-synoptic measurements, or to their assumption that the distribution of fish larvae is simulated by passive surface drifters. Through active vertical swimming larvae can encounter different currents at different depths, and the potential for an active component in larval dispersal has long been recognized for estuarine species (for reviews see Norcross and Shaw (1984), Sulkin (1984), Mann (1986a), Stancyk and Feller (1986)). Chaetognath vertical migrations can retard horizontal transport on Georges Bank (Lough and Trites 1989), and a behavioral mechanism may be involved in the retention of the larvae of Georges Bank herring (Iles and Sinclair 1982), cod, and haddock (Lough and Bolz 1989).

If vertical swimming behavior is important to the retention of fish larvae on Georges Bank, sea scallop larvae should be retained to a lesser extent. Swimming speeds of sea scallop larvae (< 1.7 mm s^{-1}; Silva and O'Dor 1988), are on the low side of the planktonic groups examined to date on Georges Bank. Small herring larvae for example (ca 10 mm length) can cruise at 10 mm s^{-1}, and have maximum speeds of 30 mm s^{-1} (Blaxter, 1965). The vertical distribution of sea scallop larvae on Georges Bank suggests that any active component to larval scallop dispersal is likely to be minimal (Chapter 2). If sea scallop larvae do vertically migrate on Georges Bank, the amplitude is less than about 10 m, and is probably diel rather than tidal. It seems unlikely that such a migration would dramatically alter the dispersal pattern expected from that of a passive particle transported by the residual currents. Given that the dispersal of sea scallop larvae should be largely a function of the major spawning locations and the residual circulation, these aspects are briefly reviewed.

3.2 Distribution and abundance of adult sea scallops

The generalized distribution of sea scallops in the Georges Bank region is depicted in Fig. 3.1. Landings by the fishery (Table 3.1) are a coarse index of the relative abundance of scallops in these areas, since fishing effort is high (Sinclair et al. 1985). Differences in the total effort among areas, and management measures such as restrictions on the total allowable catch and enterprise allocations (initiated for Georges Bank in 1986) limit the value of landings for the detection of small year to year fluctuations in abundance. Nevertheless the much larger catch on Georges Bank from 1984 to 1988 indicates scallops are most abundant there. Scallops also tend to be more concentrated on Georges Bank, a trend reflected by catch per unit effort during stock surveys (Table 3.2). Scallop fishing on most of the Scotian Shelf can be characterized as sporadic, highly localized and opportunistic (Jamieson et al. 1981, Robert et al. 1989a). The exception is the Sable Island Bank area, where landings have been fairly regular in recent years (Table 3.1)

On Georges Bank, three main fishing areas were recognized by Serchuk et al. (1979) and Sinclair et al. (1985): the Northeast Peak, the southeast part, and the South Channel. The Northeast Peak is generally the most productive area in terms of the fishery, contributing ca 70% of the total catch since 1944 (Serchuk et al. 1979, Serchuk and Wigley 1988). For 1985-1988 the figures are 71 %, 63 %, 77 %, and 62 % (Table 3.1). Annual Canadian stock surveys of sea scallops on the Northeast Peak show that animals between the ages of 3 and 11 years are most concentrated in a crescent shaped area at depths of 60-100 m (Fig. 3.2). Sea scallops are in low abundance in the well mixed part (< ca 50 m) of the bank on both Canadian and U.S. sides (Serchuk and Wigley 1986).

Actual densities of sea scallops on Georges Bank are not well estimated by the scallop drags used in fishing because drag efficiency is low and related to scallop size (Caddy 1968, 1972, 1989). From camera surveys of a large bed (274 km^2) on the

Table 3.1. Recent landings (tonnes of meats) for aggregations of sea scallops on Georges Bank, the Scotian Shelf and the Bay of Fundy (see Fig. 3.1). Data for Georges Bank includes Canadian and U.S. catches. Logbook landings shown if greater than the landings recorded by Statistics Division, Dept. of Fisheries and Oceans. Bay of Fundy (BF) season runs over 2 years and the figures include landings from the previous year. Data from: Robert et al. 1989a, b; Serchuk and Wigley 1988; and F. Serchuk (National Marine Fisheries Service, Woods Ho. , Ma, pers. comm. of 1988 Georges Bank data). Areas are as follows. NE: Northern flank and Northeast Peak; SE: Southeast part of Georges; SCH: South Channel; BB: Browns Bank (including Tuskets area); GL: German/Lurcher area; BF: Bay of Fundy excluding outer reaches; SI: Sable Island Bank area; MG: Middle Grounds; BQ: Banquereau Bank.

	Georges Bank									
Year	NE	SE	SCH	Total	BB	GL	BF	SI	MG	BQ
1984	2692	691	1633	5016	30	240	717	71	12	3
1985	4804	403	1554	6761	16	37	601	76	27	0
1986	5783	654	2744	9181	5	36	425	618	51	16
1987	9009	265	2404	11678	0	1	130	416	7	1
1988	6460	835	3124	10419	5	0	1226	100	0	0

Table 3.2. Number of scallops (ages 3 yr to greater than 11 yr) per standard tow with a lined offshore scallop dredge during Canadian stock surveys. Survey stations are allocated to density strata based on commercial catches (Robert and Jamieson 1986). Shown are average catches in medium (M) and high (H) density strata. Data for Georges Bank are from Mohn et al. (1989); data for other areas are from Robert et al. (1989a)

Year	Georges Bank		Browns Bank		German/ Lurcher		Sable Island Bank		Middle Grounds
	M	H	M	H	M	H	M	H	H
1984	187	62	-	-	34	44	38	41	17
1985	537	282	-	3	22	27	65	222	10
1986	115	393	-	2	-	-	20	12	17
1987	83	207	-	-	-	-	35	122	6
1988	95	176	-	-	-	-	45	185	-

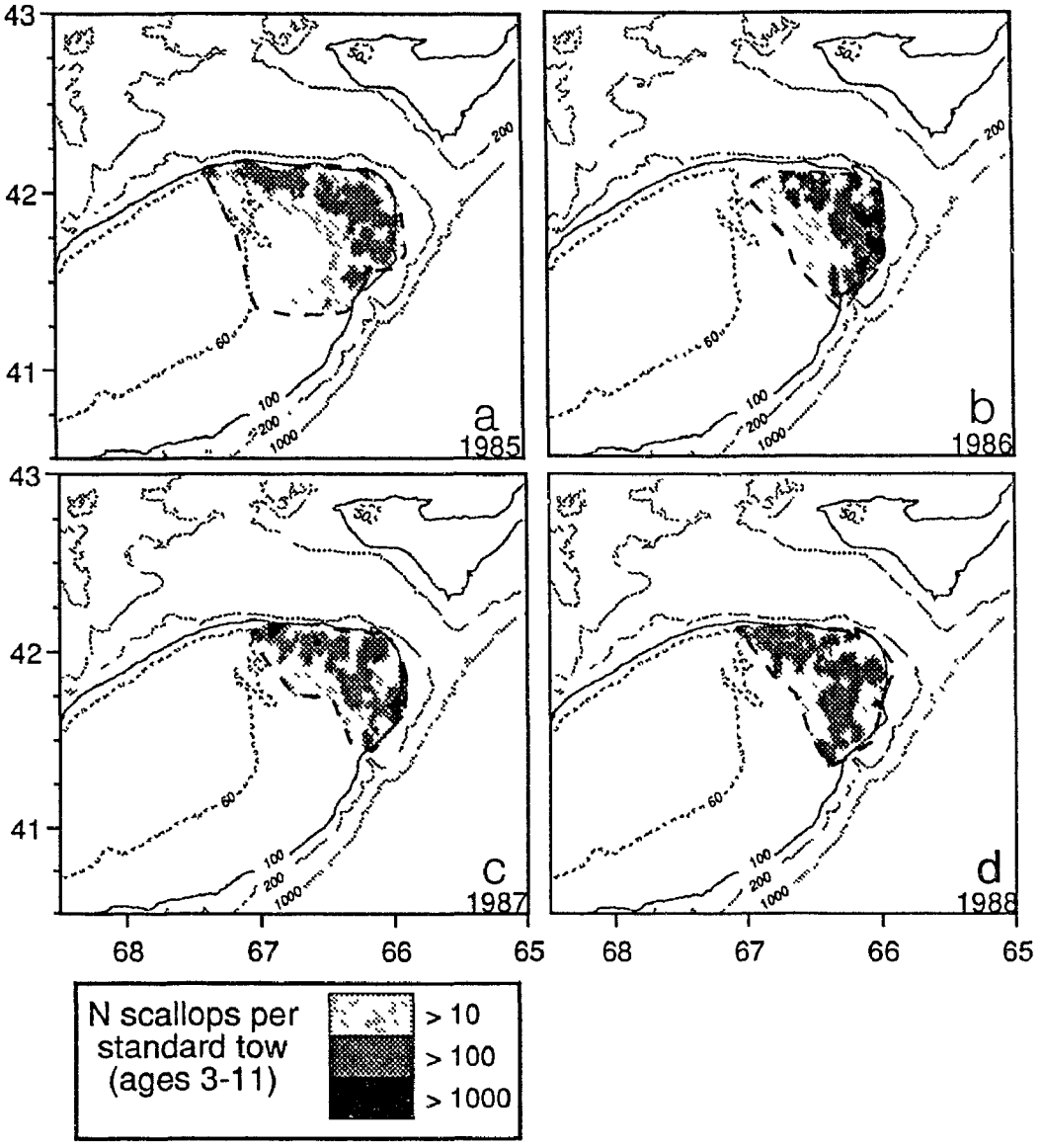

Figure 3.2. Distribution of sea scallops aged 3-11 on Georges Bank from Canadian research surveys 1985-1988. For (a), n tows = 200; for (b) - (d), n tows = 150. Heavy dashed lines indicate survey boundarys. Tows lengths are standardized to 800 m (survey methods are described in Robert and Jamieson 1986).

Northeast Peak in 1970 and 1971 the density of sea scallops averaged ca 1 m^{-2}, but reached as high as 5 m^{-2} in the centre of the bed (Caddy 1971, 1975). Using a quantitative epibenthic sled, the density of small scallops has recently been estimated to fall within a similar range (Thouzeau and Robert, unpublished data).

3.3 Circulation, residence time, and plankton distribution

The residual or mean circulation in the Georges Bank region is dominated by a series of gyres -- clockwise on Georges and Browns Banks, and counterclockwise in the Gulf of Maine (Fig. 3.3). On the Scotian Shelf north of Browns Bank, an alongshore current into the Bay of Fundy dominates the residual circulation. Seasonally related changes, tides, wind, and Gulf Stream rings will all contribute to variability in the residual circulation in these areas, and on Georges Bank, the mean circulation probably seldom occurs at any given time (Butman et al. 1987).

On Georges Bank there is significant spatial variation in the residual current speed (Fig. 3.4). The highest flows (25-30 cm s^{-1}) occur within a narrow band (10-20 km) along the Northern Flank of Georges Bank where the bathymetric gradient is steepest, and the lowest flows occur in the shallower parts of the bank. At most locations currents decline with depth. Compared to the mean currents, the semi-diurnal tidal currents, which rotate clockwise through an ellipse of 10-15 km twice per day, are considerably stronger (20-100 cm s^{-1}; Brown and Moody 1987). The effect of the semi-diurnal currents on a drifting ship is illustrated in Fig. 2.2.

The gyral circulation of Georges Bank, coupled with its large size suggest that it should tend to retain plankton, but it is important to emphasize that the Georges Bank gyre is not regarded as a barrier to cross-bank exchange (Colton and Temple 1961, Bumpus 1976, Butman et al. 1982, Loder et al. 1988). Drifters do exit from the bank, in an apparently unpredictable manner, and small cross-bank flows are measurable, although highly variable (Butman et al. 1982, Loder and Wright 1985). Georges Bank is highly

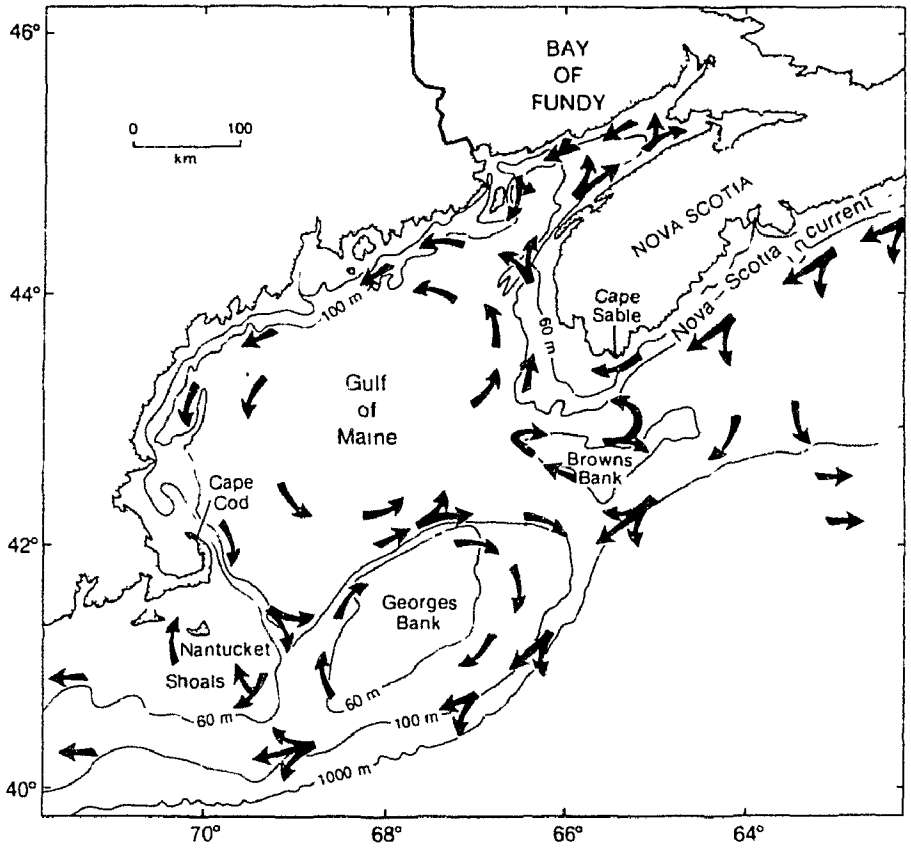

Figure 3.3. Residual circulation in the Gulf of Maine region (drawn by R. Trites).

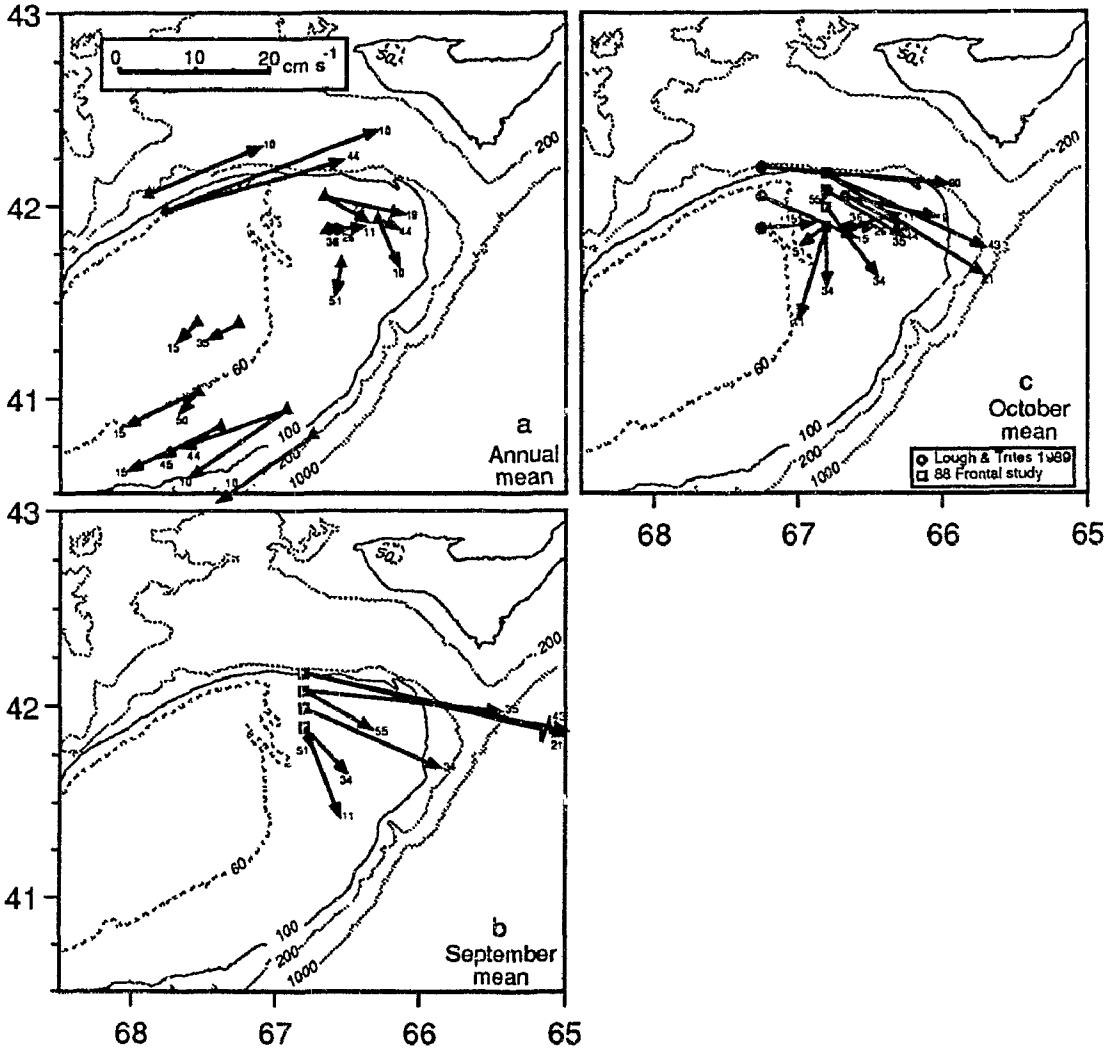

Figure 3.4. Current speed and direction on Georges Bank from moored current meter measurements. Vectors represents the mean of measurements of at least two weeks. Scale chosen reflects the distance a particle would move in five days if it travelled at the speed and direction measured at the mooring. Depths of measurements (at arrow tips) range over the depths where sea scallop larvae are most concentrated on Georges Bank (10-50 m). (a) Mean annual residual circulation for various seasons and periods (41-1113 d) from 1975 to 1979 (from Butman et al. 1982). (b) September measurements from the 1988 Georges Bank Frontal Study (J. Loder, Bedford Institute of Oceanography, pers. comm.). (c) October measurements from 1988 Georges Bank Frontal Study (first 14 d only) and Lough and Trites (1989; Oct 17-30, 1978).

retentive compared to other submarine banks in the region however (Loder et al. 1988). The impact a particular gyre is likely to have on the distribution of drifting organisms can be estimated by comparing the residence time (a measure of cross-isobath exchange which gives the average time that particles will stay over the bank) to the recirculation time (time for particle to complete a circuit of bank). Of four banks (Georges, Browns, Southeast Shoal, Flemish Cap) considered by Loder et al. (1988), only Georges Bank is estimated to have a residence time which is both (i) equal to or greater than the recirculation time, and (ii) greater than a few weeks. Therefore larvae which remain planktonic for more than a few weeks, such as the larvae of sea scallops, have the potential to recirculate on Georges Bank.

Residence time on Georges Bank is greatest in late summer and early autumn, when sea scallop spawning occurs (Posgay and Norman 1958, Sinclair et al. 1985). At this time of year passive particles in the central, well mixed area of the bank will remain the longest (> 60 d), while those on the periphery of the bank will remain ca 20 d (Loder et al. 1982, Colton and Anderson 1983, Loder et al. 1988). Maximum subsurface (15-75 m) around-bank flow also occurs in late summer and early fall (Butman et al. 1982), when the recirculation time of drifters deployed at 10 m is estimated to be 33-55 days (Loder et al. 1988). It is perhaps significant that these estimates of residence and recirculation times overlap the estimated duration of the planktonic period of sea scallop larvae (4-6 weeks; see section 3.4.5). The summer recirculation and residence times for other banks in the area are considerably less (10 and 14 d respectively on Browns Bank; Smith 1989).

Given the above information on the residual circulation and the distribution of adult sea scallops, the dispersal pattern of sea scallop larvae should be apparent from their distribution. Retention of sea scallop larvae on Georges Bank should be reflected in two ways: (i) a decline in larval abundance off the edge of the bank; and (ii) higher larval

abundance on Georges Bank than any of the surrounding areas, because spawning biomass is much higher on Georges Bank. On Georges Bank itself, examination of spatial and temporal shifts in the abundance and length frequency of sea scallop larvae may indicate the extent to which the larvae are advected in the direction of the residual circulation.

3.4 Methods

3.4.1 Surveys

The samples used to describe the broadscale distribution of larvae were obtained during 6 cruises in September or October over four years (Table 3.3). Most samples were collected during the October cruises of 1985, 1986 and 1987, with additional samples obtained by opportunity on cruises undertaken in early September 1987 by the United States National Marine Fisheries Service (NMFS), and in late August 1988 by the Department of Fisheries and Oceans (Table 3.3). Also included here are limited data from the 1988 Georges Bank Frontal Study (Chapter 4) to better depict the seasonal distribution of sea scallop larvae on Georges Bank.

The survey design was systematic and stations were either on transects (1985, 1988) or a grid (1986, 1987). In October 1985 stations were sampled every seven nautical miles on a series of transects from inshore to offshore on the Scotian Shelf, extending on to Georges Bank. Cruises in October 1986 and 1987 were based on a systematic survey grid with 10 nautical mile spacing (Fig. 3.5). During these cruises the Georges Bank stations were sampled twice, and they are therefore divided into two periods (Table 3.3). Stations in September 1987 were those of a NMFS plankton survey (MARMAP), while those sampled in 1988 were from transects on the Northern Flank of Georges Bank (Chapter 4).

Table 3.3. Dates of plankton surveys during which sea scallop larvae were collected. Ship was the RV Lady Hammond except for the September 1987 survey when samples were obtained from the RV Delaware II (during U. S. National Marine Fisheries Service MARMAP survey). In 1986 and 1987 parts of the survey grid were sampled twice (a and b). The 1988 cruises were part of the Georges Bank Frontal Study, and were restricted to the Northern Flank and Northeast Peak.

Year	Date
1985	Oct 8-11
1986	(a) Sept. 30 - Oct 8
	(b) Oct 8-13
1987	Sept. 5-7
	(a) Sept. 29 - Oct. 8
	(b) Oct 12-19
1988	Aug. 27 - Sept. 1
	Oct. 5-19

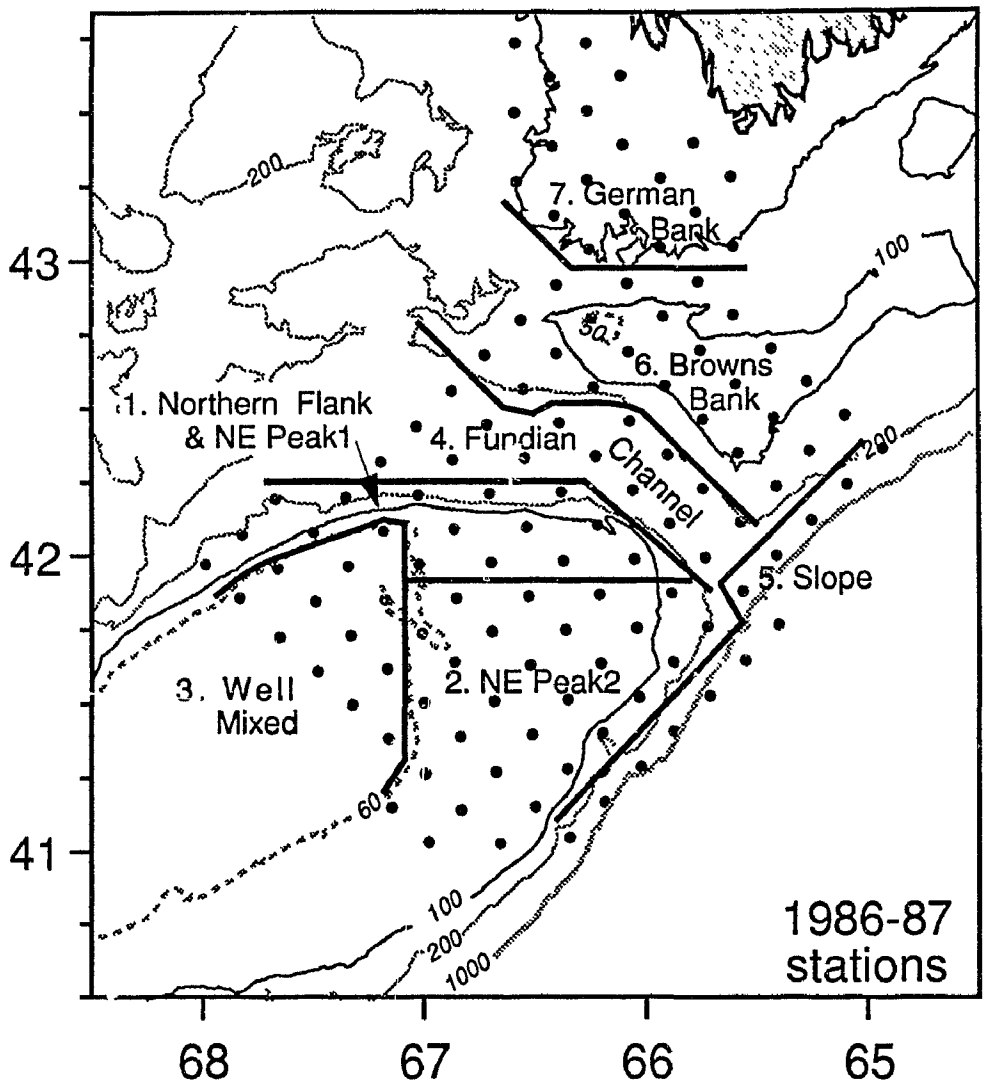

Figure 3.5. Stations sampled for sea scallop larvae in 1986 and 1987. Areas for comparison of the abundance and length frequency of sea scallop larvae are delimited.

3.4.2 Sampling methods

At each station vertically integrated plankton samples were obtained with two nets mounted on a bongo frame with two 40 cm diameter openings. Initial study indicated that replicate hauls added little to the precision of the abundance estimate (Appendix 2). Each net was 156 cm in overall length, and was fitted with NITEX mesh with openings of either 85 μm or 53 μm (see below). A removeable PVC cod end bucket was secured to the bottom of each net.

The nets were hauled from 5 to 10 m off the bottom to the surface with a usual maximum tow depth of 200 m (Appendix 3). Gear depth was measured by a mechanical or electronic meter block, with corrections for wire angle. The nets were hauled at 0.5-0.8 m sec^{-1}. A TSK flowmeter was mounted in the opening of at least one of the nets.

Samples were preserved in 4% formalin buffered with sodium borate. Sea scallop larvae and other heavier components of the plankton samples were physically separated from the lighter components using a colloidal silica (Tremblay et al. 1987). Sea scallop larvae in the samples were then identified and counted using a dissecting microscope. Subsamples were taken when the total number of larvae in the samples exceeded ca 300. The sample was split with a Motoda splitter such that a total of at least 200 larvae were counted (Appendix 1). After the larvae were transferred from the counting dish to a welled slide, their lengths were measured to the nearest 5.8 μm using an inverted microscope.

3.4.3 Data analysis

The volume (m^3) measured by the plankton net flowmeters was used to standardize the larval abundance per m^2 of sea surface as follows:

$$N\ m^{-2} = \text{count/volume} * \text{water column depth}$$

where water column depth = the lesser of the station depth, or 200 m. Prior to the above calculation, clearly spurious flowmeter readings (about 10% of all tows) were eliminated to minimize errors in volume estimation. For these samples, volume was estimated from

prediction equations developed for tows where the volume was reliably estimated. The length of wire out and the wire angle were used as predictor variables after regression on the volume estimated from the flowmeters (Appendix 4).

The length measurements of each sample were used to estimate the number per m^2 within each 5.8 μm size class from 104 μm to 292 μm. Length frequencies of sea scallop larvae retained by an 85 μm net versus a 53 μm net indicated that the former was not effective at retaining larvae less than about 124 μm. Correction factors were developed (see Appendix 5 for details) and the abundance estimates for larvae less than 124 μm were increased by factors of 2.8 (120.8 μm), 15.8 (115 μm) and 22.4 (<=109 μm).

To facilitate comparison of length frequency and abundance, the sampling area was divided into seven areas based on bathymetry and current structure (Fig. 3.5). The first three areas are on Georges Bank: (1) Northern Flank and Northeast Peak 1; (2) Northeast Peak 2 and (3) Well Mixed Area (< 50-60 m). The remaining four areas, sampled less intensively are as follows: (4) Fundian Channel; (5) Slope southeast of Browns Bank and off Georges Bank; (6) Browns Bank; and (7) German Bank and Lurcher Shoals area. To estimate overall length frequencies of sea scallop larvae within these broad areas, the length frequencies were weighted by the abundance of larvae per m^2 at each station.

Initial statistical analyses of differences among areas in the abundance of sea scallop larvae indicated that a non-parametric approach was required, as residuals from analyses of variance indicated that the variance was not stable, and log transformation did not improve matters. Non-parametric Kruskal analysis of variance was used for each of the October surveys of 1985, 1986 and 1987 and pairwise comparisons were then made using the Mann-Whitney test. To correct for the number of comparisons to be made within any one set of data, the pairwise significance level was adjusted for the number of comparisons to be made by the Bonferonni procedure (Wilkinson 1987, Neter et al. 1985). In this

procedure t. . pairwise significance level equals the chosen overall significance level (0.05) divided by the number of comparisons.

3.4.4 Data plotting

The spatial variation in the abundance (N m^{-2}) of sea scallop larvae is depicted with two types of plots: expanding symbols and shaded contours. The expanding symbols plots were used to depict the abundance of larvae over the whole sampling area during each sampling period. Shaded contour plots were used for examining the distribution of 'patches' of sea scallop larvae on Georges Bank in 1986 and 1987, when the bank was sampled twice. In this type of plot, a surface is formed by defining triangles where the data points (number of scallop larvae m^{-2}) form the vertices of triangles connecting adjacent data points (Mohn et al. 1989). Because the shading at any one station is influenced by the surrounding stations, the time period of the data for any one plot was narrowed to increase its synopticity. For 1986 stations were excluded if they were not sampled within the periods Oct 2-6 and Oct 8-11. Stations which were sampled twice in 1986 were separated by 4-6 d. For 1987 the two periods were Oct 2-6 and Oct 12-19, and stations sampled twice were separated by 10-15 d.

3.4.5 Growth of sea scallop larvae in hatcherys

To interpret the length frequency distributions of sea-caught larvae, it is necessary to have an estimate of the larval growth rate. Growth rates under different environmental conditions of temperature are currently unavailable (Tremblay 1988), so what follows is the typical development rate under hatchery conditions (12-15 °C, *ad libidum* feeding) from a variety of sources (Culliney 1974, Couturier 1986, Hurley et al. 1987, Tremblay 1988, A. Mallet, pers. comm.). Sea scallop eggs are negatively buoyant, and the first swimming stage (trochophore) is reached 24-48 h after fertilization. The earliest shelled stage ('D' shape, or straight hinge) is ca 105 µm in length, and is reached after 4 d.

Metamorphosis can occur after an additional 25-30 d, although some delay of metamorphosis is possible. Prior to the size when sea scallop larvae are competent to metamorphose (ca 235 μm) a growth rate of 5-6 μm of shell length per day is implied. Given that most sea scallop larvae on Georges Bank are found at within a temperature range of 10-13.5 °C (Chapter 2), the growth rate to metamorphosis is expected to be 4-6 μm d^{-1} if the larvae are not food-limited. If food-limited, larvae would still increase in shell length but at a lower rate. Even starved larvae can grow for a few days at 1-2 μm d^{-1} (Chapter 5).

3.5 Results

3.5.1 Abundance and length frequency of sea scallop larvae

Surveys on Georges Bank in late summer indicate that spawning had begun recently (Fig. 3.6). Sea scallop larvae were present in late August and early September, but larvae greater than about 200 μm were lacking in both 1987 (Fig. 3.6c) and 1988 (Fig. 3.6f). Larvae were less abundant in early September 1987 than in October (Fig. 3.7c-e), and peak spawning probably occurred around mid-September. By October of 1987 and 1988 the length frequencies had shifted to larger sizes, but the presence of small larvae (<124 μm) estimated to be 6-10 d old, indicates that spawning occurred as late as the second week of October (Fig. 3.6h). Compared to 1987 (Fig. 3.6c-e), larger sea scallop larvae were more prevalent in all surveys in 1988 (Fig. 3.6f-h), suggesting that spawning occurred earlier in the latter year, or that the growth rate was higher.

Sea scallop larvae were much more abundant on Georges Bank than in the Fundian Channel (area 4), on the Slope (area 5), and on the Scotian Shelf (areas 6-7) (Figs. 3.5, 3.7). These differences were statistically significant in each survey for which there were sufficient data for testing (Table 3.4). The mean number of larvae within the different

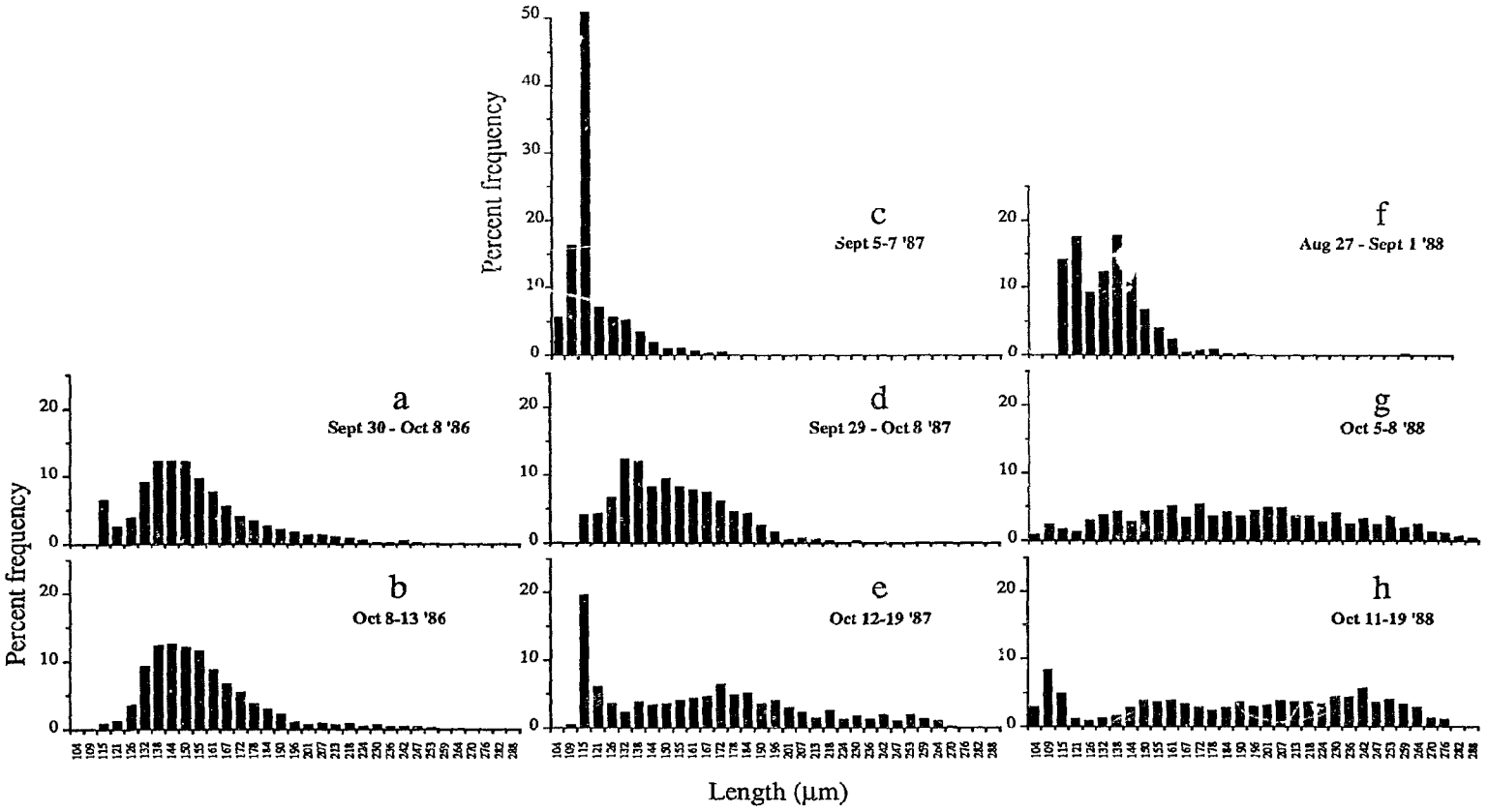

Figure 3.6. Temporal changes in the length frequency of sea scallop larvae on Georges Bank. Each histogram is based on a total of 370-4600 measurements from stations where sea scallop larvae were present. (a) - (b): Northern Flank, Northeast Peak, and Well Mixed area during two sampling periods in 1986; (c) - (e): same areas during three sampling periods in 1987; (f) - (h): Northern Flank and part of Northeast Peak during three sampling periods in 1988.

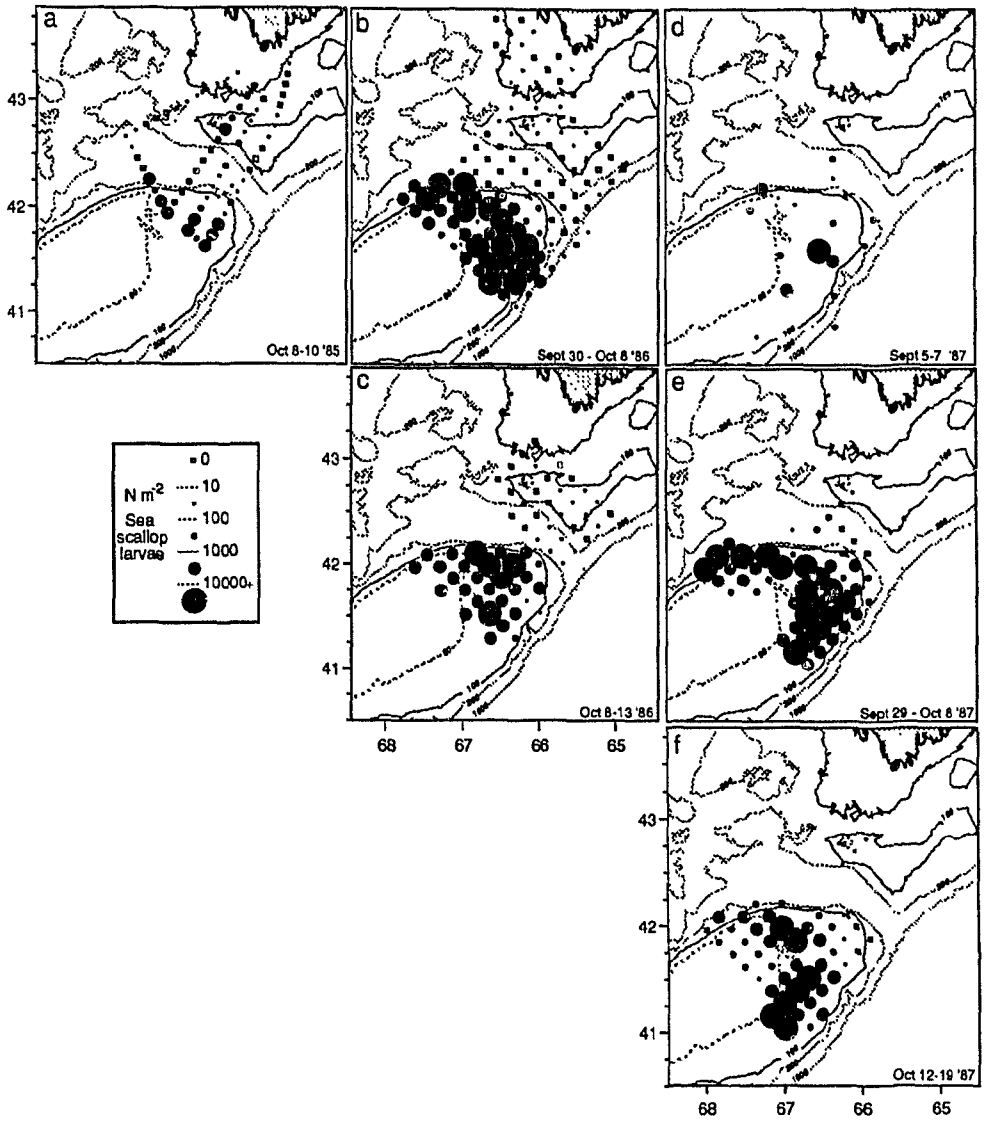

Figure 3.7. The abundance of sea scallop larvae in the Georges Bank region as estimated by plankton surveys. Shown are expanding symbol plots of the number of sea scallop larvae m^{-2} for six sampling periods from 1985-1987. (a): 1985; (b)-(c): 1986; (d) - (f): 1987.

Table 3.4. Abundance of sea scallop larvae in the Georges Bank region. Shown is mean and coefficient of variation (%, in brackets) of the number of larvae m^{-2} for areas depicted in Fig. 3.5. Mann-Whitney comparisons were done between areas within years. Areas with the same superscripted letters had distributions which were not significantly different using a P value of 0.05/N, where N is the number of comparisons within the year. [1]insuffucient number of stations for comparison. Areas are as follows. 1: Northern Flank & Northeast Peak 1; 2: Northeast Peak 2; 3: Well Mixed; 4: Fundian Channel; 5: Slope southeast of Browns Bank and off Georges Bank; 6: Browns Bank; 7: German Bank and Lurcher Shoals.

	Survey period					
	1985	1986		1987		
Area	Oct 8-10	Sept 30-Oct 8	Oct 8-13	Sept 29-Oct 8	Oct 12-19	
1	1273 a b (152)	7929 a (123)	6868 a (87)	9069 a b (130)	2161 a	(167)
2	2225 a (71)	20080 a (131)	4260 a (93)	16757 a (160)	6646 a	(115)
3	- -	3183 a (95)	2499 a (82)	1880 b c (155)	1201 a	(105)
4	17 c (135)	2 c(200)	22 b (118)	169 c (158)	-	-
5	- -	161 b (181)	- -	- -	-	-
6	240 b c (190)	40 b c(223)	5 b (140)	5[1] (140)	-	-
7	23 c (117)	63 b c(205)	- -	- -	-	-

areas was positively related to fishery landings as a coarse index of spawning biomass (Fig. 3.8).

A comparison of the length frequencies of larvae from Georges Bank, the Fundian Channel, and Browns Bank during 1985 and 1986 suggests that Browns Bank was distinct from the other areas. In 1985 (Fig. 3.9a-c) larvae greater than ca 207 μm were much less frequent on Browns than on Georges Bank. In 1986 the situation was reversed -- the percentage of large larvae was greater on Browns Bank than on Georges Bank (Fig. 3.9d-f). In both years the length frequency of larvae in the Fundian Channel was more similar to Georges Bank than Browns Bank. Small larvae (< 124 μm) were present on Browns Bank during both 1985 and 1986 (Fig. 3.9c,f).

On Georges Bank itself larval abundance was significantly lower in the Well Mixed Area only during the first part of the October 1987 survey (Table 3.4). Visual inspection indicates that larvae were less abundant in the centre of the Well Mixed Area and on the extreme northeast part of the bank (Fig. 3.7).

3.5.2 Abundance of different sized sea scallop larvae

The mean numbers of sea scallop larvae m^{-2} in five size groups for Georges Bank (exclusive of the Well Mixed Area) are shown in Table 3.5. The smallest size group (<124 μm) was usually less abundant than the second size group (124-158 μm), suggesting that the correction for undersampling of the smallest larvae by the 85 μm nets (used in each year except 1988) was only partially successful. The last size group (> 233 μm) includes larvae ca 4-6 weeks in age that are capable of metamorphosis and settlement. This size group had the lowest abundance, ranging from 44 to 497 larvae m^{-2} (Table 3.5).

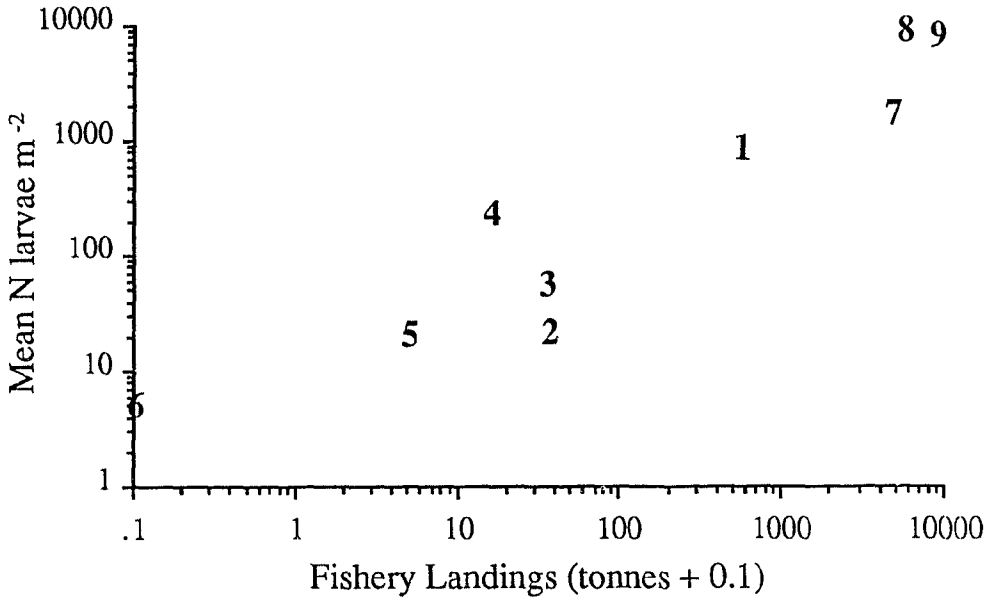

Figure 3.8. Mean abundance of sea scallop larvae (n m^{-2}) in the Georges Bank region versus fishery landings of sea scallops for different area/time combinations. **1**: Bay of Fundy Oct. 1985 (from Tremblay and Sinclair 1988); **2-3**: German Bank/Lurcher Shoals area, Oct. 1985 and Oct. 1986; **4-6**: Browns Bank, Oct. 1985-1987; **7-9**: Georges Bank, Oct. 1985-1987.

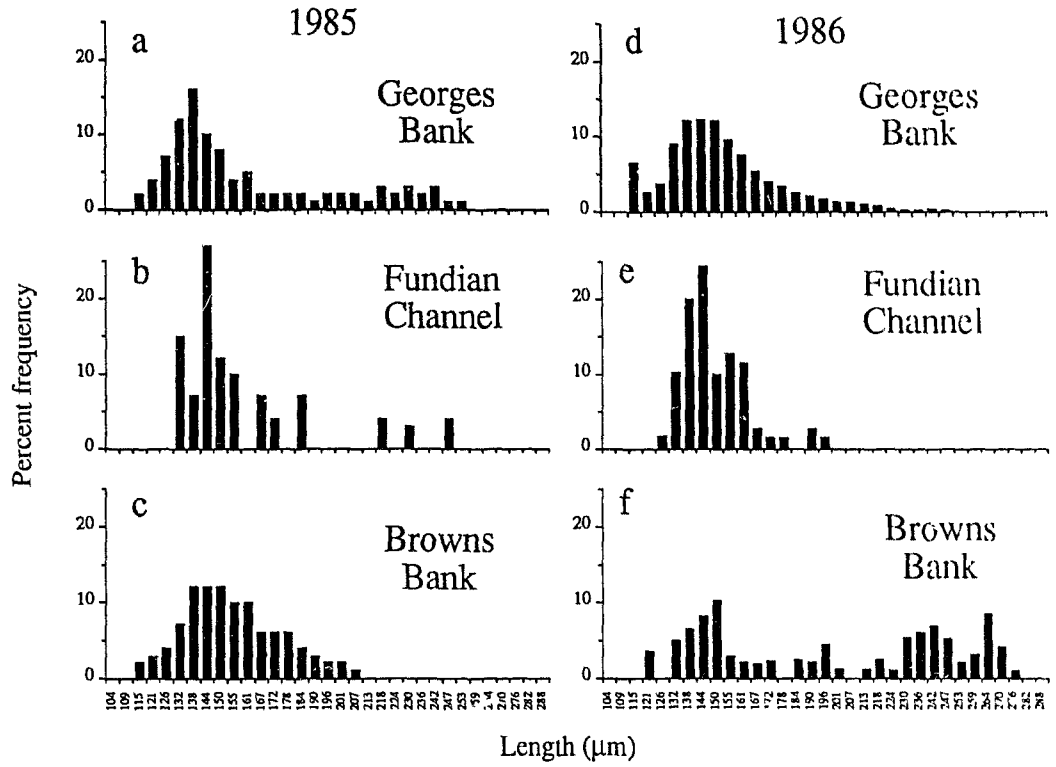

Figure 3.9. Area differences in the size structure of sea scallop larvae in the Georges Bank region. (a) - (c): Georges Bank, the Fundian Channel and Browns Bank in 1985; (d): Georges Bank, Sept 30 - Oct. 8, 1986; (e) -(f): the Fundian Channel and Browns Bank during the same period in 1986. Each histogram based on a total of 27-4600 length measurments of scallop larvae.

Table 3.5. Abundance of sea scallop within different length groups on Georges Bank (Northern Flank and Northeast Peak 1 and 2 - see Fig. 3.5). Shown is the mean number of larvae m^{-2}.

Survey period	Length (μm)				
	< 124	124-158	159-193	194-233	> 233
Oct 2-6 '86	1342	8857	3927	1047	155
Oct 8-11 '86	103	3069	1548	256	86
Oct 2-6 '87	1343	9320	5520	515	44
Oct 13-19 '87	1493	895	1499	874	497

3.5.3 Patches of sea scallop larvae on Georges Bank

3.5.3.1 1986 survey

Shaded contour plots of the abundance of sea scallop larvae are shown for the two sampling periods in 1986 in Fig. 3.10. The time separating the midpoints of the two periods was 5.5 d. Several dense patches (> 10,000 m^{-2}) of larvae were present during both sampling periods (Fig. 3.10a,b). The elliptically shaped patches were located mainly in areas with bottom depths of 60-100 m, but during the initial sampling period the patches extended beyond 200 m on the Northern Flank (Fig. 3.10a).

In relation to the concentrations of adults surveyed in 1986 (Fig. 3.2b), the patches of larvae were more towards the centre of Georges Bank. Patches a1 and a2 (Fig. 3.10) were in U.S. waters (Fig. 3.1), which were not part of the Canadian adult scallop survey in 1986 (Fig. 3.2b). There are fishable concentrations of scallops in this part of the Northern Flank (Fig. 3.1), but the landings there are usually lower than either further to the east on the Northern Flank, or in the South Channel (Sinclair et al. 1985).

There was considerable change in the distribution and extent of the larval patches between the two sampling periods (Fig. 3.10 a,b). Patch b1, on the northern half of Georges Bank, was further to the east than patches a1 and a2, which were observed earlier. A patch in the position of b1 is consistent with the advection of patches a1 or a2 in the direction of the residual current during the period separating the two sampling periods (Fig. 3.4). The largest patch observed during the Oct 2-6 period (a3), was either much reduced or absent during the Oct. 8-11 period. Patch b2 could represent a small remnant of patch a3, and is southwest of patch a3 as might be expected of the residual circulation (Fig. 3.4).

The spatial distributions of different size groups of larvae differed in detail but were similar overall. Within each survey small larvae (Fig. 3.10c, d) and large larvae (Fig. 3.10e, f) had concentrations in the same areas. The abundances of these two size groups

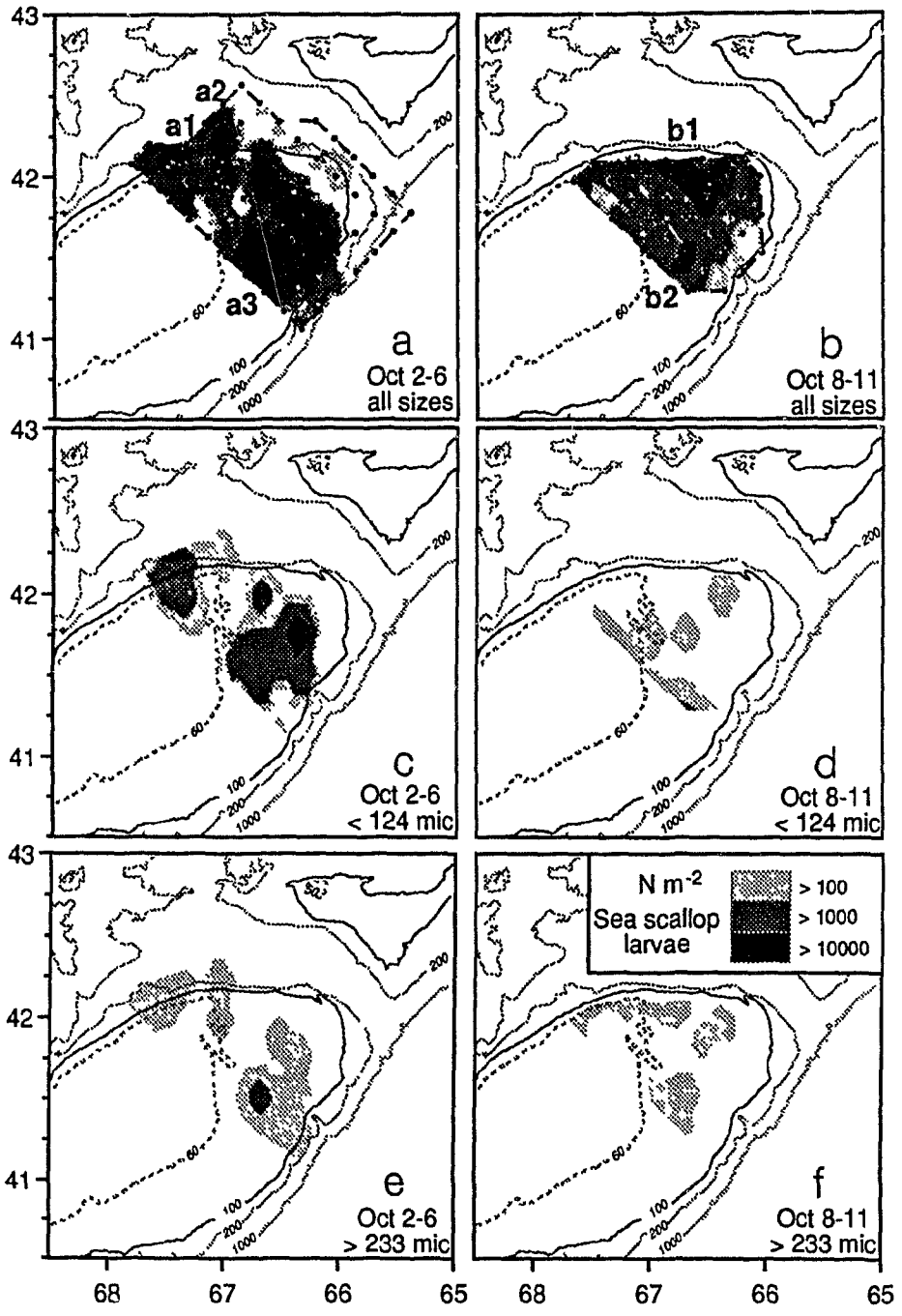

Figure 3.10. Shaded contour plots of the abundance of sea scallop larvae during two sampling periods in 1986. (a)-(b): all sizes of larvae during the two periods. High density patches of larvae (> 10,000 larvae m^{-2}) are labelled. Shown are station locations (dots) and total area sampled (dashed line). (c)-(d): small larvae (estimated to be 6-10 d old); (e)-(f): large larvae (capable of metamorphosis and settlement). mic: μm

were significantly correlated with one another, as were the abundances of all size groups (Table 3.6). The length frequency distributions of larvae at stations comprising the patches indicated in Fig. 3.10 indicate remarkable spatial coherence in size structure for the smaller patches, with clear differences among patches (Fig. 3.11). Within patches a1, a2, and b1 the length frequencies were very similar (Fig. 3.11). The length frequency distributions of larvae at stations within the larger patch (a3) were more heterogenous, but three patterns are recognizable: stations with a major mode between 130 and 160 μm, stations with an additional major mode at 115 μm, and stations with flat length frequency distributions (Fig. 3.11).

It was suggested above that patch b1 could have arisen from movement of patches a1 or a2 in the direction of the residual circulation. Comparison of length frequencies and estimates of growth rates are consistent with this interpretation. The length mode of patch b2 (155 μm) is 17 μm greater than the length mode of patch a2, and the time interval between the sampling of patches a2 and b1 was 4 d (Fig. 3.11). This would suggest a larval growth rate of 4.2 μm d^{-1}, consistent with the growth rate in hatcherys (section 3.4.5). Compared to patch a1, the length mode of patch b1 is 23 μm greater, and the time interval between sampling patches a1 and b1 was 3.5 d. If then patch b1 and patch a1 are linked, a larval growth rate of 6.6 μm d^{-1} is estimated, which is only slightly higher than that expected from hatchery growth rates (section 3.4.5). Other interpretations of these data are possible, but the linkage between patches is plausible.

3.5.3.2 1987 survey

Shaded contour plots of the abundance of sea scallop larvae are shown for the two sampling periods in 1987 in Fig. 3.12. The time separating the midpoints of the two sampling periods was ca 12 d, more than double that separating the two sampling periods in 1986, and station coverage was less than in 1986. For these reasons no attempt is made to link the patches evident during the two sampling periods in 1987.

Table 3.6. Correlations (Spearman) between abundances (n m^{-2}) of different sized scallop larvae in 1986 and 1987. N=74 for 1986; N=84 for 1987. ** $P < 0.01$; * $P < 0.05$.

1986	Length of larvae (µm)				
	< 124	124-158	158-193	193-233	>233
< 124	1.00				
124-158	0.38**	1.00			
158-193	0.26*	0.90**	1.00		
193-233	0.35**	0.81**	0.86**	1.00	
>233	0.34**	0.65**	0.67**	0.73**	1.00

1987	Length of larvae (µm)				
	< 124	124-158	158-193	193-233	>233
< 124	1.00				
124-158	0.61**	1.00			
158-193	0.56**	0.87**	1.00		
193-233	0.53**	0.50**	0.75**	1.00	
>233	0.31**	0.14	0.38**	0.69**	1.00

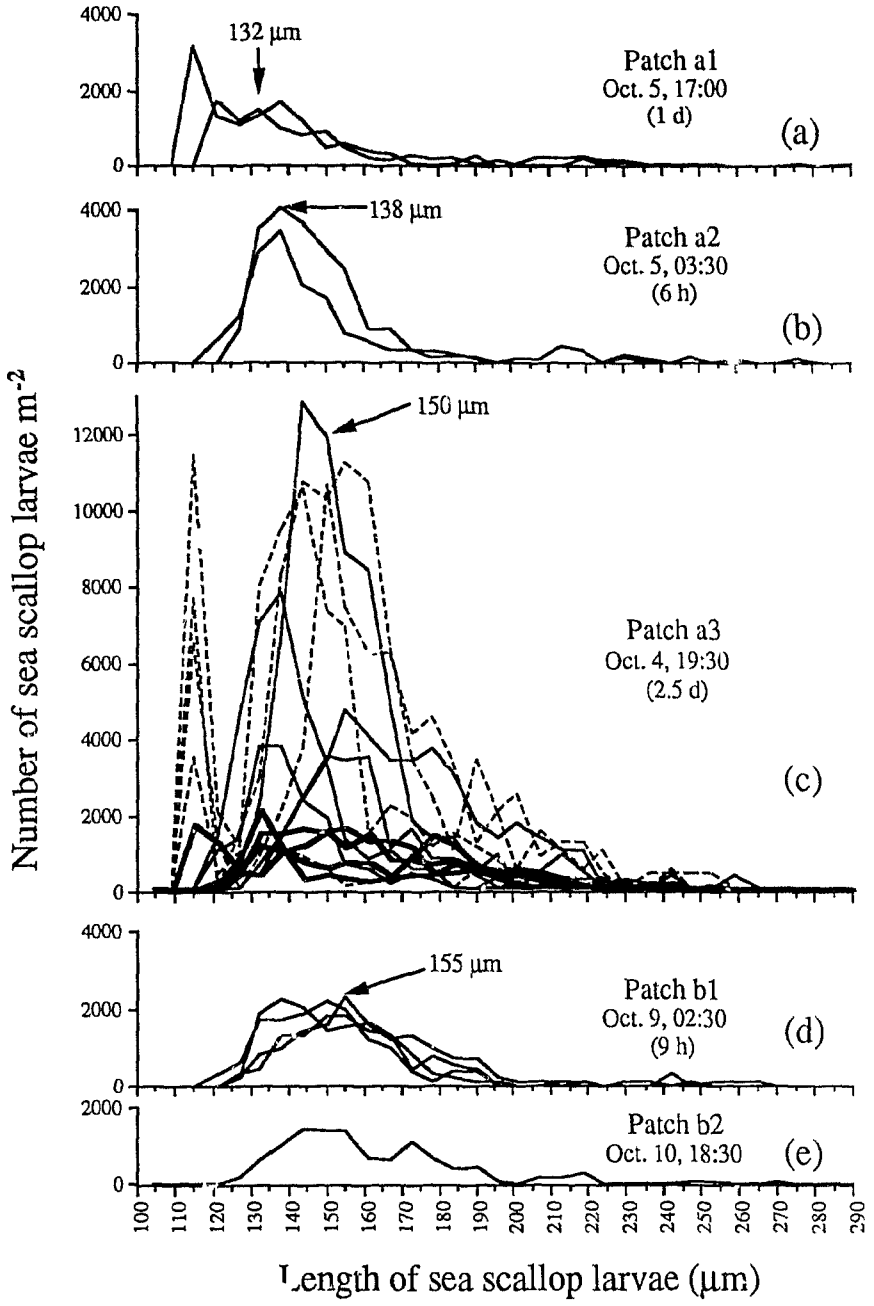

Figure 3.11. Length frequency of sea scallop larvae at stations within high density patches in 1986 (see Fig. 3.10). (a) Patch a1. Text shows date and time of midpoint of sampling of stations, and time over which sampling occurred. (b)-(e): Patches a2, a3, b1 and b2, with same information as given in (a). For each patch the major length mode of the combined data is highlighted with an arrow. Different line patterns in (c) show the 3 length frequency distributions within the large patch a3 (see text).

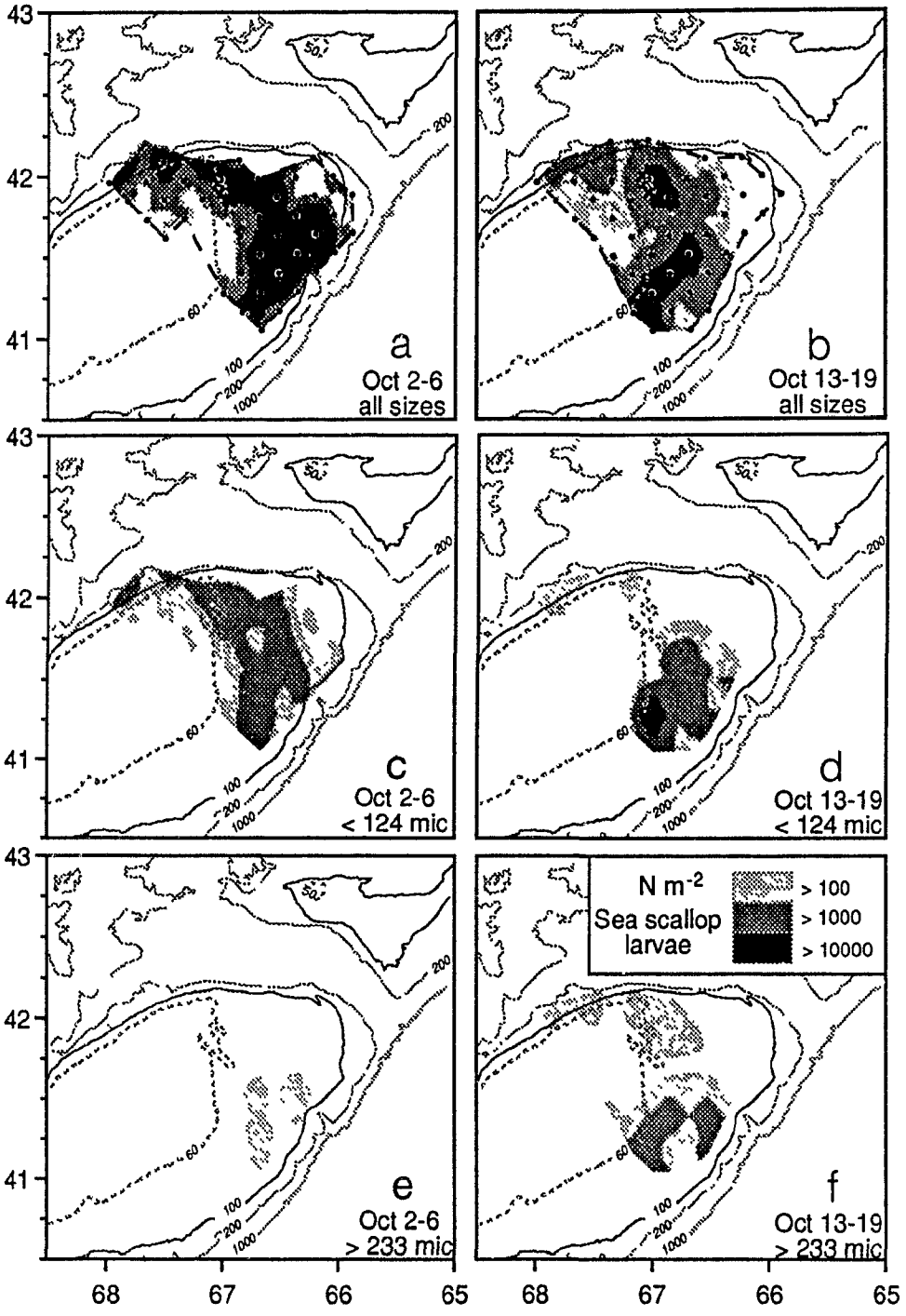

Figure 3.12. Shaded contour plots of the abundance of sea scallop larvae during two sampling periods in 1987. (a)-(b): all sizes of larvae during the two periods. Shown are station locations (dots) and total area sampled (dashed line). (c)-(d): small larvae (estimated to be 6-10 d old); (e)-(f): large larvae (capable of metamorphosis and settlement). mic: μm.

In general the distribution of sea scallop larvae in 1987 (Fig. 3.12a, b) was very similar to that of 1986. The distribution of larvae again overlapped that of the fished aggregations (Fig. 3.2e), but the larvae were more concentrated towards the centre of Georges Bank. As in 1986 there was a reduction in patch size between the 2 sampling periods. Again the spatial distributions of different size groups of larvae were similar overall (Fig. 3.12 e,f), and the abundances of different size groups were positively correlated (Table 3.6).

Unlike 1986, small larvae were widespread during the initial period in October 1987, but were intensely concentrated in the southern most part of the study area between Oct 13-19 (Fig. 3.12d). This indicates that some scallop spawning occurred as late as the first week of October. In spite of this pulse of small larvae, the length frequency distributions of scallop larvae in 1987 (Fig. 3.6d,e) indicate a clear shift to larger sizes from early to mid-October.

3.6 Discussion

3.6.1 The timing of spawning on Georges Bank

Since scallops eggs are externally fertilized, both mate proximity and spawning synchrony may influence reproductive success and ultimately recruitment (Sastry 1979, Langton et al. 1987, Paulet et al. 1988, Caddy 1989). Individual beds of sea scallops on Georges Bank can at times release most gametes almost synchronously (Posgay and Norman, 1958). Some evidence for this from the current study comes from the dense, highly localized concentrations of small larvae during some surveys (Figs. 3.10c, 3.12d), but the scale of this study cannot resolve how synchronous spawning is within beds. Scallops on Georges Bank may 'dribble spawn' as in coastal Newfoundland (Naidu 1970) and Maine (Langton et al. 1987), or may spawn synchronously more than once.

Depending upon seasonal variability in factors such as temperature, circulation, food, and predation, these different spawning strategies may affect the probability of larval survival.

The scale of the present study is best for addressing the timing of sea scallop spawning on Georges Bank as a whole. Shifts in the size frequency distribution and abundance of larvae in 1987 and 1988 indicate that peak spawning was in the second half of September, but that some spawning occurred as early as mid-August and as late as early October. Spawning of most other populations of sea scallops also occurs within this time period (Dickie 1955, Naidu 1970, Robinson et al. 1981, MacDonald 1984) although there appears to be an additional early summer spawning in some inshore populations (Naidu 1970, Savage 1980). An earlier spawning on Georges Bank may occur, but gonad indices suggest that it is of secondary importance, and variable among years (G. Robert, Dept. of Fisheries and Oceans, Halifax, pers. comm.).

The fall spawning of sea scallops on Georges Bank coincides with the period when retention and survival of larvae should be maximized. During September physical residence time is near the annual maximum, increasing the probability that larvae spawned on Georges Bank will remain there. Temperature is also near the annual maximum, which will shorten larval development and the period of the life history when mortality rates are presumably at their highest. A coincidence between the timing of the larval period, warm temperatures and high physical retention was also noted for Bay of Fundy sea scallops (Dickie 1955). He suggested that good recruitment to the fishery occurred if temperatures during the larval period were higher than average, increasing both larval retention and survival.

3.6.2 Retention of sea scallop larvae on Georges Bank

Sea scallop larvae appear to be largely retained on the northeast part of Georges Bank. Sampling in the deep water north of the bank west of about 67° longitude was too sparse to evaluate retention for that part of the bank. Inevitably some scallop larvae are lost

from Georges Bank, but for the northeast part of Georges Bank (east of about 67° longitude), these losses would appear to be small. First, few larvae were found in the middle of the Fundian Channel. Plankton samples extended down to 200 m over the edge of the bank, and larvae should have been collected if present. On the Northern Flank dense patches of sea scallop larvae do extend beyond the edge of the bank (200 m) but such patches are not necessarily lost from Georges, since the Northern Flank front moves back and forth in this area (Chapter 5), and the mean cross-frontal circulation (north-south) is actually directed on-bank (Fig. 3.4). Station coverage in the slope waters south of the bank was low, but larval abundance generally declined beyond the 100 m contour of the Southern Flank (Fig. 3.7b-f).

Further evidence for larval retention on Georges Bank is the correlation between mean larval abundance and the index of spawning biomass (fishery landings) for each area (Fig. 3.8). The observed correlation is surprising given that fishery landings are a crude index of spawning biomass. No such correlation would be expected if there was large scale export of larvae from Georges Bank to Browns Bank. The last line of evidence indicating limited export of larvae from Georges Bank is the distribution of larval length frequencies, which differed between Georges and Browns Banks.

Like sea scallop larvae, the larvae of several species of fish are found on Georges Bank and Browns Bank, but not generally between (haddock larvae: Walford 1938, Smith and Morse 1985, Hurley and Campana 1989, herring larvae: Schnack and Stobo 1973, Bumpus 1976, cod larvae: Hurley and Campana 1989). Several studies have suggested that larval behavior may be involved in the retention of fish larvae on Georges Bank or the surrounding area (Iles 1971, Iles and Sinclair 1982, Stephenson and Power 1988, Lough and Bolz 1989). The fact that sea scallop larvae are associated with the pycnocline may enhance retention, because current speed declines with depth. However sea scallop larvae do not appear to 'use' the vertical shear through vertical migration (Chapter 2), and

therefore the physical retentiveness of Georges Bank (Loder et al. 1988) is probably the primary factor determining larval retention there. Swimming behavior of other more mobile larvae may enhance retention, but such behavior is probably of secondary importance. Selection for behaviors which enhance retention of planktonic larvae (Burton and Feldman 1982) may not be necessary for Georges Bank.

3.6.3 Distribution of scallop larvae on Georges Bank and water movement

Some sea scallop larvae must be transported in the direction of the residual circulation on Georges Bank, given (i) the strong residual circulation on the Northern Flank, and (ii) sea scallop larvae do not undertake extensive vertical migrations to utilize current shear (Chapter 2). Evidence that such transport occurred during the present study is only indirect. Consistent with larval transport are the inferred links between patches during successive sampling periods in 1986, but such links are dependent on the following assumptions: (i) that growth rates on Georges Bank are similar to hatchery-reared larvae; and (ii) that patches of larvae maintain some integrity over a 4-6 d period in spite of the dynamic circulation on Georges Bank. These assumptions are reasonable, but other interpretations of the 1986 data are possible. Changes in the distribution and abundance of larvae during October 1987 do not bear directly on the question of larval transport, because of the greater number of days separating the 2 sampling periods.

The evidence linking patch movements and the residual circulation in 1986 may be as strong as can be expected from this type of study given that (i) groups of larvae appear to be spawned at different times and in different areas of Georges Bank, making tracking of individual patches difficult, and (ii) the residual circulation depicted in Figs. 3.3 and 3.4 represents mean conditions. Strong northeast winds are common during the autumn period, and over periods of a few days, near-surface drifters (10 m) can travel in a direction opposite to the mean current (K. Drinkwater, Bedford Institute of Oceanography, pers. comm.). Such events will contribute to variability in the distribution of sea scallop

larvae over periods of a few days to a week but over the 4-6 weeks of the larval period, net dispersal will probably be in the direction of the residual currents.

Other evidence for transport of larvae in the direction of the residual circulation is the observation of high concentrations of larvae in the northwestern part of the sampling area (Figs. 3.10, 3.12), where adult scallop concentrations are thought to be low, and strong residual currents are directed eastward (Fig. 3.4). These larvae may have originated upstream, in the South Channel or on the southeast part of the Georges Bank.

Comparison of the length frequencies of larvae at stations within the 1986 patches (Fig. 3.11) indicates there is strong coherence in size structure over distances of 20-40 km (10-20 nautical miles) and at time scales of less than a day (Fig. 3.11a,b,d). Tidal mixing must contribute to this coherence, given the size of the tidal ellipses and speed of the current (section 3.3). Over distances of 60-80 km (30-40 nautical miles) and time scales of several days, the coherence in length frequencies breaks down, and strong differences in size structure can be expected (Fig. 3.11c).

The positive correlations between the abundances of different sized larvae (Fig. 3.10, 3.12, Table 3.6) indicates that the factors affecting spatial distribution were not size specific, and that differences in time and place of larval origin were secondary to the processes which affect distribution one to several weeks after spawning. Physical processes may aggregate all larvae in some way, or the survival rate of larvae may be greater in certain areas of Georges Bank. A physical aggregation mechanism is consistent with observations that different sized scallop larvae have similar vertical distributions (Chapter 2), and thus should be subject to the same currents.

The lower abundance of larvae in the centre of the Well Mixed Area may be due to a lower supply of larvae, or to lower larval survival. The low abundance of adults in the Well Mixed Area suggests local supply would be low but some immigration of sea scallop larvae into the centre of the bank cannot be ruled out. Larval gadoids move into shallower

waters during spring, perhaps aided by on-bank currents near the bottom and dispersion by rotary tidal currents (Lough and Bolz 1989).

3.6.4 Implications for population structure and the recruitment process

The sea scallop larvae which seed the productive Northeast Peak may originate from all over Georges Bank. Some may originate in the South Channel or on the southeast part of the Georges Bank. Other sea scallop larvae may originate on the Northeast Peak and return there after making a complete circuit of the bank. Given the circulation time of 33-55 d, and a larval period of 4-6 weeks, this scenario is probable. Other larvae which originate on the Northeast Peak may be displaced only a few 10's of km if they are spawned towards the centre of the bank, where currents are lower (Fig. 3.4). The actual dispersal of a given patch of larvae on Georges Bank is probably a complex function of hatching location and factors which cause variation in the current field over a period of weeks (e.g. wind events, spring-neap tidal cycle). A similar situation occurs elsewhere. In the Bay of Fundy, a gyre in the outer part of the bay retains some scallop larvae, while other larvae appear to be transported to the inner bay and then returned to the outer bay by the residual circulation (Tremblay and Sinclair 1988). Haddock larvae on Browns Bank can be either physically retained, or transported to the inner Scotian Shelf (Campana et al. 1989).

Mixing among the three fishing areas on Georges Bank (the Northeast Peak, the southeast part and the South Channel) is probably not complete, but is likely sufficient to affect recruitment levels on an annual basis. Modelling of stock and recruitment dynamics on Georges Bank also suggests that considerable exchange occurs among the fished aggregations of scallops (McGarvey 1990). If the abundance of scallop larvae is correlated with recruitment to fishable sizes, then Georges Bank may best be characterized as a single recruitment unit for sea scallops, a concept which has implications for the management of this species which straddles the Canadian and U.S. sides of Georges Bank.

The supply of pelagic larvae can determine the structure of some intertidal invertebrate communities (Connell 1985, Gaines and Roughgarden 1985, Sutherland 1987), and is thought to limit the abundance of some marine fish (e.g. Victor 1986) and scallops (Sause et al. 1987). If on Georges Bank scallop recruitment is linked to larval supply, then reductions in the spawning biomass of scallops in one area could affect recruitment elsewhere on the bank.

It is probable that larval supply limits scallop recruitment in offshore areas such as Browns Bank, where recruitment to fishable sizes is low and sporadic. On Browns Bank local production of larvae is low due to the low spawning biomass, and immigration of larvae from other areas is also low. Those larvae which are produced there have a high probability of being lost, because physical retention there is weak (Loder et al. 1988).

On Georges Bank, a rough estimate of the seasonal production of late stage sea scallop larvae suggests that subsequent mortality is high. On the Northern Flank and Northeast Peak (areas 1 and 2 in Fig. 3.5) the mean abundance of late stage sea scallop larvae ranged from ca 40 to 500 individuals m^{-2} over the course of this study (Table 3.5). Given that this range of abundance occurs for at least 21 d, and that the average duration of this part of the larval period is 7 d, a coarse estimate of the total annual production of late stage larvae for this part of Georges is 120-1500 individuals m^{-2} (21 d * 40 m^{-2}/7, 21 d * 500 m^{-2}/7). This is much greater than the maximum density estimates for recent recruits within scallop beds on Georges Bank (1-5 individuals m^{-2} - section 3.2). Substantial mortality must occur during metamorphosis, settlement, and the early juvenile stages.

Processes associated with larval settlement must be important to the population structure of sea scallops. Hedgecock (1986) posed a series of questions to determine the effectiveness of pelagic larvae as agents of gene flow among populations. The first is whether migration of individual larvae is successful. Emigration of larvae from Georges Bank to the Gulf of Maine and Scotian Shelf, appears limited, but extensive exchange of

larvae does appear to occur among aggregations on Georges Bank. To better understand its importance, larval exchange should be quantified by incorporating the biological data presented here into a physical model. The next question posed by Hedgecock (1986) is whether dispersing larvae successfully survive settlement and actually reproduce, or become 'vagrants' in the sense of Sinclair (1988). Answering this difficult question hinges on the development of new sampling techniques and approaches.

3.7 Summary

The horizontal distribution of sea scallop larvae on the northeast part of Georges Bank and adjacent waters is described for late summer and fall from 1985 to 1988. The pattern of larval dispersal is inferred from the distribution of larvae, their source, and the residual circulation. The evidence indicates that sea scallop larvae are largely retained on the northeast part of Georges Bank: (i) few larvae were collected off the edge of the bank; (ii) the mean abundance of larvae for different areas was correlated with a coarse index of spawning biomass (fishery landings); and (iii) the length frequency of larvae differed between Georges Bank and the surrounding area. Scallop larvae appear to be retained primarily by physical processes. Swimming behavior of other more mobile larvae may enhance retention, but such behavior is probably of secondary importance for Georges Bank. On other banks in the area, the supply of sea scallop larvae may be limited by lower physical retention.

On Georges Bank there is strong coherence in size structure over distances of 20-40 km and at time scales of less than a day, probably due to strong tidal mixing. The abundances of different sized larvae were positively correlated, indicating that the factors affecting abundance were not size specific. Changes in the position and size structure of high density larval patches suggest that some sea scallop larvae are transported in the direction of the residual currents, and that larval exchange among adult scallop

aggregations on Georges Bank probably occurs. The larvae which seed the productive Northeast Peak may originate locally or on other parts of Georges Bank, and thus the bank may be a single recruitment unit for sea scallops.

A coarse estimate of the annual production of late stage larvae on the Northern Flank and Northeast Peak is 120-1500 m^{-2}. Since the densities of settled scallops 1-2 yr later are at most 5 m^{-2}, considerable mortality must be associated with metamorphosis, settlement, and the early juvenile period.

Chapter 4

Sea scallop *Placopecten magellanicus* larvae on Georges Bank: distribution across the frontal zone of the Northern Flank

4.1 Introduction

The major aggregations of sea scallops in the Gulf of Maine area tend to occur in the vicinity of frontal zones between vertically well mixed and stratified waters (Sinclair et al. 1985, Horne et al. 1989). The mean location of these shallow sea frontal zones is predictable because of the dependence of vertical mixing on surface heat flux, water column depth, and tidal current strength (Simpson and Hunter 1974, Garrett et al. 1978, Pingree 1978, Loder and Greenberg 1986). Wind mixing may also affect the location of frontal zones in the Gulf of Maine region (Loder and Greenberg 1986).

Fronts are characterized by strong gradients in physical and biological variables and may play an important role in the ecology of planktonic larvae of continental shelf species. Components of the plankton which can be more concentrated, abundant or productive around shallow sea fronts include phytoplankton and crustacean zooplankton (Pingree et al. 1974, Pingree et al. 1976, Pingree 1978, Bowden 1981, Holligan 1981, Fournier et al. 1984, Holligan et al. 1984, Le Fèvre 1986, Richardson et al. 1986, Kiørboe and Johansen 1986, Kiørboe et al. 1988), and the planktonic larvae of invertebrates and fish (Kiørboe et al. 1988). Many other species are largely confined to either the mixed or stratified side of the front (Boucher et al. 1987, Taggart et al. 1989, Perry et al. 1990).

Major questions related to the effects of frontal processes on zooplankton and planktonic larvae include (i) whether increased biomasses result from enhanced rates of production or survival within the frontal zone, or from physical accumulation there, and (ii) the role of swimming behavior in determining zooplankton distribution in relation to frontal features. There are observations of apparently passive convergence of

zooplankton at fronts (Pingree et al. 1974, Le Fèvre 1986), as well as increased production (Kiørboe et al. 1988). The species-specific nature of the distributions of zooplankton and larval fish in relation to fronts suggests that swimming behavior may be important (Boucher et al. 1987, Taggart et al. 1989, Perry et al. 1990), and the 'use' of frontal circulation by plankters to effect retention has been suggested (Wroblewski 1982, Iles and Sinclair 1982, Sinclair et al. 1985).

Broadscale surveys of the October abundance of sea scallop larvae on Georges Bank indicate that larvae are more abundant on the Northern Flank than in either the shallow well mixed zone or the deep stratified waters of the Gulf of Maine (Chapter 3). Cross-frontal exchange of these larvae appears to be low, but the scale of sampling was too coarse to establish whether a decline in larval abundance was associated with any particular feature of the frontal zone (section 4.2). Sea scallop larvae have the ability to vertically migrate (Chapter 1), but on Georges Bank this behavior appears to have limited effect on their vertical distribution (Chapter 2). On the Northern Flank, sea scallop larvae are found in the upper 40-50 m, which usually corresponds to temperatures of 10 to 13 °C (Fig. 2.5). Sea scallop larvae are often most aggregated within the region of the pycnocline, and vertical differences in the centre of mass (ZCM) of larvae are associated with differences in pycnocline depth. An interaction between vertical migratory behavior of sea scallop larvae and current shear (Sinclair et al. 1985) cannot be ruled out, but seems unlikely.

The objective of the present study is to relate the abundance of sea scallop larvae to the frontal zone on the Northern Flank of Georges Bank during October. Physical processes at the front may affect the distribution of sea scallop larvae directly, or gradients in physical or biological features associated with the front (e.g. temperature, food) may affect the growth and survival of sea scallop larvae. Alternatively, the abundance of scallop larvae within the frontal zone may be no different from that of other parts of

Georges Bank. This study was part of a larger effort (Georges Bank Frontal Study) directed at understanding the physical and biological dynamics of the frontal zone.

4.2 Characteristics of the Georges Bank frontal zone

From spring to autumn, a transition from tidally well mixed to more stratified waters occurs in a ring around the central shallow area on Georges Bank. Well defined features of the front include a sea-surface temperature gradient during summer, which is often apparent in satellite images (Yentsch and Garfield 1981, Loder and Greenberg 1986), and a subsurface temperature front intersecting the bottom at depths of 75-175 m. The latter feature corresponds to the transition from Georges Bank Water to Gulf of Maine Intermediate Water and may to be due to factors other than tides (Flagg 1987).

The different features of the Georges Bank frontal zone have led to different definitions of its location. It has been defined with the Simpson and Hunter (1974) stratification parameter (Garrett et al. 1978, Loder and Greenberg 1986), the extent of density stratification (Horne et al. 1989), and the horizontal gradients in surface temperature (Yentsch and Garfield 1981), and bottom temperature (Lough and Trites 1989). Horne et al. (1989) emphasize that the the Georges Bank tidal front should be thought of as occurring as a zone of 10-40 km wide, rather than a precise location. Defining the frontal zone as the area where the density difference between the surface and 50 m is 0.2 to 1.5 sigma-t units, the front is diffuse on the eastern part of the bank but intense on the Northern Flank, due to the rapid transition from shallow well mixed waters to the deep stratified waters of the slope (Fig. 4.1). In the present paper the the vertical gradient in temperature (as a proxy for density) is used to distinguish mixed and stratified waters.

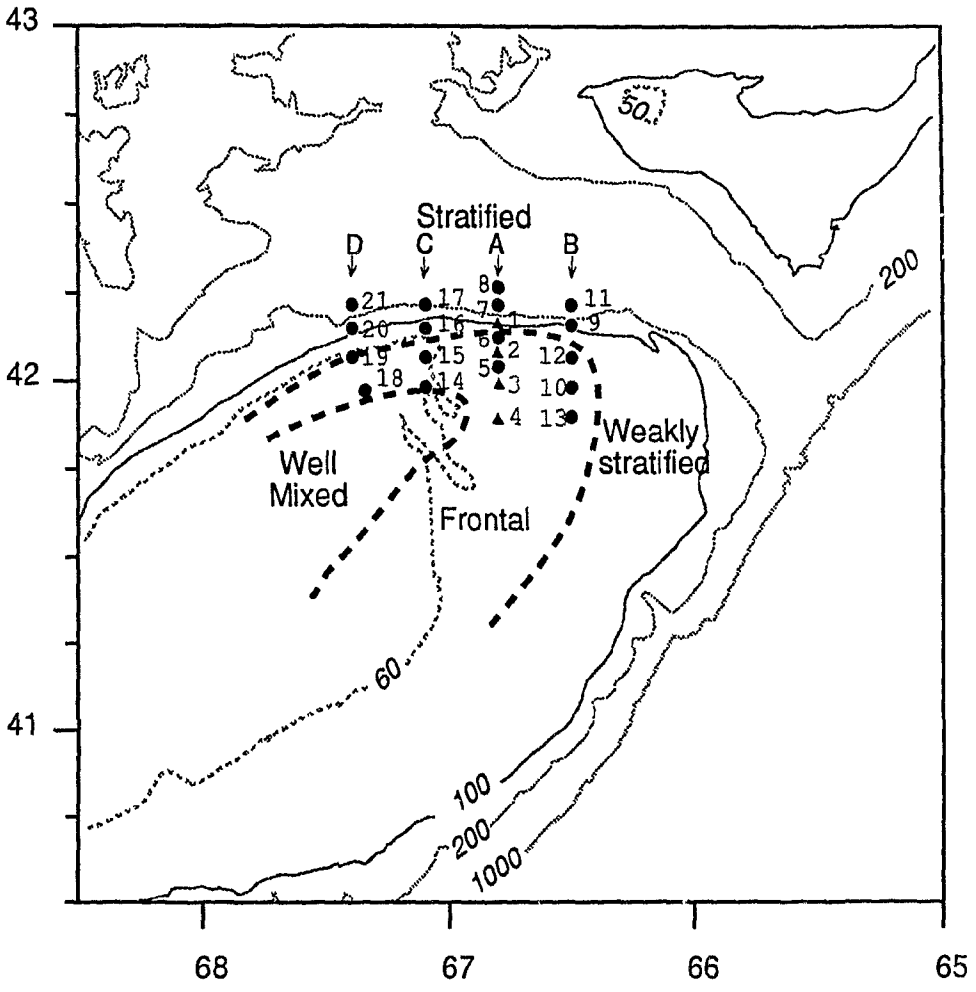

Figure 4.1. Map of Georges Bank showing sampling locations. Plankton samples were obtained at stations 1-21 on Lines A-D. Current meters were moored at stations 1-4 (triangles). The July location of the frontal zone (defined as the zone where the density difference between 0 and 50 m ranges from 0.2 to 1.5 sigma-t units; Horne et al. 1989) is between the dashed lines.

Among the potential mechanisms for physical exchange across the frontal zone are the residual circulation, baroclinic eddies, and changes in the frontal position due to the spring-neap tidal cycle (Loder and Platt 1985, Horne et al. 1989). The movement of internal wave packets through the frontal zone at tidal frequencies adds to the dynamic nature of the circulation. Observational (Butman et al. 1982) and theoretical studies (Loder and Wright 1985) agree that the cross-frontal component of the residual current is much lower and more variable than the strong along-frontal component. Measurements of currents on the Northern Flank during October indicate that the cross-frontal residual current in the upper 50 m is in the on-bank direction (Fig. 3.4).

The front appears to be important to the high primary production of Georges Bank. Phytoplankton biomass is lower in the frontal zone than in the well mixed area, but total primary production and new production (nitrate-based production) are higher in the frontal zone (Horne et al. 1989). Preliminary estimates of the physical transfer of nitrate across the tidal front suggested that various mechanisms could supply about 9% of the total nitrogen demand of the well mixed area during summer (Loder and Platt 1985). More recent estimates indicate that the on-bank flux of nitrate may be 10 times greater (Horne et al. 1989).

4.3 Methods

4.3.1 Sampling

Sea scallop larvae were collected on the Northern Flank of Georges Bank from the RV Lady Hammond from 5 to 19 Oct. 1988 (Table 4.1, Fig. 4.1). As part of the concurrent physical oceanographic study, current meters were moored at stations 1-4 on Line A, the area expected to encompass the maximum on- and off-bank excursions of the front based on previous studies. Sea scallop larvae were sampled at stations 1-8 on Line A, and on Lines B, C, and D to examine the along-frontal variation (Fig. 4.1).

Table 4.1. Transects of the Northern Flank of Georges Bank for the collection of sea scallop larvae. Transect number is consecutive, Line identifies location (see Fig. 4.1). Duration: time from start of transect to completion; Dir: direction of ship on transect. Dates and times are in GMT.

Transect no	Line	Date	Gear	No sta	Start time	Duration	Dir
1	A	5-6 Oct	net	7	23:30	4:40	S
2	B	6 Oct	net	5	07:00	4:10	S
3	D	7 Oct	net	3	10:15	1:15	N
4	C	7 Oct	net	3	13:00	1:20	S
5	A	8 Oct	net	5	02:05	2:40	N
6	A	10 Oct	pump	8	11:25	10:30	S
7	A	10-11 Oct	pump	7	23:00	7:20	N
8	A	12 Oct	net	8	00:25	7:50	S
9	C	12 Oct	net	4	13:10	2:10	N
10	A	19 Oct	net	7	13:30	7:45	S

Sampling for sea scallop larvae was on a 24 h basis, and was to some extent opportunistic, due to weather conditions and the requirements of other parts of the sampling program. Eight transects were completed with plankton nets, and two with a plankton pump. Nets were used when the weather was rough or when time was short. Two nets, each 156 cm in overall length and fitted with NITEX mesh (53 μm), were mounted on a bongo frame with two 40 cm diameter openings. A TSK flowmeter was mounted in the opening of at least one of the nets. The nets were hauled at 0.5-0.8 m sec^{-1} from 5 to 10 m off the bottom to the surface with a maximum tow depth of ca 100 m (see Appendix 3 for details). Gear depth was measured by an electronic meter block, and corrected for wire angle.

The pump system used for sampling scallop larvae (Chapter 2) consists of an electric centrifugal pump with suction hose capable of delivering 250-400 l min^{-1}. Volume is monitored by an in-line paddlewheel flowsensor, and the depth of the pump intake is controlled by a winch operator monitoring the output from a CTD, which is mounted with the pump intake. On deck, the pump outflow was directed first through a coarse mesh net (333 μm) to remove larger particles, and then through an 53 μm mesh net for sample collection. Sea scallop larvae are found mainly between 10 and 45 m (Chapter 2), and to ensure that adequate numbers of sea scallop larvae were obtained, only this depth range was sampled.

Larval samples from the plankton nets were preserved in 4% formalin buffered with sodium borate; those from the pump were stained with Oil Red O (Chapter 5) after fixation in formalin. Formalin-preserved sea scallop larvae were physically separated from the lighter components using a colloidal silica (Tremblay et al. 1987). Sea scallop larvae were then identified and counted using a dissecting microscope. Samples with total number of larvae exceeding ca 300 were split with a Motoda splitter such that a total of at least 200 larvae were counted (see Appendix 1). The lengths of the larvae were measured

in welled slides to the nearest 5.8 μm using an inverted microscope. Those sea scallop larvae in Oil Red O stain were first assessed for lipid content (Chapter 5) and then processed in much the same way as the formalin-preserved larvae.

4.3.2 Physical data.

Temperature, salinity, and current data were obtained from measurements at the moored current meters (stations 1-4), which were removed from the water on Oct. 14. The physical data were processed and made available by the Physical and Chemical Science Branch, Bedford Institute of Oceanography. Temperature and salinity data from the Applied Microsystems CTD, which was mounted on the pump intake frame, were used during sampling, but the current meter data are presented here because they give a synoptic picture across the front. Physical data were unavailable when bongo net samples were done on Lines B to D.

4.3.3 Data analysis

The volume (m^3) measured by the plankton net flowmeters was used to standardize the larval abundance per m^2 of sea surface as follows:

$$N\ m^{-2} = \text{count/volume} * \text{water column depth}$$

where water column depth = the lesser of the station depth, or 100 m. Prior to the above calculation, spurious flowmeter readings (about 10% of all tows) were eliminated to minimize errors in volume estimation. For these samples, volume was estimated from prediction equations developed for tows where the volume was reliably estimated. The length of wire out and the wire angle were used as predictor variables after regression on the volume estimated from the flowmeters (see Appendix 4).

The length measurements done on each sample were used to estimate the number per m^2 or number per m^3 within each 5.8 μm size class from 104 μm to 292 μm.

4.4 Results

4.4.1 Physical conditions in the frontal zone during October

Temperature sections on Line A for periods when sea scallop larvae were sampled are shown in Fig. 4.2. Transects took 2-10 hr to complete (Table 4.1), a time period over which the frontal zone can move appreciably, and therefore two sections are presented for each tidal period closest to the time of sampling -- one when the frontal zone was at its most southerly, on-bank position, and one when it was at its most northerly, off-bank position. The times corresponding to these maximum frontal excursions were determined from the current meter data at stations 2 and 3. When the hourly mean current changed from south to north the frontal zone was near its most southerly position; when it changed from north to south the frontal zone was near its most northerly position.

There was no single isotherm which could be used to define the front, since the transition from mixed to stratified waters was gradual (Fig. 4.2). In the upper 40-50 m, where sea scallop larvae are found, the horizontal temperature gradients were not strong. Most striking in Fig. 4.2 is the decline in on-bank stratification which occurred between 8 and 10 October. During high on-bank stratification, colder water (< 9 °C) more typical of the Gulf of Maine occurred as far up on the bank as station 3 (Fig 4.2a-d), and differences due to tidal stage were small. During low on-bank stratification (after Oct.9), cold water was limited to the edge of the bank and differences due to tidal stage were greater (Fig. 4.2e-j).

The temperature difference from near surface to ca 64 m (Fig. 4.3a) provides a more detailed picture of the temporal change in on-bank stratification. During the 5 to 9 Oct. period even the shallowest station (4) had vertical temperature gradients of ca 3 °C. This is in contrast to the periods immediately before and after, and much of the June to

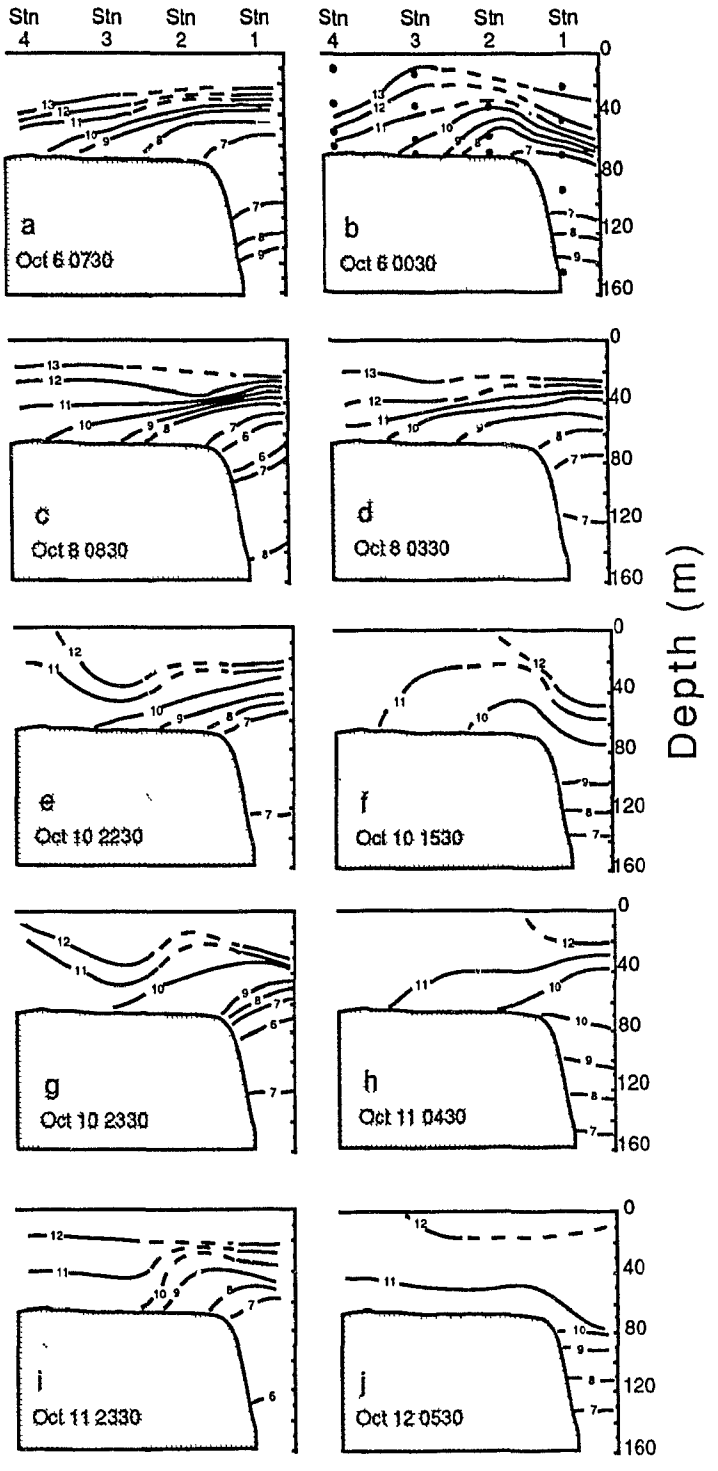

Figure 4.2. Temperature sections on Line A during October 1988. Left and right panels show extremes in frontal position during a tidal cycle (see text). The front is in the maximum on-bank position in sections on left, and in maximum off-bank position in sections on right. Depths of current meters indicated by solid circles in (b).

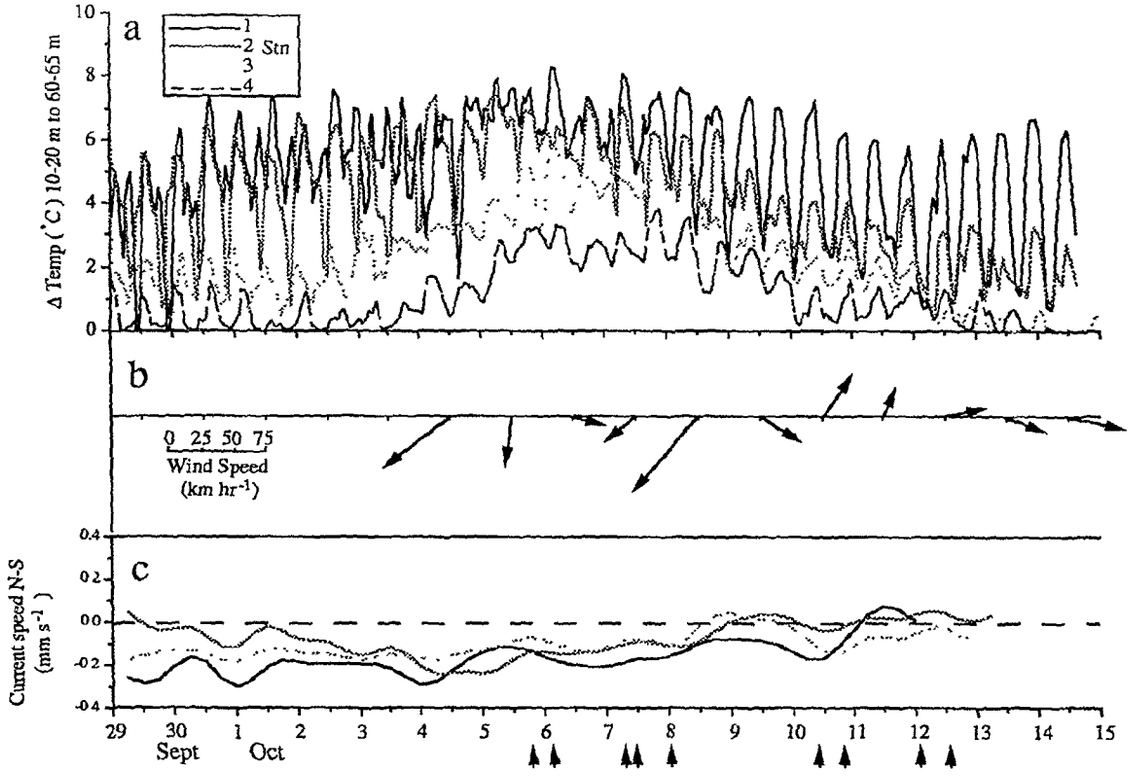

Figure 4.3. Temporal changes in physical conditions when sea scallop larvae were collected within the Georges Bank Frontal Zone. (a): hourly changes in temperature gradient from near surface to near bottom for moorings at stn 1-4. (b): mean daily wind speed and direction from ships logs. (c): Cross-frontal current with tidal component removed. From moorings at stn 1 (21 m), 2 (35 m) and 3 (34 m). Arrows at bottom indicate time of transects 1-10 for the collection of scallop larvae. Temperature data unavailable after October 14 because moorings retrieved.

September period (Perry et al. 1990, Georges Bank Frontal Study, unpublished data). The higher on-bank stratification coincided with strong winds from the north (Fig. 4.3b), and currents in the on-bank direction (Fig. 4.3c). Northerly winds subsided after 8 Oct., and on-bank stratification became progressively less.

The advective effect of the semi-diurnal tidal currents is also apparent from the vertical temperature gradients (Fig. 4.3a). At a given location in the frontal zone there is a semi-diurnal cycle in the extent of temperature stratification as the position of the front is advected back and forth in a N-S direction. Tidal changes in the vertical temperature gradient at the deep mooring (station 1) were much less during the period of high on-bank stratification.

4.4.2 Distribution of sea scallop larvae across the frontal zone

Seven of the 10 transects continued more than 1 km north of the bank edge (Fig. 4.4). On 6 of these, the abundance of sea scallop larvae declined over the slope. During the period of high on-bank stratification (Oct. 5-8), sea scallop larvae peaked in abundance within 7 km of the bank edge (200 m contour) on each of the 5 transects (Fig. 4.4a-e). The coefficient of variation (CV) of station abundances for any one transect, an indicator of larval patchiness, ranged from 70 to 110% for the 5 transects (Table 4.2). The abundance peaks on Lines C and D were closer to the bank edge than were those of the more easterly Lines (A and B) and it is not known how abundance changed beyond the bank edge (since sampling did not continue into the deep water).

For Line A, the abundance peak occurred where the vertical temperature gradient was almost as great as the deepest station (5-7 °C from 10 to 60 m; Fig. 4.4a, e). A broad size range of larvae was present at all stations (Fig. 4.5), but on Lines A and B the decline in larval abundance close to the bank edge was associated with larger larvae (Fig.4. 5a, b, e). On Lines C and D larvae there was no clear trend in length frequency from the inner to outer stations, but Line D was dominated by small larvae (Fig. 4.5c, d).

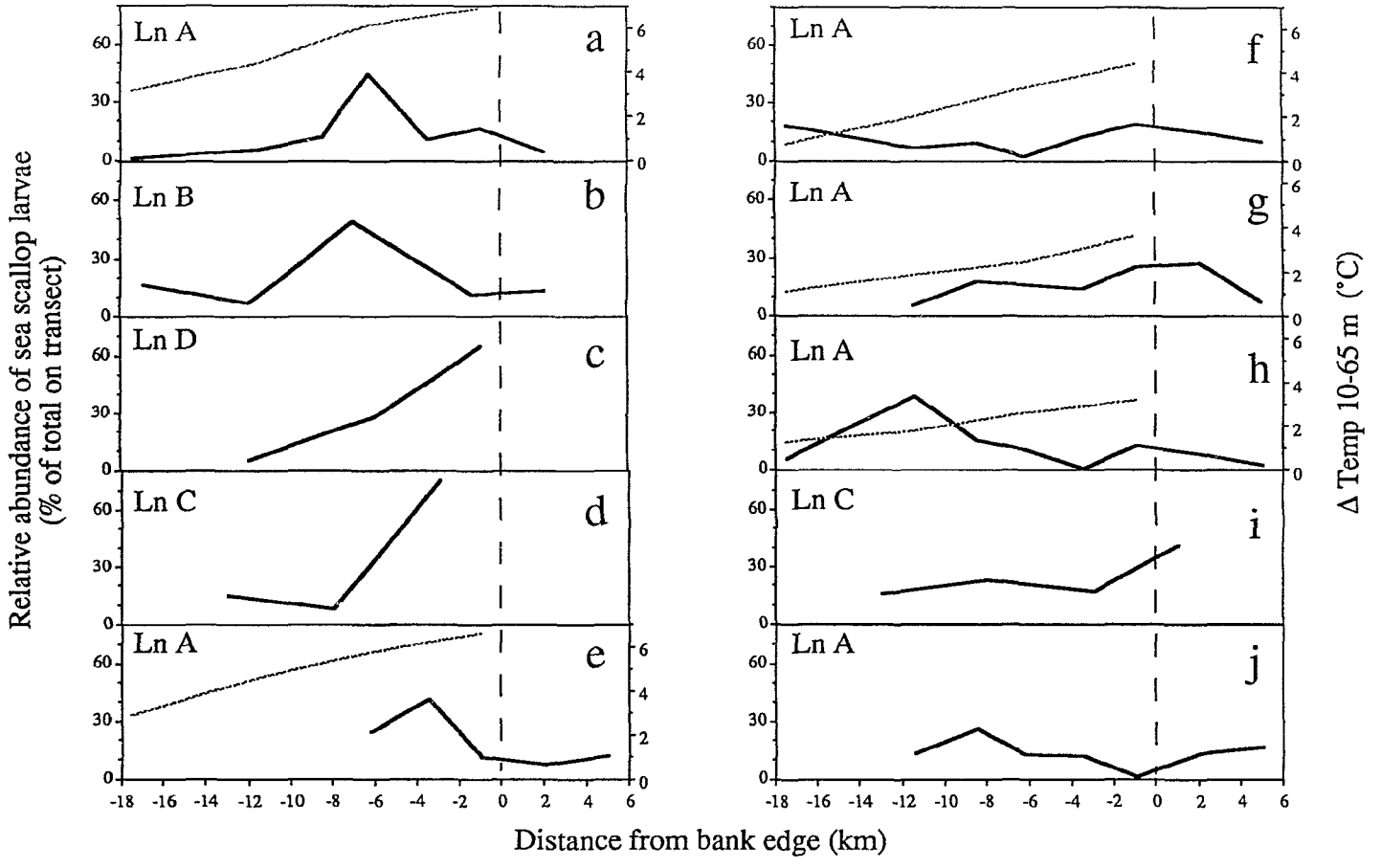

Figure 4.4. Relative abundance of sea scallop larvae for each of 10 transects of the Northern Flank. Line (Ln) identifer is indicated for each transect. Temperature difference from near surface to near bottom shown for stations 1-4 on Ln A. Station positions are related to distance from the bank edge (200 m contour). (a) to (j) corresponds to transects 1 to 10.

Table 4.2. Abundance and patchiness of sea scallop larvae across the frontal zone. Shown for each transect is peak abundance, and coefficient of variation (CV) of abundances for all stations on the transect. H: high; L: low. [1]Estimated from integrated pump samples between 10 and 40 m. [2]Stratification assumed to be low for transect 10; temperature data was unavailable.

Transect no	On-bank stratification	Abundance at peak (n m^{-2})	CV
1	H	15615	102.2
2	H	2596	83.7
3	H	11212	91.0
4	H	33512	109.6
5	H	17687	69.1
6	L	11160[1]	44.9
7	L	8490[1]	55.7
8	L	34898	95.7
9	L	14803	47.2
10	L[2]	9877	50.8

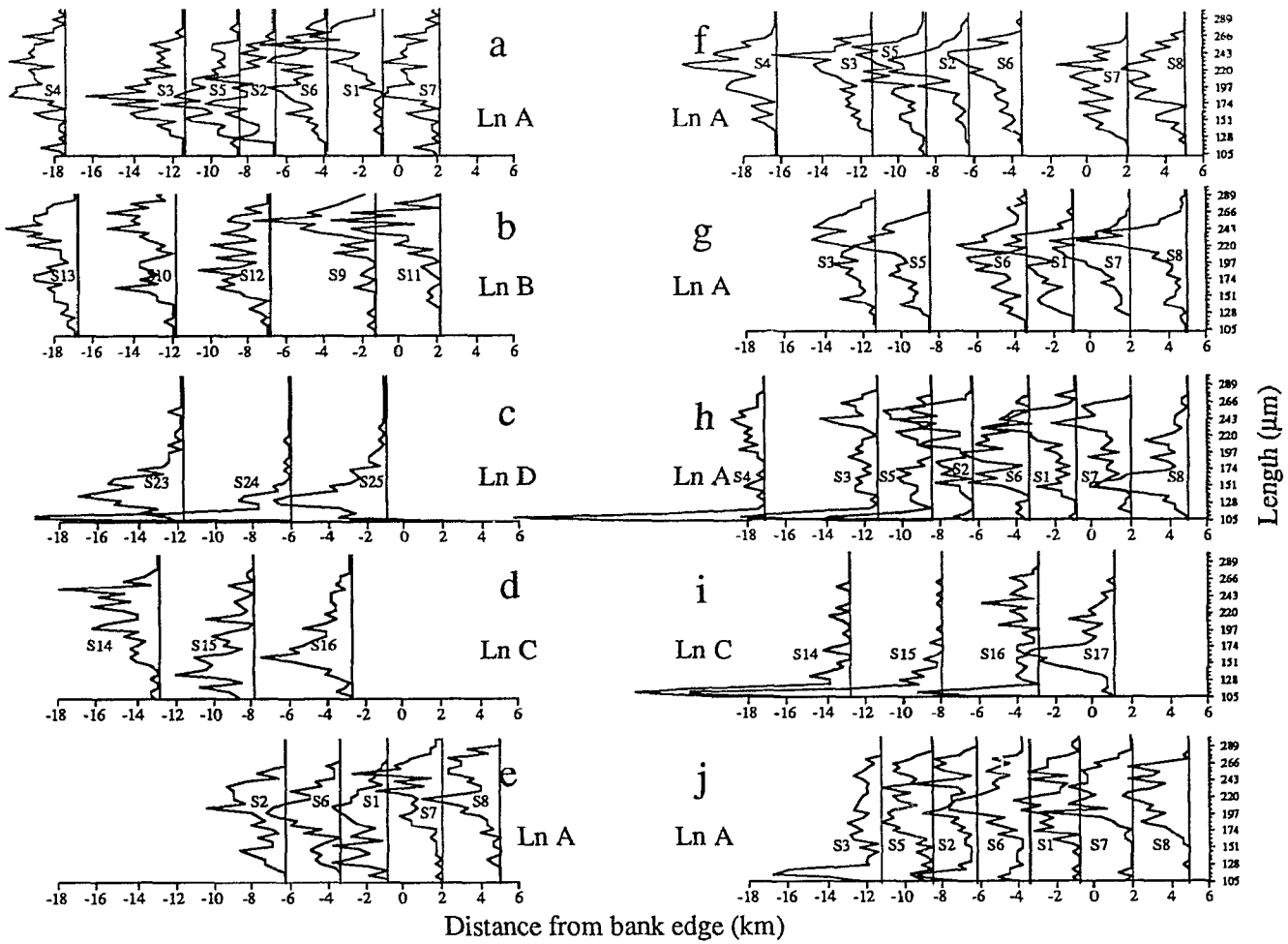

Figure 4.5. Length frequency distributions for sea scallop larvae on 10 transects of the Northern Flank. Shown for each station (S#) is percent length frequency. (a) to (j) corresponds to transects 1 to 10.

During the period of low on-bank stratification (after Oct 9), peaks in the number of sea scallop larvae (per m^2 or per m^3 in the case of pump samples) were less prevalent and not associated exclusively with the stations near the bank edge (Fig. 4.5f-j). The CV's of station abundance for the transects after Oct. 9 (45-96%, Table 4.2) indicate that patchiness was lower than during the period of high on-bank stratification. Repeat transects of Line A (Fig. 4.4f, g) indicate the trend in abundance was stable for almost 2 tidal cycles. The length frequency distribution of larvae on these 2 transects was fairly uniform (Fig. 4.5f, g), but by Oct. 12 the inner stations of both Lines A and C were dominated by a pulse of small larvae (< 115 μm, or 1-3 d veliger larvae; Fig. 4.5h, i). One week later, a mode of small larvae was still evident at the inner stations on Line A (Fig. 4.5j).

Along the front, there were relatively more large larvae on easterly Lines A and B than on westerly Lines C and D (Fig. 4.5), but no consistent pattern of abundance (Table 4.2).

4.5 Discussion

During October, the frontal zone on the Northern Flank of Georges Bank is not as well defined as in summer, and is subject to considerable variation over periods of a few days. Given the correspondence between temperature stratification, wind, and currents (Fig. 4.3) it is probable that wind contributes to this variation. An alternate explanation for the change in on-bank stratification is the spring-neap tidal cycle on Georges Bank, which causes variation in tidal current strength (and thus the extent of the mixed area).

Variability in temperature stratification was also apparent over periods of less than a day, due to tidal effects. Plankton sampling resolution was too coarse to detect differences due to tidal advection of the front, but the close match in the cross-frontal

abundance of larvae for consecutive transects of Line A (Fig. 4.4f, g) indicates that the 'smearing' of the abundance trend over a tidal cycle was not a major problem .

Two trends in the abundance of sea scallop larvae on the Northern Flank are of interest: (i) the decline off the edge of the bank during most transects and (ii) the greater patchiness during high on-bank stratification due to peaks in abundance close to the bank edge (Fig. 4.4, Table 4.2). The low abundance of larvae north of the bank edge is consistent with the broadscale surveys, which collected few larvae within the Fundian Channel (Chapter 3). The decline probably results from a lack of local production of larvae there (scallop beds are increasingly rare below 100 m), coupled with limited loss of larvae from the Northern Flank. An alternate explanation would be rapid mortality of larvae off the bank edge, but there is no reason to infer this.

Limited loss of scallop larvae from the Northern Flank may be explained by the cross-frontal component of the residual current, which was low but directed on-bank (Fig. 4.2c). Northerly winds may have increased the on-bank flow by pushing Gulf of Maine water onto the bank (Fig. 4.2), further decreasing the losses of scallop larvae from the Northern Flank.

Differences in the length frequency of larvae across the frontal zone (Fig. 4.5) suggest that physical exchange across the front is limited, because rapid exchange should homogenize the length-frequency distributions. Local larval production clearly leads to some variation in length across the frontal zone (Fig 4.5 h,i). Variation in size structure across the frontal zone may also result from the rapid movement of patches of larvae along the bank edge. Some of these patches may originate upstream, in the area of the South Channel (Chapter 3).

To compare the patchiness of sea scallop larvae on transects of the Northern Flank during October 1988 with other areas of Georges Bank, the CV of station abundances (Table 4.2) can be used. The data from pump sampling (Chapter 2) is comparable, since

profiles of larval abundance obtained while drifting are analogous to sampling with nets along a transect (Table 4.2). The CV's of larval abundance from pump profiles ranged from 33 to 69% for the mixed area of Georges Bank, 38 to 76% for the weakly stratified area, and 94% for a single set of profiles in an intense part of the frontal zone (Table 2.2). The high CV's of larval abundance during the period of high on-bank stratification of the present study (69-110%; Table 4.2) indicate that the patchiness of larvae at that time was relatively high. During the period of low on-bank stratification the patchiness of larvae in the frontal zone was of the same order as in the weakly stratified part of Georges Bank.

The peaks in larval abundance on Line A occurred where the vertical temperature gradient was ca 6 °C (Fig. 4.4). This is equivalent to a vertical density gradient of greater than 1.5 sigma-t units, which is on the stratified side of the frontal zone using the criterion of Horne et al. (1989; 0.2-1.5 sigma-t units). Possible explanations for the peaks in larval abundance close to the shelf edge include those related to physical mechanisms alone, those which invoke larval behavior to 'use' the circulation in the frontal zone, and those related to increased survival of larvae. Convergence occurs within frontal zones (Simpson 1981) and passive accumulation of zooplankton by convergence at fronts has been hypothesized (Pingree et al. 1974, Le Fèvre1986), as has passive transport modulated by behavior (Herman et al. 1981). Whether physical convergence occurs on Georges Bank at this time of year is currently under study. The abundance peaks observed during high on-bank stratification might also be related to the northerly winds pushing water and larvae up onto the bank.

Enhanced survival of larvae on the stratified side of the front due to increased food availability or reduced predation might explain the abundance peaks. For these mechanisms to operate, cross-frontal exchange would have to be sufficiently low for increased survival rates to have a measurable effect on abundance.

The along-frontal increase in length from west to east is consistent with advection of larvae in the direction of the residual circulation (Chapter 3) but this length increase cannot be explained by the residual current alone. The length frequencies at the outermost stations on Lines D, C, A, and B on Oct 6-7 (Fig. 4.5a -d) show major modes of respectively 132 μm, 161 μm, 253 μm and 265 μm. Such length differences would not occur from growth during downstream transport at residual current speeds.

Physical models of the frontal circulation on the Northern Flank are necessary to evaluate whether the apparent retention of sea scallop larvae, and the periodic increases in larval patchiness, can be explained in terms of the physical circulation, or whether biological factors such as variation in larval survival are important. With improvements to the Oil Red O condition index (Chapter 5), a hypothesis related to enhanced larval survival in the area of the abundance peaks could be tested.

4.6 Summary

To relate the abundance of sea scallop larvae to the frontal zone on the Northern Flank of Georges Bank, 10 transects were completed in October 1988. Larval abundance was not consistently related to any feature of the frontal zone per se. In October the frontal zone is not as intense as in summer, particularly in the upper 40 m where sea scallop larvae are most concentrated. Rapid declines in larval abundance usually occurred in the area of the bank edge (200 m isobath), probably because of limited loss of larvae from the Northern Flank. This view is supported by the on-bank direction of the cross-frontal component of the residual current, and by cross-frontal differences in the size structure of sea scallop larvae.

Temporal changes in on-bank temperature stratification are important to trends in the abundance of sea scallop larvae on the Northern Flank. Five transects were completed from 5 to 8 October when on-bank stratification was high, probably due to strong winds

from the north pushing Gulf of Maine water onto Georges Bank. The abundance of sea scallop larvae on these transects was very patchy, with peaks in abundance within 7 km of the bank edge. The remaining 5 transects were completed from 10 to 19 Oct. after northerly winds had subsided. At this time temperature stratification on the Northern Flank was reduced, with near isothermal conditions at the shallow station. On these transects the abundance of sea scallop larvae was no more patchy than for other parts of Georges Bank.

Chapter 5

The application of a lipid-based condition index for assessing the condition of sea scallop *Placopecten magellanicus* larvae

5.1 Introduction

It is generally accepted that the enormous fecundity of marine species which produce planktotrophic larvae is balanced by high mortality during the larval and immediate post-larval periods. A female sea scallop 5 yr of age produces upwards of 100 million eggs annually (Langton et al. 1987) and only 2 of these need to survive to maintain the population size. Estimates of mortality rates for naturally occurring planktonic larvae are wide ranging (2-90% per day) and dependent upon species, developmental stage, season, location and the methods used to generate the estimate (May 1974, Dahlberg 1979, Hewitt et al. 1985, Hines 1986, McGurk, 1986, Taggart and Leggett 1987, Morse 1989). The causes of mortality amongst planktonic larvae are usually thought to be starvation, predation, and transport related losses of larvae to unfavorable habitats, but disease and environmental stress may also play a role (Hjort 1914, Thorson 1950, Hunter 1976, Iles and Sinclair 1982, Shepherd et al. 1984, Simpson 1987, Wooster and Bailey 1989).

Starvation does occur in larval fish under certain conditions (Shelbourne 1957, O'Connell 1980, Theilacker 1986) but it is generally thought to be less important than predation as a source of mortality (Rothschild and Rooth 1982, Peterson and Wroblewski, 1984, Morse 1989). For invertebrate larvae, Thorson (1946) wrote that 'a considerable part of the waste in planktotrophic pelagic larvae is due to starvation' but he agreed with Korringa (1941) that predation was probably the major source of mortality, because many larvae could feed on a variety of food sources, and some could survive starvation for a few days in the laboratory. Later authors have argued that starvation of

invertebrate planktotrophic larvae is rare because of well developed abilities to survive without food (Vance 1973), because food (phytoplankton) is rarely in short supply (Mann 1988b), and because invertebrate larvae can utilize bacteria and dissolved organic matter (DOM) to some extent (Manahan and Crisp 1982, Olson et al. 1987). Based on in-situ experiments, the hypothesis of larval starvation was rejected for echinoderm larvae from the tropics (Olson 1987a) and from the antarctic (Olson et al. 1987). This is one of the few studies to investigate starvation in invertebrate planktotrophic larvae however, and starvation may be restricted to certain species and or critical stages of development (Hines 1986). In a recent review of food limitation, Olson and Olson (1989) suggest that food limitation may be linked to trophic level -- herbivorous invertebrate larvae which can also utilize DOM may be less food-limited, while larvae which feed upon herbivores may be more food-limited.

Even if starvation is rare, it has long been recognized that food limitation can have indirect effects which lead to mortality. Reduced food may lead to a decline in the ability of larvae to avoid predators (Jones 1973, Hunter 1984), or to reduced growth and prolongation of the larval period. Thorson (1950, stated 'The most common effect of poor food conditions, low temperatures, or lack of suitable substratum on the waste of larvae will be an indirect one, namely a retardation of the metamorphosis of the larvae, that is, a longer stay in the plankton exposed to large crowds of voracious enemies'. Vance (1973) also took this view, and Houde (1987, 1989) has emphasized that small differences in larval growth rates (which may be due to poor food) could increase larval mortality dramatically because of the prolongation of the larval period, when mortality is presumed to be highest.

Studies of whether food limits the rates of growth and development in marine invertebrate larvae are few. Paulay et al. (1985) showed that growth and development rates were increased in several species when natural seawater was supplemented with

cultured algae. Olson et al. (1987) on the other hand cultured antarctic echinoderm larvae in situ, and reported that for these larvae, developmental rates in nature are only slightly lower than the developmental rates of larvae which are well fed.

Among the approaches available for investigating the occurrence of food limitation (including the extreme case of starvation) are physiological condition indices. These indices can integrate the biological and physical variation a planktotrophic larva is likely to experience. In many species of invertebrate larvae, neutral lipid is the primary endogenous source of energy when food is low, when environmental conditions are adverse, or during metamorphosis (Bayne 1965, Millar and Scott 1967, Holland and Spencer 1973, Holland 1978, Lucas et al. 1979). Stored protein can also be an important energy source during periods of stress (Mann and Gallager 1985, Rodriguez et al. 1990), but as long as lipid is also utilized it should be a useful index of condition.

To make direct measurements of neutral lipid reserves in bivalve larvae would require a substantial number because of their low weight (ca 0.2-2 μg) and because generally less than 10% of the dry weight is neutral lipid (Gallager et al. 1986, Whyte et al. 1987). Given that separating 100-1000 larvae from a plankton sample at sea is impractical, and since the individual variability in lipid content is important (Gallager and Mann 1986a) an alternate approach is necessary. In bivalve larvae lipid is stored in the form of coalesced droplets which accumulate during development until their number is reduced by starvation or metamorphosis (Bayne 1965). Oil droplets (or "oil sacs") have been visually quantified to assess feeding condition in copepods (Corkett and Mclaren 1969) and cladocerans (Tessier and Goulden 1982). To better assess these visual lipid reserves in bivalve larvae, a technique was developed based on the lipid-specific stain Oil Red O (Gallager and Mann 1981). Larval bivalve shells are transparent and the distribution of the Oil Red O (ORO) is readily apparent with light microscopy.

An ideal stain for monitoring lipid energy reserves would dissolve only in neutral lipids. There is still some doubt which lipid classes ORO stains most intensely, and the extent to which structural lipids (phospholipids) are stained (Gallager and Mann 1986a, Mann 1986a). Although ORO may stain some structural lipid, it does detect changes in endogenous energy reserves, probably because neutral lipids comprise 30-80% of the total lipid in bivalve larvae (Gallager et al. 1986, Whyte et al. 1987). The lipid stained by ORO (ORO lipid) declines if bivalve larvae are starved, fed a non-nutritious diet, or reared at high temperatures (Gallager and Mann 1981, 1986a, Gallager et al. 1986), and the ORO lipid in bivalve eggs is a good indicator of subsequent survival (Gallager and Mann 1986b).

In the present chapter I evaluate the Oil Red O stain as an index of condition in sea scallop larvae by measuring ORO lipid in fed and starved hatchery-reared larvae. I also assess the condition of sea scallop larvae on Georges Bank using the ORO lipid index.

5.2 Methods

Hatchery-reared sea scallop larvae for the present study were from the Department of Biology, Dalhousie University, and the aquaculture research hatchery at Fink Cove, Nova Scotia (Table 5.1). Larvae from Dalhousie University were reared specifically for this study. Larvae from the Fink Cove hatchery were reared for other purposes, and were obtained opportunistically. All sea-caught larvae were from Georges Bank (Table 5.1).

5.2.1 Effects of starvation and temperature on ORO lipid

To examine the effect of food regime and temperature on ORO lipid in sea scallop larvae, a factorial experiment was run in the hatchery of the Department of Biology, Dalhousie University. The experiment had two levels of temperature (11 and 14 °C), two levels of food regime (fed or starved) and a nested factor (two culture containers per

Table 5.1. Sea scallop larvae stained with Oil Red O (ORO). Shown are sources of larvae, size of larvae, the method of quantifying the ORO stain, and the factors examined. PC: pixel count; GV: globule volume; meas.: measurement error; chl: chlorophyll.

	Source	Date	Larval length (μm)	ORO lipid measure PC	GV	Factors examined for effect on ORO lipid
1.	Dalhousie University	Nov. 1986	108-217	√	-	temperature, starvation, meas.
2.	Fink Cove Aquaculture	May 1989	195-285	√	√	measurement error
	Research Hatchery	Sept. 1989	190-265	√	-	starvation
3.	Georges Bank	Oct. 1988	228-300	√	√	chl *a*, oceanographic regime

treatment combination). Using the methods described in Hurley et al. (1987), sea scallops (5 females and 5 males) were spawned on October 31, 1986. Fertilized eggs were then incubated at densities of ca 30 ml^{-1} in 20 l buckets containing 2 µm filtered seawater at a temperature of 14 °C. On day 4, when most surviving larvae had reached the straight hinge stage, they were allocated to sixteen 20 l buckets at densities of ca 2.5 larvae ml^{-1}.

Eight buckets were then placed in each of two water baths in which the temperature was thermostatically controlled and measured once a day. One water bath was maintained at 14 °C (mean: 14.3 °C, SD: 0.62, n: 23 days), the other at 11 °C beginning on day 6 (mean: 10.9 °C, SD: 0.35, n: 21 days). The water in all buckets was changed every 2 days during the experiment. Feeding was initiated on day 4, and carried out within 2 hours of changing the water every two days thereafter until starvation was imposed on the larvae in some buckets (see below). The species of algae, and their approximate initial concentrations within each 20 l bucket were as follows: *Chaetoceros calcitrans* (30,630 cells ml^{-1}); *C. gracilis* (6,320 cells ml^{-1}); and *Isochrysis galbana* (13,050 cells ml^{-1}).

The effect of starvation on ORO lipid was investigated by starving the larvae within replicate buckets at each temperature. One 'starvation series' was initiated on day 12, the other on day 22. Larvae from 8 buckets were sampled during each starvation series: 2 replicates from each of the 4 temperature/food regime combinations. All buckets during the first starvation series were terminated on day 18, those in the second series on day 26. Samples of at least 30 larvae per bucket were stained with ORO using the methods described in section 5.2.3.

The larvae from the above experiment ranged in size from 108 to 217 µm -- most were less than 160 µm. To measure ORO lipid in large well-fed larvae for comparison with sea-caught larvae, samples were obtained from the Fink Cove hatchery. Larvae 28 d

post-fertilization were obtained in May and September of 1989 (Table 5.1). Some of the larvae obtained in September were then starved for 6 d.

5.2.2 Collection of sea scallop larvae from Georges Bank

Sea scallop larvae were obtained on Georges Bank in 1988, in conjunction with the Georges Bank Frontal Study (Chapter 4). Larvae were obtained by pump from a mixed location on Oct. 6 and Oct. 15, a weakly stratified location on Oct. 6 and Oct. 14, and the Northern Flank frontal zone on Oct. 10-11 (Fig. 5.1). Samples from one of the 2 pump transects of the Northern Flank, and additional net samples obtained by opportunity were used to develop the methodology for quantifying ORO lipid in sea-caught larvae.

The pump system is fully described in Chapter 2. Briefly, it consisted of a submersible pump with 6 cm PVC suction hose, a frame upon which the pump intake and CTD were mounted, and on-deck readouts of intake depth, water temperature and salinity, and volume sampled. To collect larvae for measurement of condition, the pump intake was moved through the 10-45 m depth interval until a sample of ca 10 m^3 was obtained. To assess the variability in ORO lipid associated with different samples in the same general location, consecutive samples were obtained from the mixed and stratified locations while drifting for ca 6 h. In order to assess within sample variability in ORO lipid, 2 fractions from each plankton sample were stained using the methods described in section 5.2.3. The remainder of the sample (unstained) was preserved in formalin so that the total number of sea scallop larvae per drift sample could later be determined.

To relate the measure of ORO lipid to the quantity of food available for the larvae, water samples for chlorophyll *a* were obtained at the same time as the larval samples. These chlorophyll *a* samples were obtained from three depth intervals (45-30 m, 30-20 m, and 20-10 m) via a garden hose connected to the pump manifold. Chlorophyll *a* within the < 15 μm size fraction was later determined using the methods described in Chapter 2.

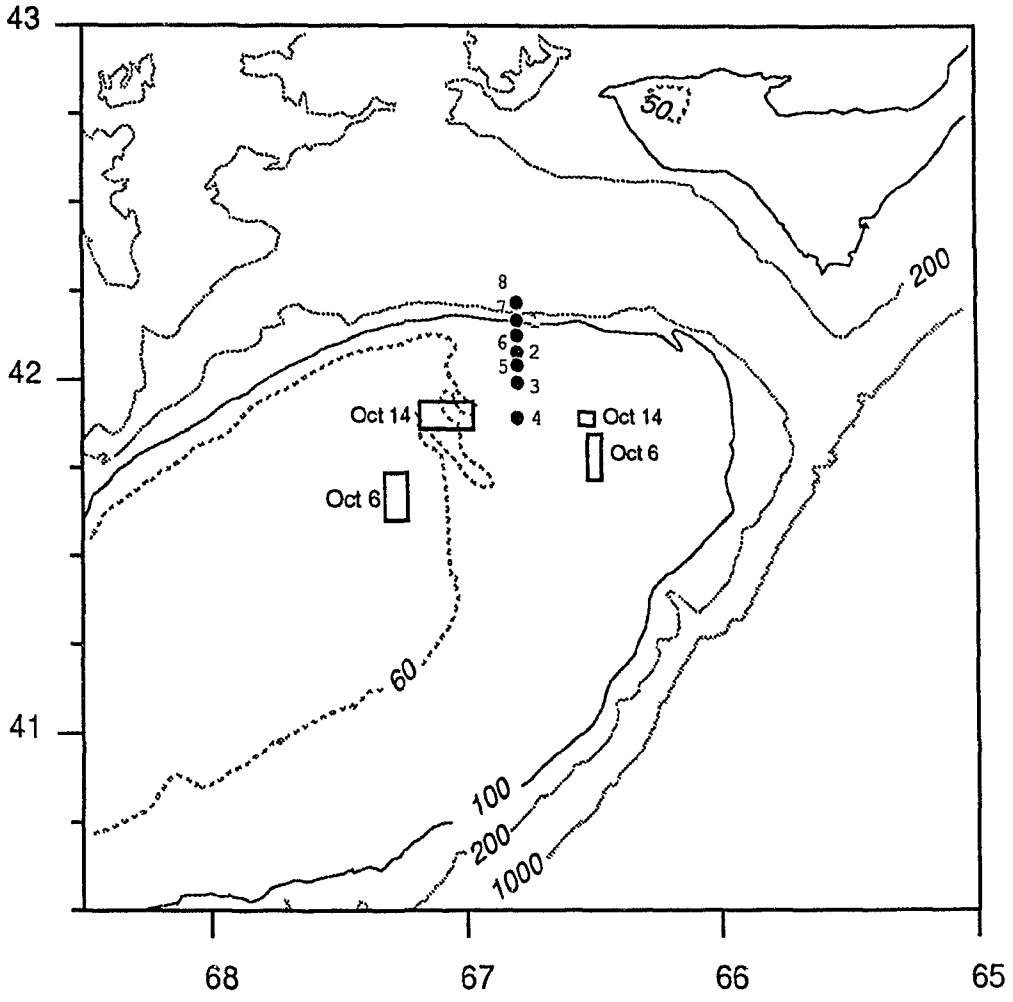

Figure 5.1. Locations on Georges Bank where sea scallop larvae were collected for staining with Oil Red O. Boxes outline areas where drift sampling carried out.

5.2.3 Staining procedures

Sea scallop larvae were stained with Oil Red O using the methods of Gallager and Mann (1981) and Gallager et al. (1986). A saturated solution of the stain was made by dissolving 0.75 g of ORO in 100 ml of propylene glycol heated to 60 °C. The solution was filtered hot through Whatman no. 2 paper, refrigerated, then filtered again. Larvae to be stained were removed from the batch culture (or plankton sample, see below) concentrated on a screen (44, 55 or 64 μm) and then backwashed to a petri dish with a small amount of seawater. The larvae were then narcotized over a period of 10-30 min by adding drops of 7.5% MgCl solution to the petri dish, and periodically pipetting off the excess fluid. This gradual increase in the percentage of MgCl solution was meant to relax the larvae such that they would not clamp their shell valves together prior to addition of the stain. When the larvae were relaxed, or 30 min had passed, a few drops of 4% formalin were added to the petri dish. The larvae were then transferred to a small screen, and the excess fluid was removed by blotting on a paper towel. The screen with larvae was then transferred to a 20 ml vial and enough ORO stain added to immerse the larvae.

For sea-caught larvae the procedure differed only in the first step, that of concentrating the larvae. On board ship, the identification and removal of enough sea scallop larvae from individual plankton samples was difficult and time consuming. Instead, the scallop larvae were stained along with other dense components of the plankton sample. Portions of the plankton sample were poured into a large petri dish (ca 16 cm in diameter) which was then swirled such that the heavier components of the plankton sample were concentrated towards the centre of the dish. Bivalve larvae were always part of this central component, but the extent to which they were separated from other suspended particles, and from phytoplankton in samples which it dominated, varied from sample to sample. The total volume of plankton stained in one vial never exceeded

ca 2 ml, and was usually much less. Two fractions were stained for each plankton sample.

Samples were processed in the laboratory 6-15 months later. To reduce the effects of any measurement bias, individual samples (or sample fractions) of larvae from the 3 sources (Table 5.1) were done in random order. Excess stain was removed from the sea scallop larvae by multiple transfers in ethylene glycol over a period of ca 24 h. The larvae were then mounted on slides in ethylene glycol and the stain quantified within 24-48 h using the methods described below.

5.2.4 Quantification of ORO stain

The lipid stained by ORO (ORO lipid) was quantified indirectly using an image analysis system. The system consisted of an IBM compatible PC equipped with a video digitizer board which was interfaced to a compound microscope (Campana 1987). ORO stain was taken up mainly in the region of the digestive gland (Fig. 5.2) and 2 measures of ORO lipid were used: pixel count and globule volume (see below). The length of each larva was also determined using the image analysis system.

Photographs of representative larvae from the Fink Cove hatchery and from Georges Bank (Table 5.1) were made with a 35 mm camera mounted on a compound microscope within 24 h of ORO lipid quantification. Exposures and lighting conditions varied somewhat from specimen to specimen. The original photos were on slide film (Ektachrome, ASA 160, tungsten) and prints of individual larvae were made from the slides. Individual slides were then mounted together to form groupings which were rephotographed.

5.2.4.1 Pixel count measure of ORO lipid

The pixel count measure of ORO lipid utilized the darker red colour of the stained area and the grey-level threshold feature of the image analysis system. After positioning the larva in the centre of the field at a magnification of 160, the stained area was

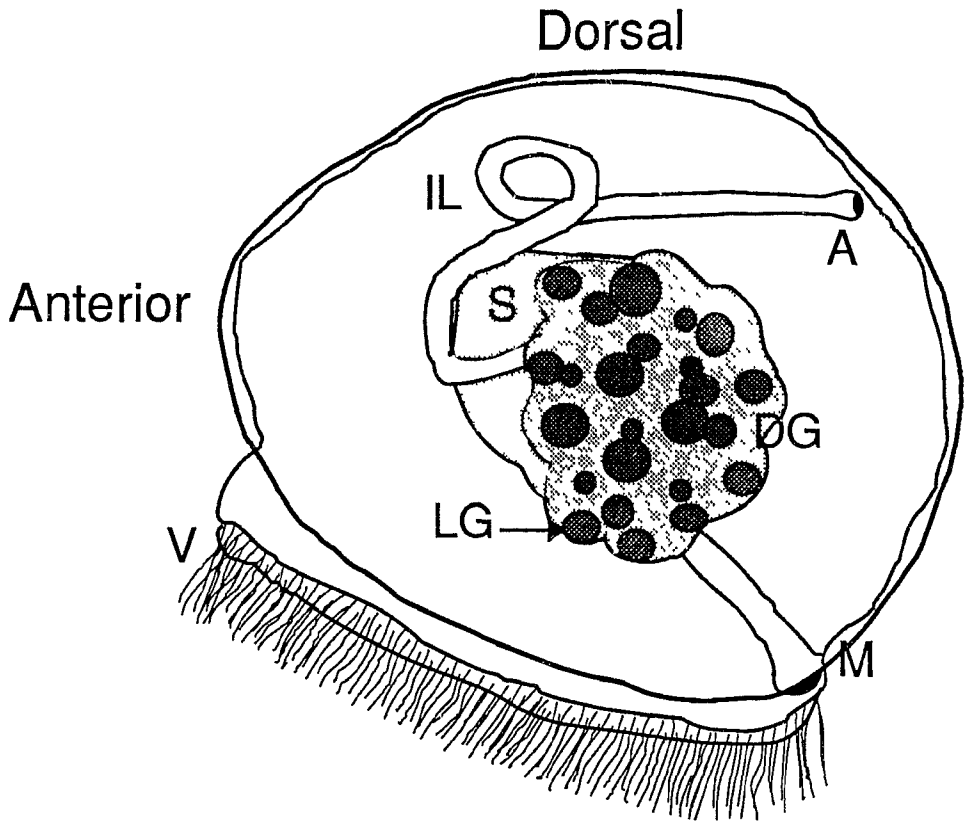

Figure 5.2. Sea scallop larva with velum extended showing simplified view of digestive system. Larval length ca 230 μm. IL: intestinal loop; A: anus opening into mantle cavity; S: stomach; DG: bilobed digestive gland; LG: lipid globule; M: mouth; V: velum.

highlighted by eliminating all pixels in the image which were above (lighter than) the selected grey-level threshold. Once the stained area was highlighted, the pixels comprising the image were automatically enumerated. This measure of ORO lipid will be referred to as the pixel count.

Pixel count measurements of ORO stain for larvae from the factorial experiment were made at a fixed grey-level threshold of 63, after initial examination indicated this level would effectively highlight the stained area in most larvae. Care was taken to make lighting conditions as consistent as possible from one measurement session to another.

For sea scallop larvae from the Fink Cove hatchery and from Georges Bank, a green filter over the light source was used to enhance the red colour of the stained area, and a lower threshold of 34 was used. An additional pixel count measurement due to variable background absorbance of the stain was done at thresholds ranging from 27 to 33 depending upon the specimen. Only this latter pixel count measurement is retained for statistical analysis.

5.2.4.2 Globule volume measure of ORO lipid

This measure of ORO lipid was used for larvae from the Fink Cove hatchery and from Georges Bank. The method involved estimating the mean size and total number of lipid globules (Fig. 5.2) in larger sea scallop larvae (> 220 μm). The mean size of globules within two size classes (ca 2-6 μm and > 6 μm in diameter) was estimated from measurements of at least 5 globules within each size class at a magnification of 400. The number of globules within the two size classes was counted as the plane of focus was moved through the larva. When there were a large number of globules, a subset of the total was counted (at least 20%) and the fraction not counted estimated. Data on the number and size of globules were then used to estimate the total volume (μm^3) of lipid within globules for each larva.

5.2.5 Data analysis

All data were analyzed using SYSTAT version 3.1 (Wilkinson 1987). In examining the effects of starvation on ORO lipid, the distributions of the pixel count were characterized with the coefficient of variation (CV), and with skewness, since Gallager and Mann (1986a) found these to increase in stressed larvae. Parametric analyses were used where the assumptions of normality and homoscedasticity could be verified. Where they could not be verified, non-parametric analyses were performed.

5.3 Results

5.3.1 Error associated with the measurement of ORO lipid

Repeated measures of the pixel count of ORO lipid on different specimens over a 5 d period indicate that variability due to specimen placement and light variation were low (Table 5.2). The coefficient of variation of such measurements was less than 13% except for one high value (44%) when ORO lipid was very low. The measurement error of globule volume was substantially higher, ranging from 15-44% (Table 5.3).

5.3.2 Factorial experiment: effect of starvation and temperature on ORO lipid

The length and pixel count data for each culture container on days 14, 16, 18, 24 and 26 are shown on Fig. 5.3. The effect of starvation at both temperatures is clearest for larvae on day 18, when starvation had continued for 6 d. The pixel count data for each measurement day (days 14, 16, 18, 24 and 26) of the factorial experiment were initially analyzed separately. Pixel count increased with larval length (Fig. 5.4) and therefore it was necessary to account for length differences between the larvae in different culture containers. Analysis of covariance (ANCOVA) with length as the covariate is the preferred statistical approach. Using the nested ANOVA in Underwood (1981) as an

Table 5.2. Measurement error of pixel count (an index of the quantity of ORO lipid per larva). Shown are results of repeated measures of single specimens completed over 2-5 days. CV: coefficient of variation (%). Specimens were from 2 culture containers; length shown is the mean for each container.

Length (μm)	N	Pixel count mean	CV
131	5	552	10
131	7	813	7
131	5	41	44
131	7	437	13
131	7	1536	11
161	7	5288	3
161	7	4783	3
161	7	4823	3
161	7	1433	3

Table 5.3. Measurement error of lipid globule volume. Shown are results of repeated measures of single specimens completed over 2 days. CV is coefficient of variation (%).

Length (μm)	N	Globule volume (μm^3) mean	CV
239	4	13111	44
237	4	8149	15
243	4	14859	30
241	4	12063	30
232	4	10708	27
235	4	9500	18

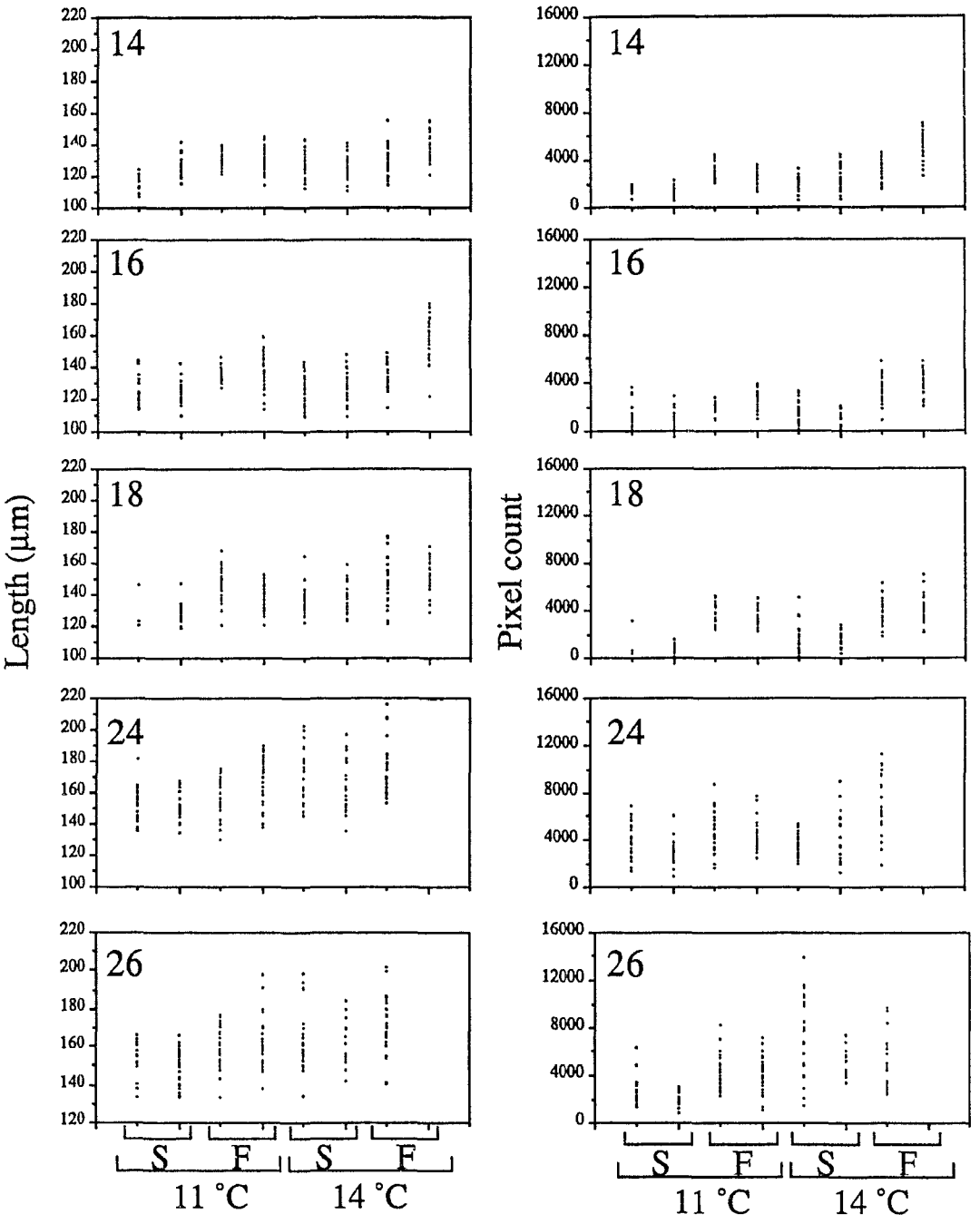

Figure 5.3. Sea scallop larvae reared at 2 temperatures and fed (F) regularly or starved (S) for 2-6 d. Shown is length and pixel count for each larva within each culture container. There were usually 2 culture containers per treatment combination. Number in upper left is age in days since fertilization.

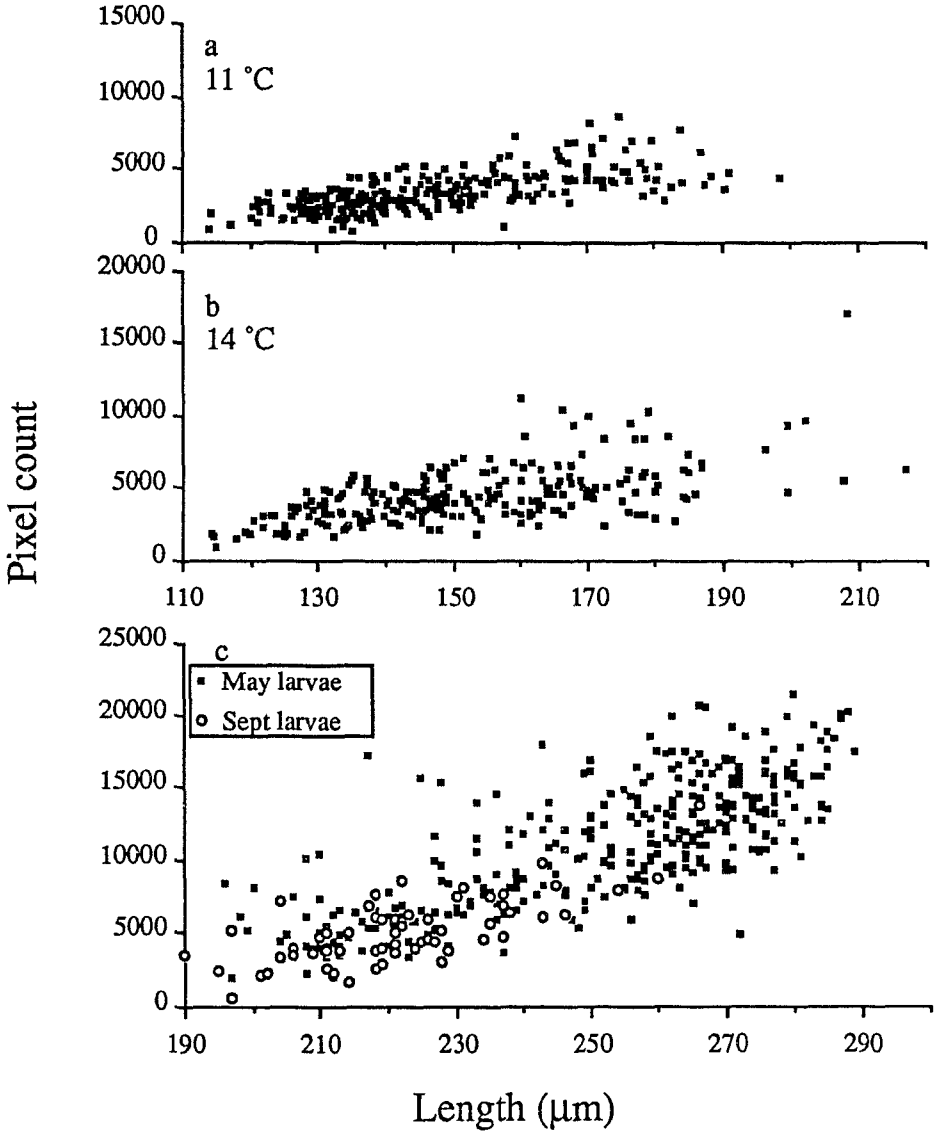

Figure 5.4. Pixel count versus length for hatchery-reared sea scallop larvae (starved larvae not included). (a): 11 °C larvae from Dalhousie hatchery; (b): 14 °C larvae from Dalhousie hatchery; (c): larvae from Fink Cove hatchery in May and September of 1989. Note different length scale.

example, the statistical model for the data for each measurement day (days 14, 16, 18, 24 and 26) of the factorial experiment is as follows:

$$P_{ijkl} = \mu + L_{ijkl} + F_i + T_j + FT_{ij} + C_{k(ij)} + e_{l(ijk)} \qquad (1)$$

where P_{ijkl} is the pixel count of individual larvae; L_{ijkl} represents the effect of length, the covariate; F_i (i = 1 or 2) represents the effect of the i th feeding regime, T_j (j = 1 or 2) represents the effect of the j th temperature; FT_{ij} represents the interaction between feeding regime and temperature, $C_{k(ij)}$ (k = 1 or 2) represents the effect of the k th culture container at feeding regime i and temperature j, and $e_{l(ijk)}$ represents the error associated with the l th larva (l= 1...n; mean n = 28) in the k th culture container.

ANCOVA assumes that the relationship between the dependent variable and the covariate is the same for each treatment (Kleinbaum and Kupper 1978). This assumption was tested by adding terms for the interactions with length to Equation 1. Estimation of the parameters using SYSTAT indicated that there were significant interactions between length and the main factors ($p < 0.001$). ANCOVA was therefore inappropriate.

The next choice for statistical analysis was analysis of variance (ANOVA) of both pixel count and length using the model described in Equation 1 with the covariate removed. To test for the assumption of homogeneity of variance, I used Levene's test, which is much less sensitive to non-normality in the data than is Bartlett's (Snedecor and Cochran, 1980). Ten tests were performed---one for length and one for pixel count on each of the 5 measurement days. Nine of the ten tests indicated that the assumption of homogeneous variance was not met. Six of nine tests were significant at a probability level of 0.001, one at a level of 0.01 and two at a level of 0.05. As a result of these tests, a non-parametric approach was used to assess the effect of starvation and temperature on ORO lipid.

To examine the effect of starvation, comparisons were made only within groups of larvae that had been fed the same number of days at the same temperature. Within each of

the 3 groups the number of days starved varied, but length differences were reduced (Table 5.4). Mann-Whitney comparisons of (i) length and (ii) pixel count were first made between replicate culture containers within the same treatment. Those replicates which were not significantly different ($p < 0.05$) were combined for the between treatment comparisons. For the between treatment comparisons, the criterion for a significant effect was more conservative ($p < 0.05/N$, where N is the number of comparisons).

Lower pixel counts occurred with increasing levels of starvation (Table 5.4). Length was not a factor in these differences, since larvae tended to continue growing as they starved (larvae fed 8 d at 14 °C) or remained the same length (larvae reared at 11 °C). Pixel count did sometimes differ between replicates within treatment, but the differences were generally not as great as between treatments (Table 5.4). The coefficient of variation (CV) of pixel count increased with starvation, but not the skewness of pixel count (Table 5.4).

To examine the effect of temperature on ORO lipid, comparisons were made among fed larvae reared at the 2 temperatures on each of days 14, 16, 18, and 26 (Table 5.5). Mann-Whitney comparisons were made in the manner described above. Larvae at 14 °C had significantly higher pixel counts on 3 of 4 days, but the effect of temperature on ORO lipid was confounded with the effect of temperature on length (Table 5.5). The CV and skewness of pixel count were not affected by temperature (Table 5.5).

5.3.3 ORO lipid in larger hatchery-reared larvae

ORO lipid was readily apparent in the larvae obtained from the Fink Cove hatchery (Plate 5.1). Most of the ORO stain was taken up in the area of the digestive gland (Fig. 5.2) where it tended towards a deep red or black colour. Lipid globules were most prevalent in the largest larvae from the Fink Cove hatchery (> 250 μm; Plate 5.1). Pixel count again increased with the length of the larvae (Fig. 5.4c).

Table 5.4. Effects of starvation on ORO lipid in scallop larvae. Shown are 3 groups of scallop larvae reared under different conditions. Each line of data is from a single culture container. Results of within-group pairwise comparisons using the Mann-Whitney test are depicted with superscripted letters. Replicate lengths or pixel counts with the same superscripted letter were not significantly different at a probability level of 0.05. Lengths or pixel counts in different treatments with the same superscripted letter were not significantly different at a probability level of 0.05/N, where N is the number of comparisons. T: temperature; CV: coefficient of variation (%); S: skewness (positive values of S indicate distribution is skewed to the right).

T	----N Days----		Age	N	---Length (μm)--		---------Pixel Count--------		
(°C)	Fed	Starved	(d)		Mean	CV	Mean	CV	S
11	8	2	14	16	118 ^{a}	4.2	1490 ^{a}	21.5	-0.9
11	8	2	14	30	125 ^{b}	4.5	1349 ^{a}	27.8	0.3
11	8	4	16	30	124 ^{b}	7.1	928 ^{b}	98.6	1.7
11	8	4	16	30	125 ^{b}	5.0	895 ^{b}	68.0	1.6
11	8	6	18	18	128 ^{b}	4.9	718 ^{b}	55.5	0.3
14	8	2	14	30	126 ^{a}	6.9	1923 ^{a}	30.5	0.1
14	8	2	14	30	126 ^{a}	5.4	2564 ^{b}	39.2	0.1
14	8	4	16	30	127 ^{a}	7.8	1411 ^{c}	60.6	0.4
14	8	4	16	30	129 ^{a}	7.3	1044 ^{d}	57.3	-0.0
14	8	6	16	28	136 ^{b}	6.0	1552 ^{cd}	70.9	1.5
14	8	6	16	29	139 ^{b}	7.3	1479 ^{cd}	43.6	0.4
11	18	2	24	30	152 ^{a}	6.9	3644 ^{a}	38.4	0.5
11	18	2	24	22	153 ^{a}	6.2	2874 ^{b}	36.9	1.0
11	18	4	26	15	153 ^{a}	6.0	2748 ^{c}	46.8	1.5
11	18	4	26	30	150 ^{a}	6.4	2148 ^{c}	26.4	-0.0

Table 5.5. Effects of temperature on ORO lipid in 4 age groups of fed scallop larvae. Results of within-group pairwise comparisons using the Mann-Whitney test are depicted with superscripted letters. Replicate lengths or pixel counts with the same superscripted letter were not significantly different at a probability level of 0.05. Lengths or pixel counts in different treatments with the same superscripted letter were not significantly different at a probability level of 0.05/N, where N is the number of comparisons. T: temperature; CV: coefficient of variation (%); S: skewness.

T	Age	N	----Length (μm)----		--------Pixel Count-------		
(°C)	(d)		Mean	CV	Mean	CV	S
11	14	30	132 a	3.5	2894 a	21.8	0.9
11	14	30	131 a	6.1	2566 a	24.5	0.1
14	14	30	130 a	6.4	2772 a	34.1	0.3
14	14	30	140 b	6.0	5003 b	22.4	-0.4
11	16	30	136 a	3.7	1901 a	24.4	-0.5
11	16	30	138 a	7.7	2656 b	26.2	-0.5
14	16	24	135 a	7.4	3554 c	31.6	-0.3
14	16	30	159 b	8.3	3925 c	25.3	-0.2
11	18	30	147 a b	6.6	3645 a	23.1	0.2
11	18	30	139 c	5.7	3567 a	22.6	0.5
14	18	30	146 a c	9.7	3850 b	26.3	0.2
14	18	30	152 b	6.4	4240 b	25.2	0.5
11	26	30	161 a	6.6	4250 a	31.9	1.0
11	26	30	160 a	8.1	4100 a	33.3	-0.1
14	26	13	163 b	8.0	5252 a	25.8	0.4
14	26	30	172 b	8.8	4852 a	43.0	0.9

Plate 5.1 Large sea scallop larvae stained with Oil Red O. All were obtained from the Fink Cove hatchery and are 28 d post-fertilization. (a)-(d) are from May 15, 1989. (e)-(h) are from Sept. 25 1989. Scale bar at bottom. Variability in contrast among specimens due to both (i) differences in larval thickness and (ii) lighting conditions when individual larvae were photographed. Lipid globules of ca 5-15 μm diameter are most evident in (a) and (d).

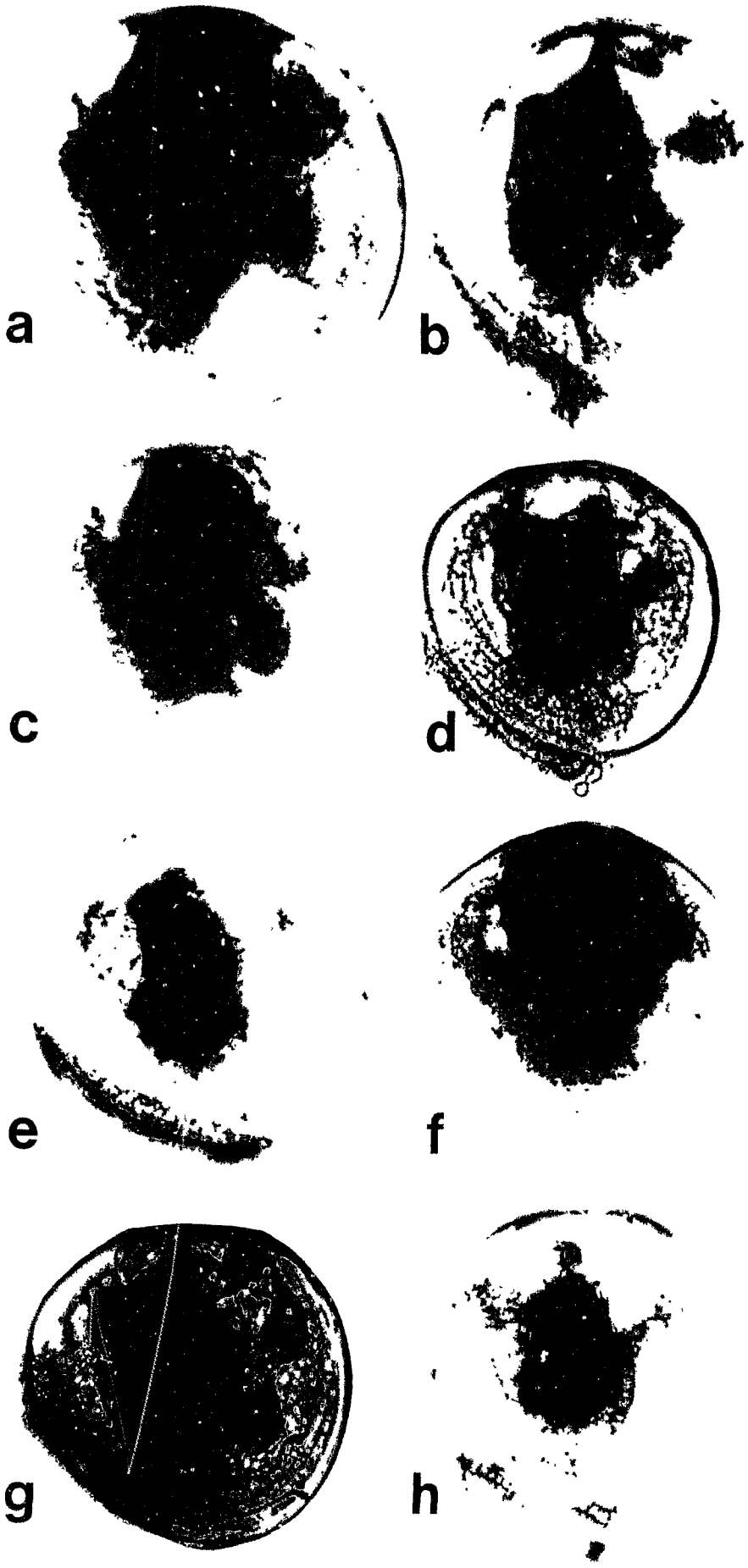

Plate
5.1

Differences in the ORO lipid between the two cultures of larvae from the Fink Cove hatchery were also apparent. Larvae obtained in May (Plate 5.1a-d) were larger and had more ORO lipid than larvae of the same age obtained in September (Plate 5.1e-f). Even larvae only ca 210 μm in length from May had numerous large lipid globules (Plate 5.1d), while in larvae ca 230 μm in length obtained in September, the lipid globules were smaller and less numerous.

Starvation reduced ORO lipid in the Fink Cove larvae after 4-6 d. This is apparent visually (Plate 5.2), and from the statistical comparisons among the starved larvae (Table 5.6). The distribution of ORO lipid within the larvae also changed with starvation. After 6 d without food the little ORO lipid which remained in the larvae was confined to a loop within the anterior region of the intestine (Fig. 5.2 and Plate 5.2e, f). The CV of pixel count also increased in starved larvae (Table 5.6).

5.3.4 ORO lipid in sea-caught larvae and stain artifacts

Examination of scallop larvae collected on Georges Bank revealed problems with the ORO stain which made the measurement of ORO lipid problematic. First, it appeared that ORO did not stain all the lipid in many larvae. Larvae less than 150-200 μm seldom had any apparent lipid globules, and often little or no ORO stain. In samples from the well mixed location there were few sea scallop larvae of any size with ORO stain. At other stations the lipid globules in large larvae appeared to be incompletely stained, since some crescent shapes were apparent rather than full globules (Plate 5.3a-d). The second problem related to the ORO stain was that many larvae had a stain precipitate, which was evident from its intense black colour and crystalline structure (Plate 5.3e). When the precipitate was at the periphery of the shell, isolated from the digestive system, as in Plate 5.3e, the lipid globules in the digestive gland were usually normally stained and ORO lipid was easily quantified using the pixel count. However in some larvae what

Plate 5.2. Starved sea scallop larvae stained with Oil Red O. All were obtained from the Fink Cove Hatchery on Sept. 25 when they were 28 d post-fertilization. (a)-(b): starved 2 d; (c)-(d): starved 4 d; (e)-(f): starved 6 d. Refer to scale bar at bottom of Plate 5.1.

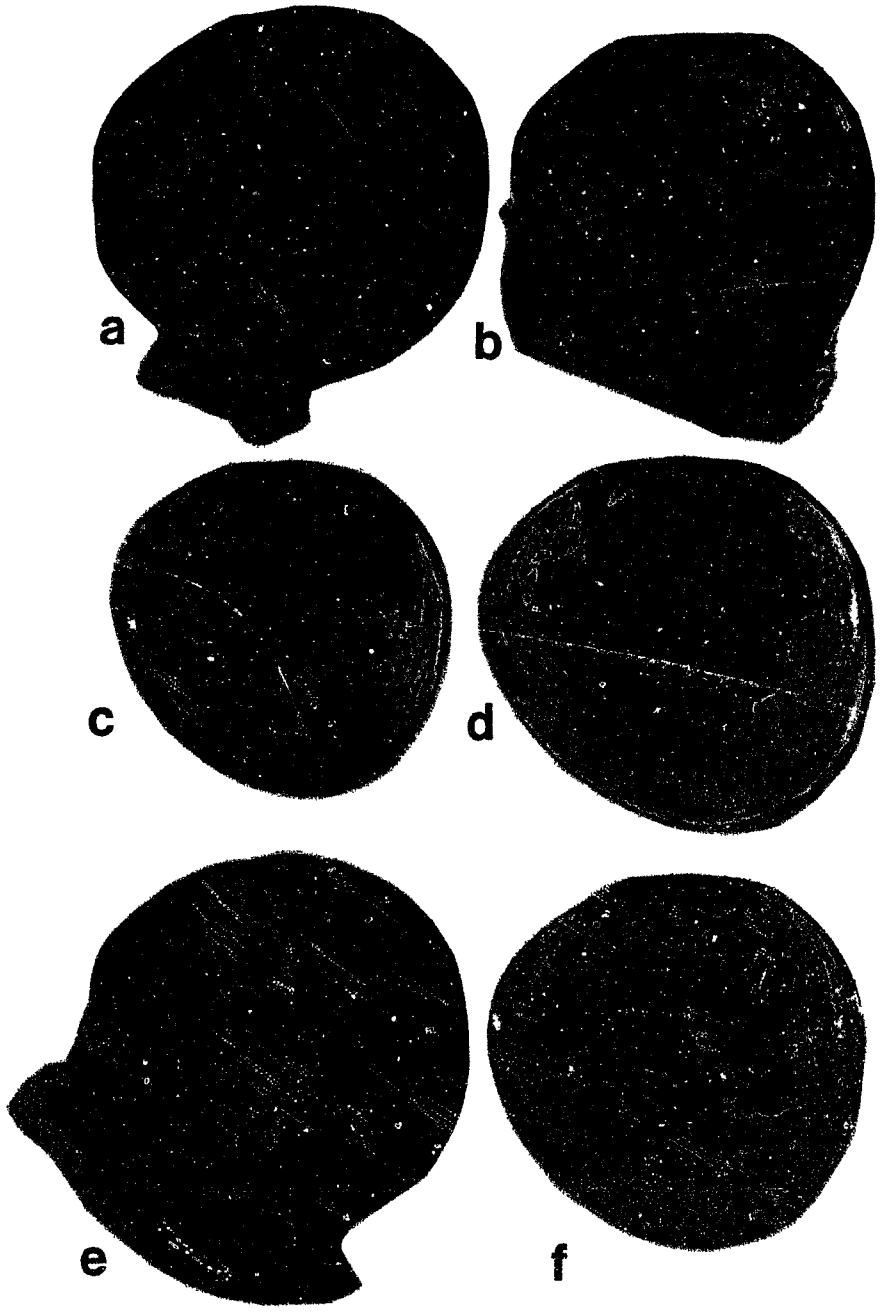

Plate 5.2

Table 5.6. ORO lipid in large (> 220 μm) hatchery-reared sea scallop larvae and effects of (i) starvation and (ii) sample preparation prior to staining. All larvae were obtained from the Fink Cove hatchery when they were 28 d old. Some were then starved (No. 4-7), and some were stained with different quantities of phytoplankton (No. 8-10). Results of within group pairwise comparisons using the Mann-Whitney test are depicted with superscripted letters for: (i) starved larvae and (ii) larvae stained with phytoplankton. Batches 1-10 are from September 1989; last 2 are from May 1989. vol: volume; CV: coefficient of variation (%); S: starved; Phyt: phytoplankton.

No.	Treatment	N	--Length (μm)-- mean	CV	----Pixel count--- mean	CV	Globule vol (μm^3) mean	CV
1.	control	21	224	6.7	4390	43	-	-
2.	control	21	218	7.9	6146	46	-	-
3.	control	22	222	5.9	4876	34	-	-
4.	S 2 d	20	224 [a]	7.7	3297 [a]	61	-	-
5.	S 3 d	20	224 [a]	6.1	5296 [a]	45	-	-
6.	S 4 d	30	220 [a]	4.5	575 [b]	206	-	-
7.	S 6 d	22	221 [a]	6.6	641 [b]	113	-	-
8.	+ 0.3 ml Phyt	22	224 [a]	5.9	3737 [a]	45	-	-
9.	+ 0.6 ml Phyt	20	220 [a]	4.7	5663 [b]	34	-	-
10.	+ 1 ml Phyt	30	220 [a]	4.6	1455 [c]	152	-	-
11.	control	21	257	3.5	8856	24	35742	40
12.	control	22	259	6.2	9640	19	28791	47

Plate 5.3. Stain artifacts in sea scallop larvae obtained from Georges Bank. (a)-(d): lipid globules incompletely stained; (e): stain precipitate away from digestive gland; (f): stain precipitate within digestive gland, coupled with incompletely stained lipid globules. Refer to scale bar at bottom of Plate 5.1.

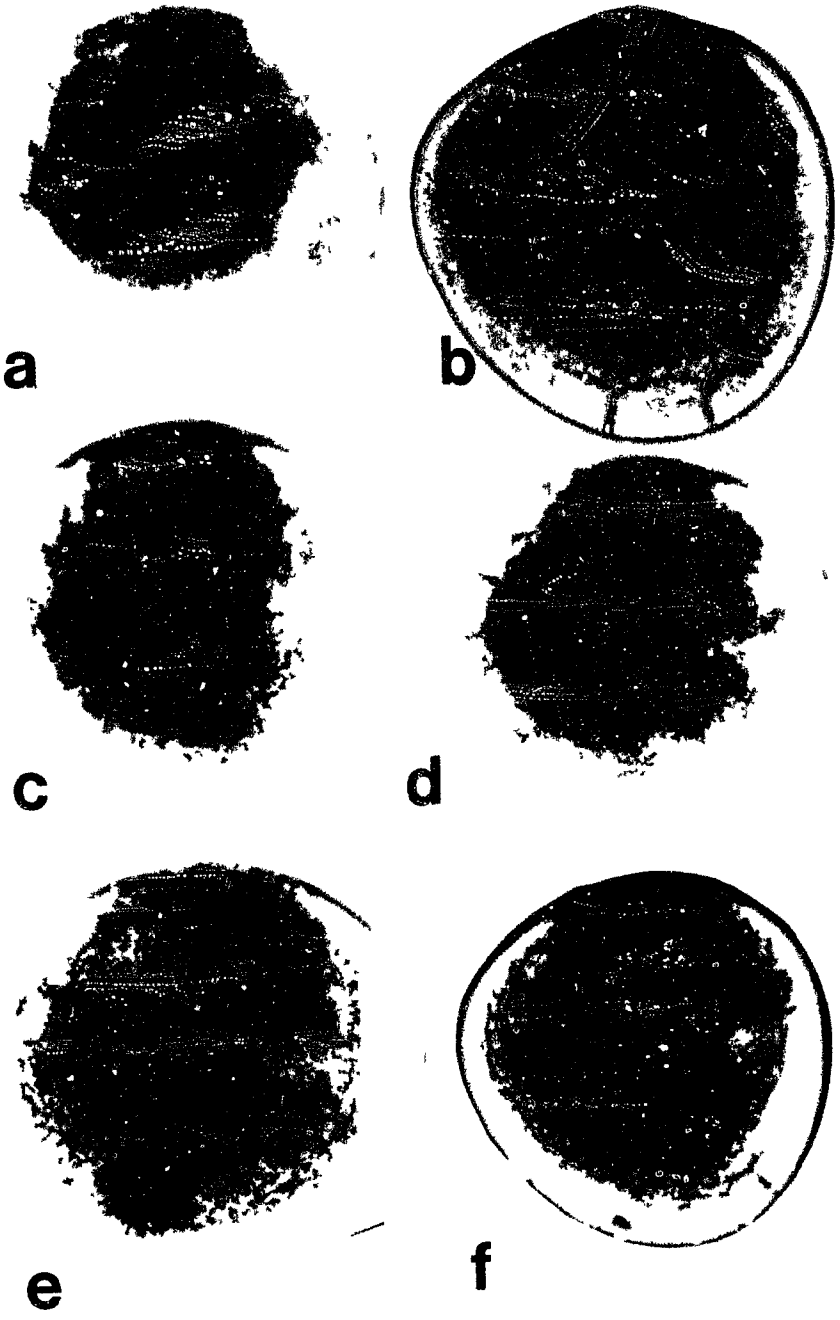

Plate 5.3

appeared to be a precipitate occurred in the digestive gland (Plate 5.3f) and in these larvae the lipid globules were usually incompletely stained as well.

The prevalence of these staining phenomena differed between stations, but in ca 2/3 of the samples the stain uptake was reduced and ORO quantification was ambiguous at best (Table 5.7). At the well mixed stations few bivalve larvae of any species showed much ORO uptake. Plankton samples from the well mixed area always had large quantities of phytoplankton, suspended particles and detritus which were difficult to separate from the bivalve larvae prior to staining. As a result a relatively large amount of wet material (up to 2 ml) was stained along with the bivalve larvae. To determine if this excess wet material could prevent the uptake of ORO stain by scallop larvae, some of the larvae obtained from the Fink Cove hatchery in September 1989 were taken aboard a small research vessel which then proceeded to the Bedford Basin. Freshly caught phytoplankton was added to samples of sea scallop larvae prior to staining. Stain uptake was unaffected by small amounts, but reduced with the addition of 1 ml of phytoplankton plus seawater (Table 5.6, Plate 5.4). In some larvae a stain precipitate was apparent, similar to that seen in sea-caught larvae.

At stations outside of the well mixed area, such as those on the slope (stations 7 and 8 -- Fig. 5.1) there was not as much wet material in the stain preparations, but many of the the larvae had partially filled lipid globules and stain precipitate (Table 5.7). The reason for these stain artifacts is not clear.

The lipid globule approach (see section 5.2.4.2) was developed to better quantify ORO lipid in larvae where (i) stain precipitate was present in the digestive gland and (ii) lipid globules were incompletely stained. Even with this method ORO lipid levels in Georges Bank larvae could be statistically analyzed only when the larvae were restricted in the following manner. First, ORO lipid was quantified only in larvae greater than

Table 5.7. Sea scallop larvae from Georges Bank and frequency of ORO stain artifacts. Remote precipitate: stain precipitate present but mostly remote from digestive gland. Low uptake: minimal stain uptake, or lipid globules less than 50% filled. P1, P2 and P3 denote consecutive plankton samples obtained while drifting at the 'stratified' and 'mixed' locations. [1]Larvae from consecutive drift samples combined (N m^{-3} is average). [2]Stain uptake was also negligible in other species of bivalve larvae. Freq: frequency. **Data from these stations retained for statistical analysis.

Oceanographic regime	Sampling dates	Stn(s)	N m^{-3}	N examined (> 230 µm)	Freq of stain artifacts (%) Remote precipitate	Low uptake
Stratified	Oct. 6	P1**	23	42	90	10
		P2**	30	40	89	8
		P3**	50	43	89	11
Mixed	Oct. 6	P1-P2[1]	< 5	3	0	100[2]
Frontal	Oct. 10	8	202	20	0	100
		7	303	42	59	40
		6	260	7	57	43
		2	64	20	85	15
		5	200	66	70	30
		3	145	56	38	44
		4	366	38	11	89
Stratified	Oct. 14	P1**	109	41	83	17
		P2**	457	42	78	19
		P3**	422	45	93	7
Mixed	Oct. 14/15	P1-P3[1]	< 10	9	22	78

Plate 5.4. Effect of sample preparation on ORO uptake. Larvae were obtained from the Fink Cove hatchery in September 1989. Freshly caught phytoplankton was added to the stain preparations. (a) and (b): 1 ml phytoplankton added; (c): 0.6 ml phytoplankton added. Refer to scale bar at bottom of Plate 5.1.

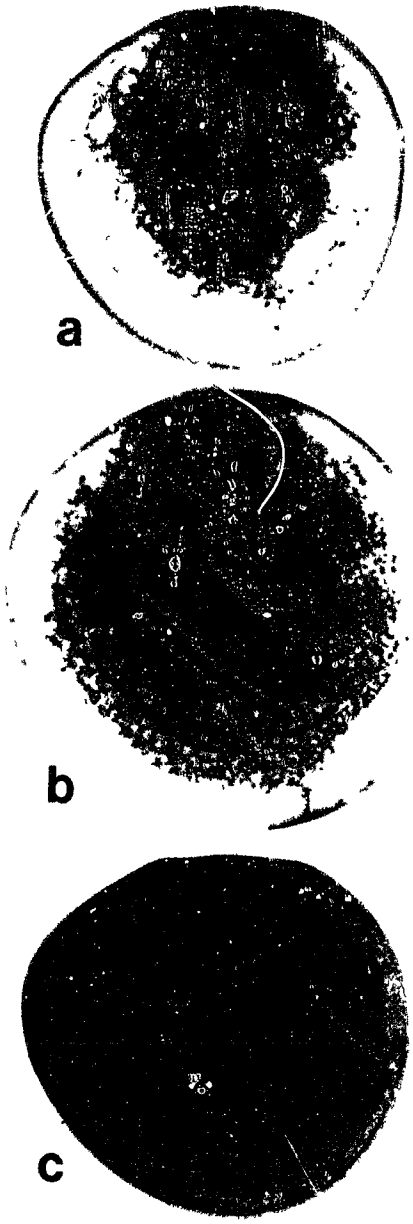

Plate 5.4

230 μm in length since at this size lipid globules were usually visible. Second, samples were retained for statistical analysis only if larvae with low stain uptake comprised less than 20% of the sample. The samples collected from the stratified locations on Oct. 6 and Oct. 14 met the latter criterion (Table 5.7). The frequency of low stain uptake was low for one other sample (station 2), but because there was no replicate sample fraction there, data from this station is not analyzed.

5.3.5 ORO in larvae from stratified locations: Oct. 6 vs Oct. 14th

Most larvae collected from the stratified location on Oct. 6 (Plate 5.5) had levels of ORO lipid comparable to the hatchery-reared larvae of similar size (Plate 5.1). Many larvae collected from the stratified location on Oct. 14 (Plate 5.6) had levels of ORO lipid which were lower than those of the hatchery-reared larvae but there was no evidence of starvation. Of the 224 larvae greater than 230 μm examined from the collections on Oct. 6 and Oct. 14, none had the characteristics of a starved larva (Plate 5.2). The greatest percentage of ORO lipid in sea-caught larvae was always in the digestive gland.

The means of both measures of ORO lipid (pixel count and globule volume) in the Georges Bank larvae (Table 5.8) were higher on Oct. 6 than on Oct. 14. To determine if this difference was significant, and to analyze variation in ORO lipid due to plankton sample and sample fraction, I used a statistical model similar to that shown in Equation 1:

$$P_{ijkl} = \mu + L_{ijkl} + D_i + PS_{j(i)} + SF_{k(ij)} + e_{l(ijk)} \qquad (2)$$

where P_{ijkl} is the pixel count of individual larvae; L_{ijkl} represents the effect of larval length, the covariate; D_i (i = 1 or 2) represents the effect of the i th sampling date, $PS_{j(i)}$ (j = 1...3) represents the effect of the j th plankton sample for sampling date i ; $SF_{k(ij)}$ (k = 1 or 2) represents the effect of the k th sample fraction for sampling date i and plankton sample j , and $e_{l(ijk)}$ represents the error associated with the l th larva (l= 1...n; mean n = 18) in the k th sample fraction. Length was included as a covariate because ORO lipid of the sea-caught larvae increased with length (Fig. 5.5), as in hatchery-reared larvae.

Plate 5.5. ORO lipid in 8 representative sea scallop larvae obtained from Georges Bank on October 6. Refer to scale bar at bottom of Plate 5.1.

Plate 5.6. ORO lipid in 8 representative sea scallop larvae obtained from Georges Bank on October 14. Refer to scale bar at bottom of Plate 5.1.

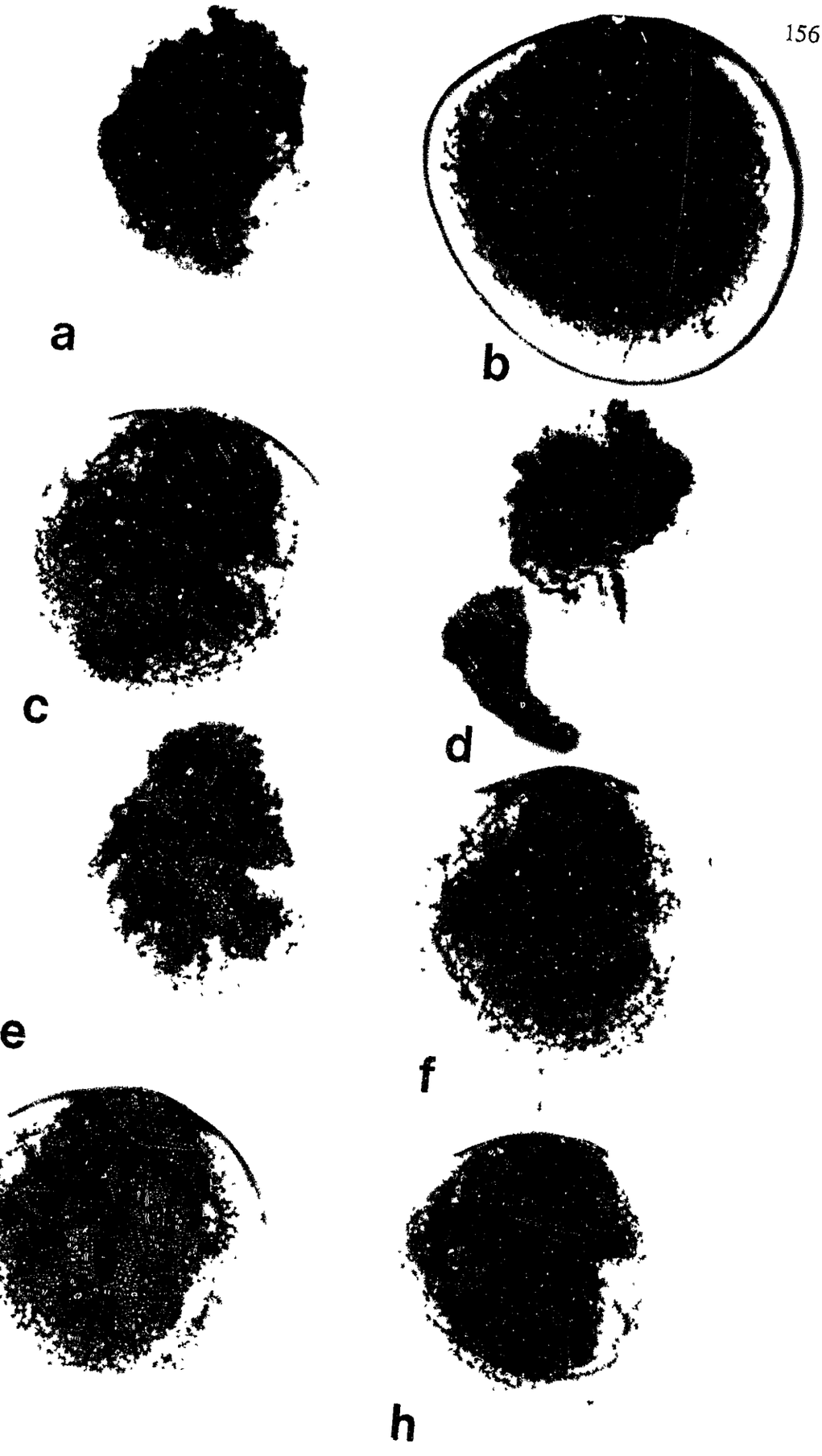

Plate
5.5

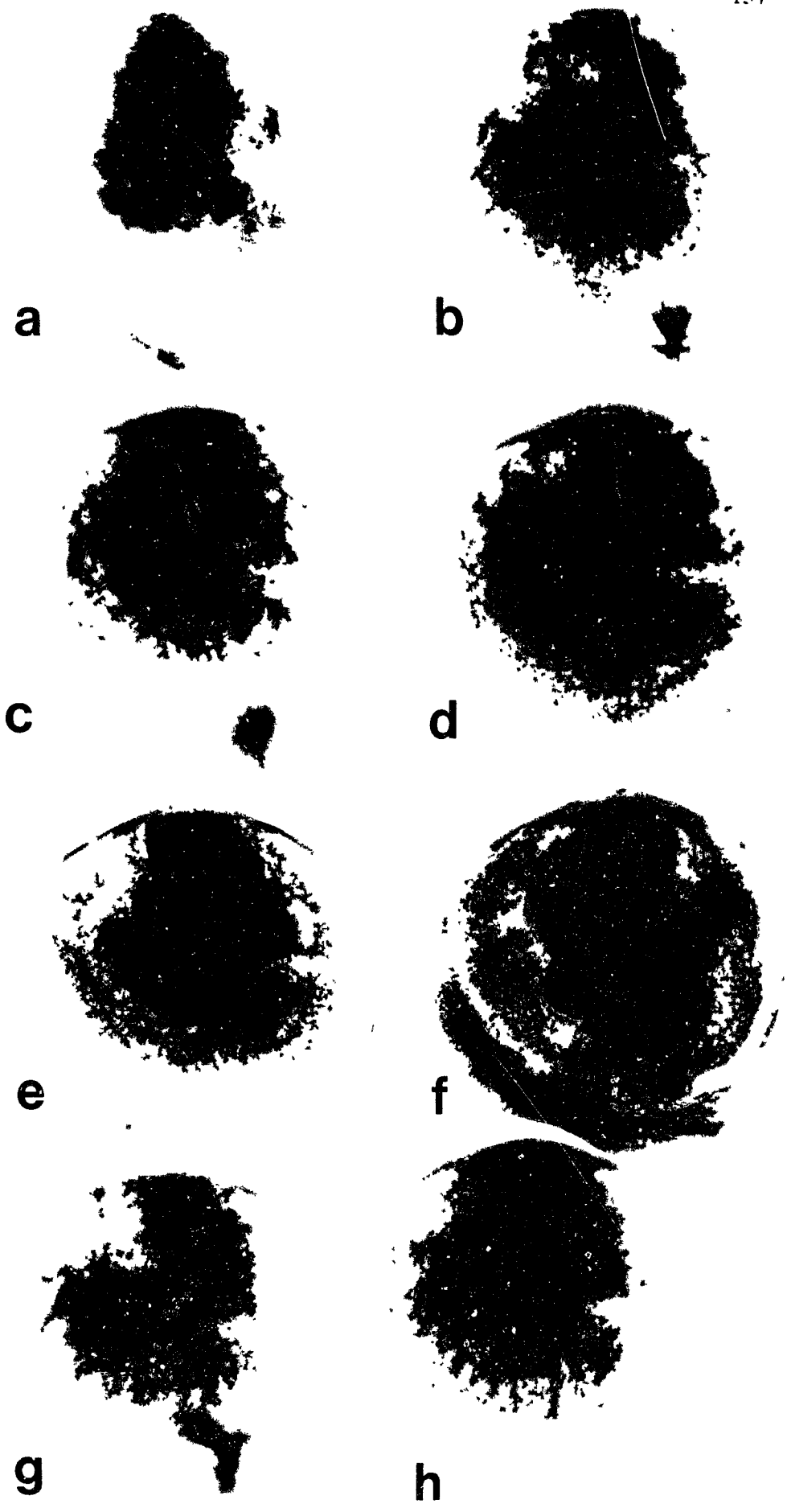

Plate
5.6

Table 5.8. Summary statistics for ORO lipid in sea scallop larvae collected on Georges Bank on Oct. 6 and Oct. 14. On each date 3 plankton samples (1, 2, and 3) were obtained while drifting. Two sample fractions (a and b) were stained from each plankton sample. CV: coefficient of variation (%); S: skewness (positive values of S indicate distribution is skewed to the right). Where N for length, pixel count and globule volume was not the same, range is given.

Date	Sample fraction	N	---Length--- Mean	CV	-------Pixel count------ Mean	CV	S	----Globule volume--- Mean	CV	S
Oct. 6	1a	18	264	8.6	10521	30.4	1.4	30156	65.0	1.3
	1b	20	279	6.5	10264	25.9	-0.5	38934	38.2	-0.2
	2a	19	271	6.4	9959	30.0	0.1	31327	45.7	0.8
	2b	18	263	7.9	10180	32.3	1.2	38929	67.7	1.0
	3a	19	263	8.1	10323	26.5	0.3	27434	84.4	1.5
	3b	19	273	5.2	9991	20.3	0.5	36872	43.1	0.4
Oct. 14	1a	18	258	5.6	7812	34.8	1.0	19521	66.9	1.5
	1b	12-15	262	5.2	7999	17.2	0.3	23817	35.2	0.1
	2a	16	264	5.7	7574	26.6	-0.0	28059	58.7	1.8
	2b	20-21	262	2.7	6244	31.9	0.6	19225	47.2	0.7
	3a	20	267	4.5	6629	27.3	0.2	24421	61.3	1.3
	3b	20-21	267	5.7	8346	27.4	0.3	21439	47.3	1.4

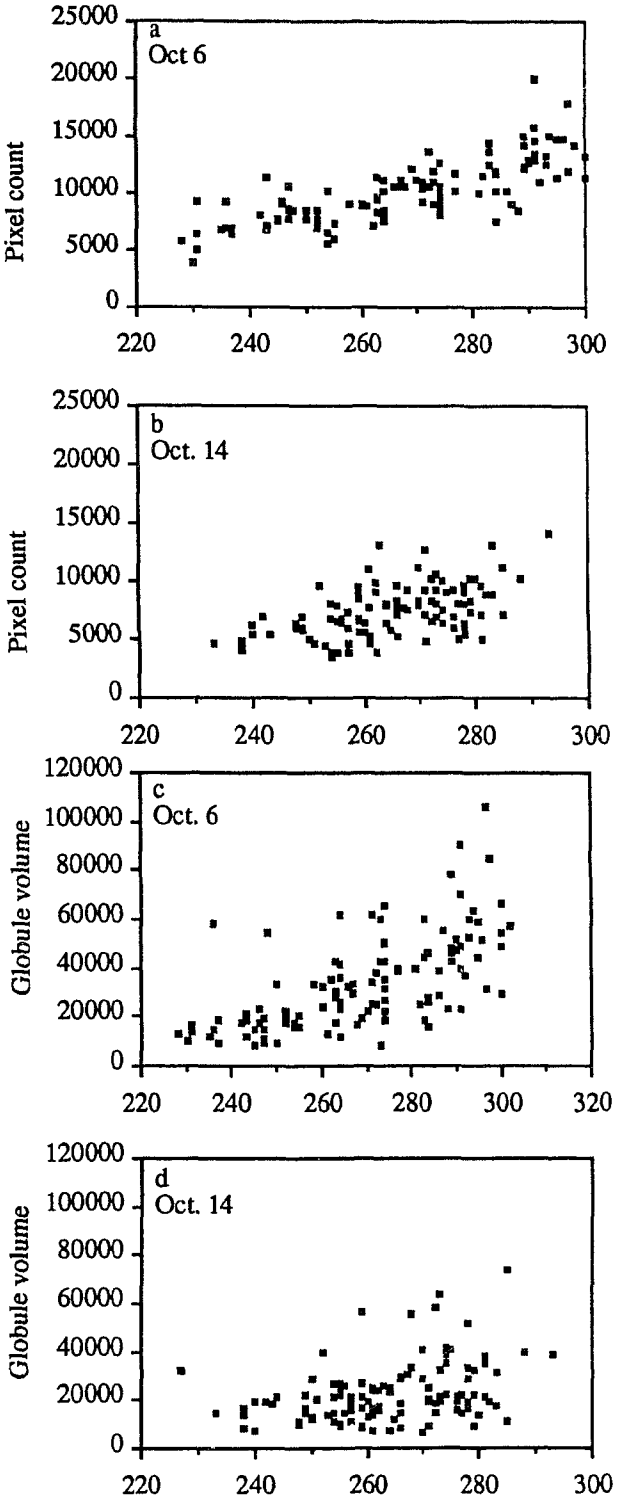

Figure 5.5. ORO lipid versus length in sea scallop larvae collected from Georges Bank. (a): pixel count for larvae from Oct. 6.; (b): pixel count for larvae from Oct. 14; (c) globule volume for Oct. 6; (d): globule volume for Oct. 14.

Variation in globule volume using the above model was not analyzed since globule volume was correlated with pixel count (Spearman rank correlation coefficient of 0.60, n = 218, $p < 0.01$).

To test for the ANCOVA assumption that the relationship between pixel count and the covariate was the same for each treatment, terms for the interactions with length were added to Equation 2. Estimation of the model parameters using SYSTAT indicated no significant interactions with length. The other assumptions of normality and homoscedasticity were also verified after estimating the model parameters without the interaction terms. Pixel count was log transformed after the initial analysis. Levene's test (Snedecor and Cochran 1980) indicated that the variance of pixel count did not differ among treatments, and a normal probability plot of the residuals indicated little deviation from normality.

The analysis of covariance (Table 5.9) shows that date had a significant effect--the larvae collected on Oct. 14 had lower pixel counts than those collected on Oct. 6. The 'Sample' factor was not significant, indicating that the variation in ORO lipid levels among larvae from 3 consecutive plankton samples was minimal. Variation due to sample fraction was significant.

There was no indication that either the coefficient of variation of ORO lipid, or the skewness of ORO lipid differed between dates (Table 5.8).

5.3.6 Physical conditions and chlorophyll *a* concentration: Oct. 6 vs Oct. 14

Physical conditions and chlorophyll *a* changed little during the 3 profiles on Oct. 6 (Fig. 5.6) and Oct. 14 (Fig. 5.7), indicating that on both dates the ship drifted within a homogenous water mass. Differences between the 2 dates with respect to chlorophyll *a* and density structure of the water column were apparent however (Table 5.10). The concentration of chlorophyll *a* on Oct. 6, when sea scallop larvae had more ORO lipid,

Table 5.9. Variation of ORO lipid in Georges Bank scallop larvae. Shown are results of an analysis of covariance (ANCOVA), with larval length as the covariate. The dependent variable (pixel count) was log-transformed prior to the analysis. See Table 5.8 for statistics on individual sample fractions.

Source	Sum of Squares	Df	Mean Square	F-Ratio	P
Length	8.742	1	8.742	222.72	0.000
Date	3.841	1	3.841	30.24	0.000
Sample (total)	0.506	4	0.127	0.51	0.305
Oct. 6	0.021	2	0.011	0.04	0.960
Oct. 14	0.485	2	0.242	0.97	0.452
Sample Fraction	1.494	6	0.249	6.38	0.000
Error	8.086	206	0.039		

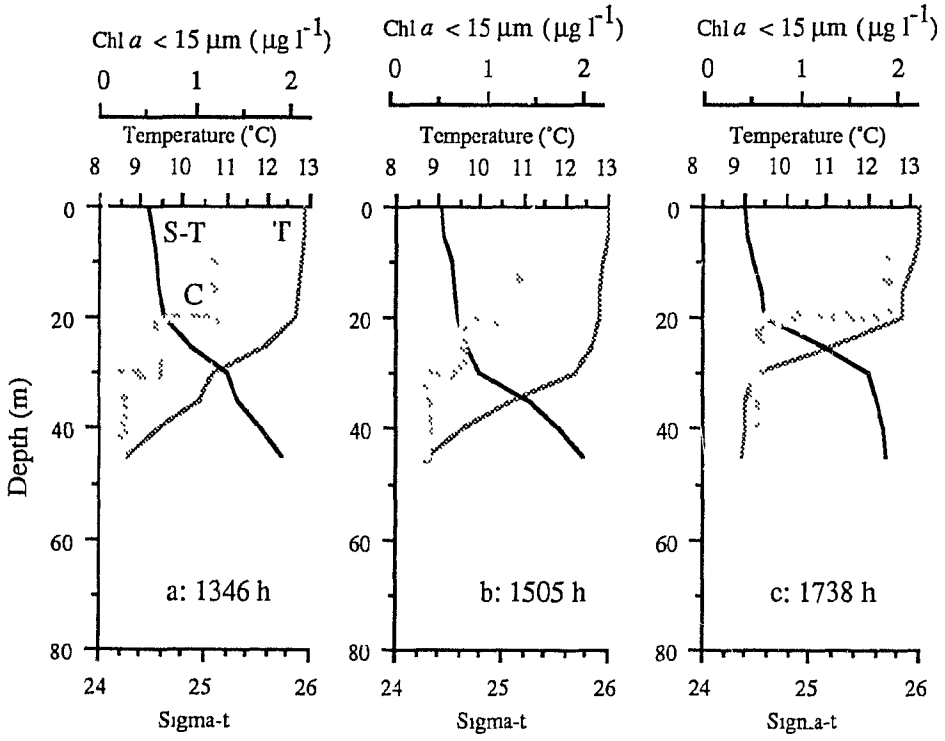

Figure 5.6. Profiles of temperature (T), sigma-t (S-T), and chlorophyll *a* (C) on Oct. 6. Each set of profiles are a composite of conditions while the ship drifted for ca 30 min.

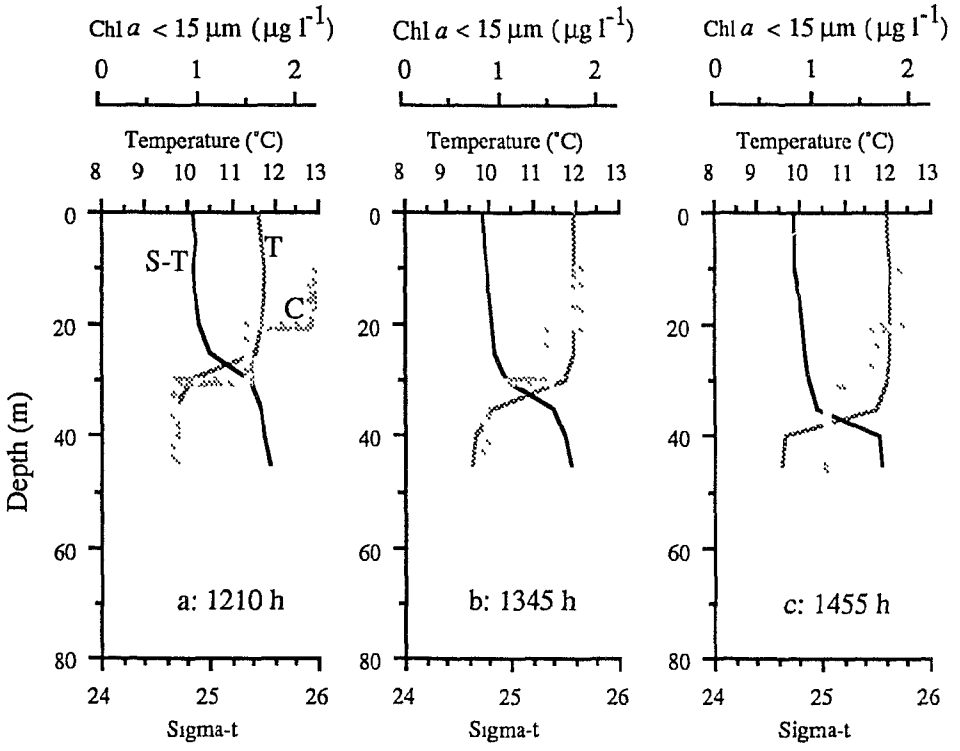

Figure 5.7. Profiles of temperature (T), sigma t (S-T), and chlorophyll *a* (C) on Oct. 14. Each set of profiles are a composite of conditions while the ship drifted for ca 30 min.

Table 5.10. Summary of physical conditions and chlorophyll *a* concentrations ($\mu g\ l^{-1}$) during collection of Georges Bank sea scallop larvae for ORO lipid measurement. Pycnocline defined as the centre of the 10 m interval where change in sigma-t is maximum.

Date	Sample	Mean chl *a* < 15 μm	ΔSigma-T/ Δ depth	Pycnocline depth (m)	Mean temperature (°C) above pycnocline
Oct. 6	1	0.75	0.028	25	12.7
	2	0.97	0.030	35	12.6
	3	0.90	0.029	25	12.8
Oct. 14	1	1.33	0.016	28	11.7
	2	1.28	0.018	33	11.9
	3	1.49	0.018	37	12.0

was about 2/3 that of Oct. 14 (Table 5.10). The density gradient was greater on Oct. 6th, and the pycnocline was shallower. The mean temperature above the pycnocline on Oct. 6 was only slightly higher than Oct. 14 (Table 5.10).

5.4 Discussion

5.4.1 Utility of ORO as a condition index in sea scallop larvae

Changes in the quantity of ORO lipid in scallop larvae were significant after periods of 2-6 d starvation, as in studies of other species of bivalve larvae (*Teredo navalis*, *Mercenaria mercenaria*, and *Crassostrea virginica*) which have used both qualitative and quantitative measures of ORO lipid (Gallager and Mann 1981, 1986a, Gallager et al. 1986). In the factorial experiment of the present study, parametric statistics were not possible, but comparisons among groups of larvae which differed little with respect to length, indicated that ORO lipid decreased when starvation was prolonged 2 d.

In larger larvae, a decline in ORO lipid was not evident until 4 d of starvation. This apparent decrease in the sensitivity of the ORO lipid measure (pixel count) for large larvae may be related to the the fact that pixel count is essentially a measure of stained area rather than stained volume. During starvation of these larger larvae, substantial declines in lipid volume may be reflected by relatively small declines in the area stained by ORO. Unfortunately measurements of lipid globule volume on hatchery-reared larvae were too scant to assess whether this measure is more sensitive.

The restriction of ORO lipid to the intestines in starved sea scallop larvae (Plate 5.2) is similar to what was observed in *Crassostrea virginica* when reared under stressed conditions by Gallager et al. (1986). They suggested that intestinal ORO lipid was less labile, but why it became more prominent with increased starvation in the present study is not clear. Whatever the explanation, it appears that the percentage of intestinal ORO lipid is a good indicator of stress in sea scallop larvae.

The higher levels of ORO lipid in sea scallop larvae reared at 14 °C is at least partially due to the increased growth rate at 14 °C (larger larvae have more ORO lipid). The experimental temperatures (11 and 14 °C) were typical of what sea scallop larvae experience in nature (Chapter 2). Temperatures higher than normal may reduce the rate of ORO lipid accumulation, perhaps because the elevated metabolic rate at higher temperatures exceeds the rate at which energy can be stored in the form of lipid (Gallager and Mann 1981, Gallager et al. 1986). Potentially as important as the effect of temperature on the level of ORO lipid is the interaction among temperature, ORO lipid, and survival. It may be that at different temperatures the level of ORO lipid necessary for the survival of short term stress differs. In studies of ORO lipid levels in nature, it would be prudent to compare only larvae from similar temperature regimes.

In addition to the percentage of intestinal ORO lipid and the mean level of ORO lipid, the coefficient of variation (CV) of ORO lipid appears useful as an indicator that a population of sea scallop larvae is stressed. The CV tended to increase with starvation in sea scallop larvae (Tables 5.4, 5.6) as reported for other bivalve larvae (Gallager and Mann 1986a). Unlike Gallager and Mann (1986a), I found no increase in skewness of the ORO lipid measure in starved scallop larvae.

Measurements of ORO lipid quantity and distribution are useful as indicators of larval condition, but questions remain concerning the lipid specificity of the Oil Red O stain (Gallager and Mann 1986a, Mann 1986a). The stain appears to have a strong affinity for neutral lipid, but the different appearance of the stain in hatchery-reared larvae suggests ORO may not stain neutral lipid exclusively. In some larvae the stain was intense red bordering on black with no apparent lipid globules in the digestive gland and lighter red elsewhere, while in other larvae lipid globules were clearly apparent. In starved larvae dark ORO was largely restricted to the intestine and no globules were apparent. Although these differences may reflect changes in storage of neutral lipid with

development and with stress, it is also possible that structural lipids are sometimes stained. This would contribute to variability in any measure of ORO lipid, and reduce its effectiveness as an indicator of energy storage. Measures of ORO lipid which rely on total stain per larva do not account for potential differences in what ORO stains. Measuring only lipid globule volume overcomes this problem, but is labour intensive and has high measurement error.

Problems with the ORO measure that are specific to sea-caught larvae are (i) the effect of staining the larvae with other components of the plankton which increase the moisture content of the stain preparation and apparently reduce stain uptake; (ii) partially stained lipid globules; and (iii) stain precipitate. The first problem should be corrected if sea scallop larvae are fully separated from the remainder of the sample. This puts restrictions on the number of larvae which can be collected given the constraints of sorting small larvae at sea. The second and third problems may also be related to moisture in the stain preparation, but since these artifacts occurred at stations where additional moisture was not an obvious problem, some other factor(s) must be involved. With regard to the stain precipitate, this is not uncommon when dyes which dissolve in tissues are used in a saturated form, as is Oil Red O stain (Humason 1972).

Alternatives to the ORO stain as a lipid index for bivalve larvae include other lipid specific stains (e.g. Nile Red) or improvements to microtechniques for lipid class analysis (Fraser 1989).

5.4.2 Condition of late stage sea scallop larvae on Georges Bank

ORO lipid was quantified only in large larvae (> 230 μm) from the weakly stratified part of the Northeast Peak of Georges Bank. Although this limits the conclusions which can be drawn about the condition of sea scallop larvae on the bank, this area is one where the abundance of all sizes of sea scallop larvae is generally high, and where the

production of large larvae is coarsely estimated as 120-1500 m^{-2} per year based on surveys in 1986 and 1987 (Chapter 3).

None of the larvae collected in 1988 had the characteristics of starved larvae from the hatchery. This indicates that this extreme form of food limitation is infrequent for these large larvae, although the possibility that starving larvae are rapidly lost from the water column because of a decline in buoyancy as lipid reserves are utilized (Gallager 1985, Mann 1986a), cannot be ruled out. If starvation of sea scallop larvae in nature occurs it is probably most important during the earlier larval stages when lipid reserves are lower, and the ability to locate food may not be as great. In the present study I observed little stain uptake in larvae less than ca 150-200 μm, but because of an inability to determine whether this lack of ORO lipid was related to problems with the stain preparation, I concentrated only on large larvae, which clearly had some ORO lipid. If in fact these small larvae have little neutral lipid, then food limitation may be severe.

ORO lipid levels for larvae collected on Oct. 6 were similar to well-fed hatchery reared larvae, while those collected on Oct. 14 were only moderately lower. This finding differs from observations on sea-caught larval fish in which lipid levels have frequently been noted to be lower than their counterparts in the hatchery, perhaps due to higher activity levels or less available food in nature (Ehrlich 1975, Blaxter 1976, Fraser et al. 1987).

The large larvae collected on Oct. 14 were not starving but did have lower ORO lipid than the larvae collected on Oct. 6. The factor(s) underlying these lower ORO lipid levels is not immediately obvious since the most obvious candidate, food concentration (as indicated by chlorophyll *a* in the < 15 μm size class), was actually higher on the latter date. Either the measure of food was inappropriate, or the decrease in ORO lipid between Oct. 6 and 14 was due to factors other than food. The food measure would be inappropriate if sea scallop larvae satisfy most of their nutritional requirements from other

food sources, or if the scale (time or space) of the phytoplankton biomass measurements was inappropriate. Bivalve larvae can utilize dissolved organic compounds (Manahan and Crisp 1982, Welborn and Manahan 1990) and other invertebrate larvae can utilize bacteria (Rivkin et al. 1986), but whether these substances form an important dietary component in nature is unresolved.

In my estimates of food availability, the implicit assumption is that the 10-15 m depth intervals over which chlorophyll *a* was measured do not average out peaks in concentration which might be important to sea scallop larvae. In Chapter 2 it is argued that subsurface chlorophyll *a* maxima are unlikely to be important on Georges Bank at this time of year. Furthermore, ambient levels of phytoplankton biomass should reflect recent feeding conditions, since high levels of chlorophyll *a* can persist in the weakly stratified part of Georges Bank for several days (Chapter 2).

In Chapter 2 it was shown that sea scallop larvae on Georges Bank were not found where phytoplankton < 15 μm was most concentrated. This suggests that food concentrations are adequate for scallop larvae throughout the upper part of the water column and that aggregations are not food related, or that the larvae concentrate within some unmeasured food resource. The lower ORO levels of the sea scallop larvae on Oct. 14 may be related to the lower stratification of the water column at that time. Lower condition of larval fish in well mixed waters has been explained by the low food patchiness associated with low stratification (Buckley and Lough 1987, Frank and McRuer 1989), but for scallop larvae, there are also non-trophic explanations. Since turbulence is generally greater when stratification is low, the suspended particulate load is greater, and particulates may interfere with larval bivalve feeding or swimming (Carriker 1986). In a more direct manner, increased vertical turbulence may increase the energetic costs of swimming to maintain position.

Whether the Oct. 14 larvae had a lower rate of survival through to settlement because of their lower levels of ORO lipid is of interest. This would occur if ORO lipid levels were below the minimum required to complete metamorphosis, but the critical levels are unknown. The lower ORO lipid levels may indicate that the larvae were developing more slowly, which would prolong the larval period when mortality is thought to be highest (Thorson 1950, Vance 1973, Houde 1987). Future studies should address whether decreased stratification results in decreased condition, and whether this leads to decreased rates of development and survival. This study is among the first to use this or any other index to quantitatively assess condition in sea-caught bivalve larvae. The scope of the measurements of ORO lipid in Georges Bank scallop larvae were limited, but indicate that with improved techniques for measuring neutral lipids, there is potential for significant advances in understanding the patterns and consequences of variation in larval condition.

5.5 Summary

A condition index for bivalve larvae based on lipid stained by the Oil Red O stain (ORO lipid) was tested on both hatchery-reared and sea-caught larvae of the sea scallop. ORO lipid per larva was quantified indirectly using an image analysis system. ORO lipid increases with larval size and thus any length differences among groups of larvae must be considered if ORO lipid levels are to be compared. In larvae reared in the the hatchery at two temperatures (11 and 14 °C), ORO lipid decreased with increasing periods of starvation. Ad-hoc experiments with older and larger hatchery-reared larvae confirmed that ORO lipid in sea scallop larvae declined in larvae which were starved. There was also an increase in the percentage of intestinal ORO lipid in these larger larvae when they were starved.

The effect of temperature on ORO lipid was difficult to separate from the effect of temperature on growth rate, because of the increase in ORO lipid with size. In studies of ORO lipid levels in nature, it would be prudent to compare only larvae from similar temperature regimes.

When the sea scallop larvae obtained from Georges Bank were examined, it was apparent that more than half the samples had larvae which were incompletely stained or had some stain precipitate. Some of these artifacts appear to be related to sample preparation at sea and the artifacts were duplicated under controlled conditions. Because of the stain artifacts, ORO lipid was quantified only in large larvae (> 230 μm in length) from stations where the stain artifacts were not severe.

Of 224 larvae obtained from weakly stratified waters on Oct. 6 and Oct. 14, none had the characteristics of starved larvae. Larvae collected on Oct. 6 had lipid levels very similar to well-fed hatchery-reared larvae of a similar size. Larvae collected on Oct. 14 had ORO lipid levels which averaged ca 2/3 those of the previous week but these lower levels were not related to measures of ambient phytoplankton biomass. Chlorophyll *a* <

15 μm was actually higher on Oct. 14 than Oct. 6. The lower ORO levels may be related to lower water column stratification and associated increased turbulence on Oct. 14. Improvements in the techniques for measuring the condition of sea-caught bivalve larvae are necessary to determine the significance of variation in larval condition.

Conclusions

Sea scallop larvae are not passively distributed in the water column, but physical processes may often override their swimming ability. Evidence that scallop larvae can exercise control over their depth by swimming vertically comes from observations of (i) diel vertical migration, and (ii) aggregations of larvae associated with the pycnocline and apparent avoidance of water below the pycnocline. Evidence that the depth regulating ability of scallop larvae is limited comes from observations that (i) subsurface aggregations move vertically with the pycnocline, and (ii) larvae are dispersed over the whole water column when there is no density stratification.

Initially it was thought that the subsurface aggregations of sea scallop larvae might be a result of feeding where phytoplankton was most concentrated. Measurements of chlorophyll *a* within a size range upon which sea scallop larvae can feed (< 15 μm) found little evidence to support this idea, since the subsurface aggregations were nearly always below the depth where chlorophyll *a* was most concentrated. This suggests that food concentrations are adequate for scallop larvae throughout the upper part of the water column, and that aggregations are not food related, or that the larvae concentrate within some unmeasured food resource.

A non-trophic explanation for the subsurface aggregations lies with the tendency of larvae to swarm and the decreased turbulence associated with the pycnocline. Perhaps it is only near the pycnocline that the aggregations are not dispersed by turbulence. Where the pycnocline was poorly developed, and turbulence was presumably high throughout the water column, sea scallop larvae did not form subsurface aggregations. The critical level of physical stratification (as indicated by the vertical gradient in sigma-t) for the formation of subsurface aggregations of scallop larvae on Georges Bank was very similar to the critical level observed at an inshore location close to Grand Manan Island.

The swimming behavior of sea scallop larvae, which is limited in scope due to low swimming speed, is likely to have only a small effect upon larval dispersal. The association of scallop larvae with the pycnocline may retard transport by currents, because current speed declines with depth. However sea scallop larvae do not appear to "use" the vertical current shear through vertical migration. Two features of vertical migration can alter the currents to which larvae are exposed: the amplitude, and the frequency. A large amplitude increases the chances that larvae will encounter different currents due to vertical shear. Migration on a tidal frequency would enable larvae to utilize strong or weak currents at particular stages of the tide. The vertical migration of sea scallop larvae can be described as small amplitude (< 10 m) and daily in frequency.

Plankton surveys conducted between 1985 and 1988 provide three lines of evidence that most sea scallop larvae are retained on the northeast part of Georges Bank: (i) few larvae were collected off the edge of the bank; (ii) the mean abundance of larvae for different areas was correlated with a coarse index of spawning biomass (fishery landings); and (iii) the length frequency of larvae differed between Georges Bank and the surrounding area. Given that the swimming behavior of sea scallop larvae has a limited effect on dispersal, the physical retentiveness of Georges Bank must be the primary factor determining larval retention there. Swimming behavior of other more mobile larvae may enhance retention, but such behavior is probably of secondary importance for Georges Bank. On other banks in the area physical retention is lower; this may limit the supply of sea scallop larvae to these banks.

On the Northern Flank of Georges Bank, a frontal zone between well mixed and stratified waters, the abundance of sea scallop larvae was not consistently related to any physical feature of the frontal zone per se. In October the frontal zone is not as intense as in summer, particularly in the upper 40 m where sea scallop larvae are most concentrated. Declines in larval abundance usually occurred in the area of the bank edge (200 m

isobath), on the stratified side of the frontal zone, where the residual current was directed on-bank. Dense patches of larvae can occur on the Northern Flank when on-bank stratification is high, but the mechanism (s) underlying the formation of these patches is not understood and could involve either physical concentration or enhanced growth and survival. On-bank stratification varies over periods of days, and is probably affected by wind.

On the weakly-stratified part of Georges Bank there is strong coherence in larval size structure over distances of 20-40 km and at time scales of less than a day, probably due to strong tidal mixing. The abundances of different sized larvae were positively correlated, indicating that the factors affecting spatial distribution were not size specific. Changes in the position and size structure of some high density larval patches over a period of 4-6 d are consistent with transport of scallop larvae in the direction of the residual currents, but the rate of movement and the precise path of any group of larvae will be a function of the hatching location and current field, which can vary over periods of days. Larval exchange among adult scallop aggregations on Georges Bank probably occurs. The larvae which seed the productive Northeast Peak may originate locally or on other parts of Georges Bank (Southeast Part or South Channel), and thus the bank may be a single recruitment unit for sea scallops.

A condition index based upon the lipid stained by Oil Red O (ORO lipid) can detect declines in condition brought about by starvation and presumably other forms of stress in hatchery-reared sea scallop larvae. Care must be taken in applying the method to sea-caught larvae because of stain artifacts. Measurement of ORO lipid in 224 large larvae from the weakly stratified part of Georges Bank suggests (i) starvation of large larvae is rare (ii) the condition of many large larvae is as good as in well fed hatchery-reared larvae and (iii) the condition of large larvae may at times be more a function of physical stratification than of the concentration of available phytoplankton. Larvae collected on

October 14 had lower ORO levels than larvae collected on October 6 even though chlorophyll *a* was substantially higher on October 14. Further measurements of larval condition using improved methods are necessary to confirm these findings.

A coarse estimate of the annual production of late stage larvae on Georges Bank is 120-1500 m^{-2}. Since the densities of settled scallops 1-2 yr later are at most 5 m^{-2}, considerable mortality must be associated with the settlement and post-settlement periods. Mortality due to starvation of these large larvae is probably not important -- food limitation probably acts in a less direct manner, by extending the planktonic period and thus increasing the exposure to predation.

Appendices

Appendix 1. Frequency with which larval scallop plankton samples were subsampled, and associated variability

Following table shows frequency of subsampling (% of total samples examined) by sampling year. Increase in subsampling after 1985 reflects increases in both the numbers of samples and number of larvae per sample

Year	Pump	Bongo nets
1985	0	5
1986	0	25
1987	19	38
1988	66	79

A partitioning of the variance between (i) station location and (ii) subsampling follows. The analysis is based on 41 stations where larvae from 2 equal sized fractions (1/32, 1/16, 1/8, 1/4 or 1/2) were enumerated and used to estimate the total number of larvae in the sample.

Source	Sum of Squares	D.F.	Mean Square	Variance Component	Percent
Station	24.685	40	0.617	0.306	98.2
Subsamples	0.229	41	0.006	0.006	1.8

Appendix 2. Larval scallop abundance and sampling variability

Data for the following tables were obtained in the Bay of Fundy in September and October of 1984, and on Georges Bank in 1985. A full analysis of the Bay of Fundy data is presented in Tremblay and Sinclair (1988).

Appendix Table 2.1 Results of hierarchical analysis of variance of larval scallop abundance estimates via pump sampling. Shown are components of variance associated with (i) station location (ii) depth interval and (iii) replicate pump samples within the same depth interval. Based on 9 stations each with 4 depth intervals and 2 pump samples per interval. Data were log transformed prior to analysis of variance.

Source	Sum of Squares	D.F.	Mean Square	Variance Component	Percent
Station location	10.220	8	1.278	0.120	41.6
Depth interval	8.612	27	0.319	0.151	52.4
Replicate	0.622	36	0.017	0.017	6.0

Appendix Table 2.2. Results of hierarchical analysis of variance of larval scallop abundance estimates via bongo net sampling. Shown are components of variance associated with (i) station location (ii) replicate plankton hauls at the same station. Based on 43 stations with 2 hauls per station. Data were log transformed prior to analysis.

Source	Sum of Squares	D.F.	Mean Square	Variance Component	Percent
Station location	41.694	42	0.993	0.457	85.4
Replicate	3.348	43	0.078	0.078	14.6

Appendix 3: Bongo sampling: Summary of gear depth and gear distance from bottom

Sampling period	Depth Range	N tows	Mean no. m off bottom	SD	Mean gear depth	SD
	<= 50	2	4.6	0.8	31.9	1.5
October	50-75	14	4.5	1.7	59.0	4.9
1985	75-100	23	4.8	1.6	80.9	6.7
	100-200	45	7.9	6.5	148.0	28.4
	> 200	19	47.4	37.9	197.5	7.2
	Total	103				
October	<= 50	18	9.4	1.3	29.5	7.5
1986	50-75	37	10.4	1.3	53.7	7.5
	75-100	53	10.4	2.2	77.3	7.0
	100-200	35	10.0	2.3	124.9	30.1
	> 200	39	782.5	75.2	199.6	1.6
	Total	182				
September	<= 50	1	9.5	-	14.5	-
1987	50-75	2	7.6	3.4	58.4	7.6
	75-100	5	7.9	2.9	77.3	7.1
	100-200	4	54.7	27.7	95.8	6.3
	> 200	4	140.9	18.1	97.6	4.6
	Total	16				
October	<= 50	21	5.6	5.5	36.1	5.5
1987	50-75	47	7.5	5.5	56.4	5.5
	75-100	29	8.7	7.5	77.8	7.5
	100-200	11	10.4	34.3	136.9	34.3
	> 200	14	52.0	6.3	193.5	6.3
	Total	122				
September	<= 50	0	-	-	-	-
1988	50-75	8	8.7	1.9	56.8	2.7
	75-100	0	-	-	-	-
	100-200	1	10.0	-	140.0	-
	> 200	2	39.1	32.2	209.4	3.8
	Total	11				
October	<= 50	5	9.2	1.1	39.0	1.0
1988	50-75	27	13.1	6.8	53.6	9.6
	75-100	6	11.8	8.6	69.7	8.5
	100-200	9	60.9	24.5	108.7	18.2
	> 200	10	123.3	48.2	113.4	37.1
	Total	57				

Appendix 4. Calculation of volumes sampled by bongo nets and editing of flowmeter data

Estimates of volumes sampled during individual bongo net hauls were based on flowmeter readings. Other correlates of the volume sampled are the length of wire out, and the size of the wire angle. The latter gives a measure of the strength of the current flowing through the nets. Flowmeters are fairly reliable, but can give spurious readings for the following reasons : (i) material entrapped in propellers which decreases the number of revolutions; (ii) wind blowing propellers when the net is not actually sampling; (iii) reader error. To estimate the volume sampled where flowmeter data were missing or spurious, the data were edited and compared in the following way.

1. Calibration curves for individual flowmeters were used to estimate the length of the water column sampled (LNGFLOW) for each tow. Spurious flowmeter readings were identified by comparison with other data (e.g. length of wire out, other flowmeter readings at the same station) and eliminated. Number of these was small (< 10%).

2. The best available data was used to develop prediction equations for the volumes sampled during tows rejected in step 1. Only the data from tows for which both flowmeter readings were available (except for 1986 when only one net was metered) and in good agreement (i. e. differing by less than 50% of the lower reading) were included in this data subset.

3. Prediction equations were developed by regressing LNGFLOW on the length of wire out (WO), and the wire angle (WA). Initial plots and regressions indicated that the form of the equation which best satisfied the assumptions of homoscedasticity and normality was as follows:

$$\text{Log (LENGFLOW)} = \text{constant} + B1\ (\text{Log(WO)}) + B2\ (\text{WA})$$

4. Extreme outliers for tows where there was no replicate flowmeter reading were identified and rejected. Regression rerun.

5. Using the final equations from step 4, the length of the water column sampled was estimated for each of the tows rejected in steps 1 and 4. To estimate the volume sampled, the following relationship was used:

$$N\ m^3\ \text{sampled} = (\pi\ r^2 \cdot \text{LENGFLOW})$$

where r is the radius of the opening of the net (= 0.2 m)

6. Finally, the number of larvae per m^2 was estimated as follows:

$$N\ \text{larvae}\ m^{-2} = (\text{sample count} / N\ m^3\ \text{sampled}) \cdot D$$

where D is the the depth of water column or 200 m, whichever was less.

The results of steps 1-6 are summarized in Table A4.1.

Table A4.1. Specifics of regression equations used to calculate volumes sampled where flowmeter data was missing or spurious. Regression coefficients are shown for the the flowmeter used in the net from which most of the larval scallop enumerations were done (identified by the raised cross). ** $p < 0.001$; * $p < 0.01$; N. S.: not significant.

Cruise	N tows	Flowmeters used	N tows with paired FLM readings	N used to develop equation	Multiple regression coefficients				
					Constant	Log(WO)	WA	R^2 (Adj)	N recalc·
1985	177	4470+, 4471	168	163	0.332*	0.983**	-0.003*	0.87	14
1986	182	4526	0	169	0.687**	0.915**	-0.006**	0.78	13
1987 (Sept)	17	4519+,4526	12	9	1.946*	N. S.	N. S.	0.52	8
1987 (Oct)	122	4519+,4526	62	53	0.766*	0.909**	-0.005	0.70	9
1988 (Sept)	4	4519+,4526	1	--	--	--	--	--	4
1988 (Oct)	69	4519+,4526	69	59	N. S.	1.062**	N. S.	0.58	10

Appendix 5. Size selectivity of sea scallop larvae in 85 µm mesh nets vs. 53 µm nets.

The following table shows the of abundance of different sized scallop larvae caught by nets of different mesh size. Data are from bongo net hauls in Oct. 1988 when a 53 µm net was on one side, and an 85 µm net on the other. In the calculation of mean selectivity for a given size class, only those hauls where some larvae were collected in the 53 µm net were included. The first 2 length classes were grouped because larvae in the 103.5 µm length class were collected in only 1 85 µm haul. From the data below, full selectivity by the 85 µm net appears to occur at a larval scallop length of ca 126 µm. Sel: selectivity.

Appendix 5. Size selectivity of sea scallop larvae in 85 µm mesh nets vs 53 µm mesh nets.

Sta. no.	24	24		25	25		4	4		14	14		3	3			
Mesh size	53	85		53	85		53	85		53	85		53	85			
N measured	147	215		151	143		113	223		111	204		235	206			
N in sample	710	226		1404	566		3232	1968		924	328		948	1208			
Leng wat col	42	55		110	100		282	277		76	61		102	95			
Vol sampled	5	7		14	13		35	35		10	8		13	12			
Sounding	48	48		178	178		60	60		48	48		64	64			
No/m2	4934	2069		19957	7310		5568	3326		5793	1655		5100	6003			
Length of Sea scallop larva	N/m2 (calc)	N/m2 (calc)	Sel. 85:53	N/m2 (calc)	N/m2 (calc)	Sel. 85:53	N/m2 (calc)	N/m2 (calc)	Sel. 85:53	N/m2 (calc)	N/m2 (calc)	Sel. 85:53	N/m2 (calc)	N/m2 (calc)	Sel. 85:53	MEAN SEL.	CORR. FACTOR
103.5 & 109.:	2719	164	0.060	1718	102	0.060	2563	0	0.000	2714	89	0.033	413	29	0.071	0.045	22.40
115.0	873	106	0.121	793	51	0.064	788	15	0.019	1357	49	0.036	760	58	0.077	0.063	15.76
120.8	201	192	0.956	1189	256	0.215	49	15	0.303	157	32	0.207	651	87	0.134	0.363	2.76
126.5	201	298	1.481	2908	665	0.229	0	0		157	89	0.570	87	117	1.343	0.906	1.10
132.3	336	395	1.176	3040	1278	0.420	0	45		313	203	0.648	109	204	1.880	1.031	0.97
138.0	302	231	0.765	2643	1380	0.522	49	30	0.605	157	154	0.985	87	58	0.671	0.710	1.41
143.8	67	212	3.154	1322	562	0.425	0	104		52	105	2.021	22	204	9.399	3.750	0.27
149.5	101	135	1.338	1454	818	0.563	148	30	0.202	104	65	0.622	152	262	1.726	0.890	1.12
155.3	34	96	2.867	925	358	0.387	99	89	0.908	0	41		22	291	13.428	4 397	0.23
161.0	0	96		661	358	0.541	0	119		0	16		195	262	1.343	0.942	1.06
166.8	0	0		793	256	0.322	49	89	1.816	209	57	0.272	217	175	0.806	0.804	1.24
172.5	34	58	1.720	925	256	0.276	0	164		104	49	0.466	130	437	3.357	1.455	0.69
178.3	0	0		132	307	2.321	0	75		0	41		174	321	1.846	2.083	0.48
184.0	34	48	1.434	396	204	0.516	0	89		0	65		239	437	1.831	1.260	0.79
189.8	0	0		396	307	0.774	49	75	1.513	52	65	1.244	130	233	1.790	1.330	0.75
195.5	0	19		264	51	0.193	49	104	2.119	0	32		87	233	2.686	1.666	0.60
201.3	0	10		132	0	0.000	197	104	0.530	0	24		195	291	1.492	0.674	1.48
207.0	0	10		0	0		49	164	3.330	52	57	1.088	174	146	0.839	1.752	0.57
212.8	34	0	0.000	132	51	0.387	148	104	0.706	157	32	0.207	152	321	2.110	0.682	1.47
218.5	0	0		0	0		99	149	1.513	0	24		130	291	2.238	1.876	0.53
224.3	0	0		0	0		148	119	0.807	104	32	0.311	87	117	1.343	0.820	1.22
230.0	0	0		132	0	0.000	99	254	2.573	0	41		109	321	2.954	1.842	0.54
235.8	0	0		0	0		197	164	0.832	0	24		87	175	2.014	1.423	0.70
241.5	0	0		0	0		246	328	1.332	0	24		130	117	0.895	1.114	0 90
247.3	0	0		0	51		148	254	1.715	0	32		195	204	1.044	1.380	0.72
253.0	0	0		0	0		197	179	0.908	104	41	0.389	130	291	2.238	1.178	0.85
258.8	0	0		0	0		49	179	3.632	0	81		87	175	2.014	2.823	0.35
264.5	0	0		0	0		49	104	2.119	0	73		43	117	2.686	2.402	0.42
270.3	0	0		0	0		49	60	1.211	0	8		109	29	0 269	0.740	1 35
276.0	0	0		0	0		49	119	2 422	0	8		0	0		2.422	0.41

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