THE RELEVANCE OF FEEDING ENVIRONMENT TO "RETENTION" OF ATLANTIC HERRING (*CLUPEA HARENGUS*) LARVAE

By

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À Mônica, Pedro e Mariana

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Abstract

Despite the economic importance of herring fisheries and several years of intensive research, proximate causes for variability in the recruitment of herring remain unclear. In this thesis, the feeding environment of herring larvae from the coastal waters off southwest Nova Scotia is evaluated and discussed in the light of current hypotheses that attempt to explain variable survival during the early life history of pelagic fish.

Throughout the North Atlantic, fall-spawned herring larvae predominantly inhabit coastal regions with tidally well mixed waters. Data from two cruises confirm that large aggregations are confined to well mixed waters off SW Nova Scotia. Physical-behavioural interactions could contribute to this pattern. The diel periodicity of vertical migration exhibited by the larvae, however, is not sufficient to explain the maintenance of their horizontal position through interaction with semi-diurnal tidal current. Alternatively, lower prey abundance in stratified waters could lead to increased mortality from starvation and account for the observed spatial distribution of the larvae. Results show that larvae in well mixed and stratified regions off SW Nova Scotia were exposed to similar concentrations of microzooplankton. Thus, variation in food concentration alone is not sufficient to explain the maintenance of the aggregations in the well mixed region.

It has frequently been suggested that relative motions of predator and prey influence the feeding rate of planktonic organisms. Dimensional analysis of relevant biological parameters describing herring life history and field data shows that tidally well mixed regions constitute a preferential feeding environment for herring larvae because turbulence enhances predator-prey encounter rates. Hence, feeding rates should be greater in well mixed regions as compared to stratified regions with similar food abundance. Indeed, measurements of RNA/DNA ratios indicate that larvae from the well mixed areas were healthier than those from stratified areas, and had similar condition throughout the water column. However, larvae from both regions were generally in good condition, supporting the initial finding that during the fall, food is adequate for larval growth throughout the coastal zone.

This thesis supports the hypothesis that tidal mixing enhances the feeding environment of herring larvae. Furthermore, it indicates that as food availability decreases towards the winter, larvae in stratified waters may be more susceptible to starvation. Therefore, differential mortality between the two regions may be the proximate cause for the apparent retention of larvae during winter in the well mixed waters off southwest Nova Scotia.

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Chapter 1

Introduction

Two hypotheses, presented by Hjort [1914], are milestones in the study of the variability of marine fish populations. The first hypothesis stresses the timing between spawning and phytoplankton blooms, and states that the cause of differential mortality between years is a result of differential food availability at critical stages of larval fish development. The second hypothesis deals with the influence of drift of eggs and larvae away from the appropriate distributional area due to interannual differences in the circulation. These hypotheses have never been falsified. Instead, they have evolved independently, have been adapted and re-stated, and have generated a debate in the literature (*e.g.* see Sinclair, 1988, and Cushing, 1990).

Since Hjort [1914] proposed that variability in recruitment was related to food availability during the early stages of the life history of fish, two main hypotheses evolved to link fish larval survival to their food. The "match-mismatch" hypothesis [Cushing, 1975] stated that survival would be enhanced by a match between food production and larval emergence. The "stable-ocean" hypothesis [Lasker, 1975] linked increased food supply to the maintenance of a stable, stratified ocean. Both of these hypotheses have a common cause of larval mortality, food limitation, and require a match between the larval and food distribution. According to Sinclair [1988], the theory of these hypotheses is conceptually attractive, but field tests undermine their validity. A key observation that led to the questioning of this

formulation is that the time of spawning for herring populations within the Gulf of Maine in the fall is not matched by a fall bloom of primary production [Iles and Sinclair, 1982].

Hjort's [1914] second hypothesis received more attention after Iles and Sinclair [1982] postulated the "herring stock hypothesis". The Iles and Sinclair hypothesis states that the number of herring stocks and the geographic location of their respective spawning sites are determined by the number, location, and extent of geographically stable larval retention areas. It decoupled fish spawning from food production. Iles and Sinclair [1982] showed that the size and location of these spawning areas correspond closely to physical features (well mixed areas bordered by fronts) that can be predicted by the Simpson and Hunter stratification parameter [Simpson and Hunter, 1974]. Sinclair and Iles [1985] argued that the relevant criterion is that maintenance of a reproductive unit is possible. Sinclair [1988] extended this hypothesis to populations of sexually reproducing marine species in general, and called it the "member/vagrant" hypothesis.

It is interesting to notice that studies of the early life history of herring were the backbone for the development of the match-mismatch and of the member/vagrant hypothesis. Cushing [1967] developed the match-mismatch hypothesis based on observations that on different areas of the North Sea herring spawning times were coincident with an increase in the production cycle. He further pointed out that for herring, plaice, sockeye salmon and cod the spawning season was fixed, with the standard deviation of the peak date of about 1 week, although the fish may spawn for a period of 2 to 3 months [Cushing, 1969], and that the standard error of the mean date is only 1–2 days [Cushing, 1990]. According to Rothschild [1986], this is important because it reflects the ability of fish not only to center their spawning activities at the most favorable time of the year, but also to extend these activities so that at least some of the spawning will coincide with the most favorable periods within the most favorable time of the year.

The problem with this interpretation rested on the fact that different herring

populations spawn at different spawning times throughout the year. Sinclair and Tremblay [1984] found it difficult to reconcile the wide range in timing of spawning with the phytoplankton literature on the timing of predictable blooms. They observed that larvae of a population develop within the specific oceanographic conditions of its retention area, and that metamorphosis occurs primarily within April to October. They noted that larvae hatched in spring and early summer have faster growth rates than larvae from the end of summer/fall spawning, and that they were able to metamorphose before October. Larvae hatched in the end of summer and fall metamorphose only in the subsequent April. They hypothesized that the timing of spawning is a function of the length of time necessary to complete the larval phase and yet metamorphose, and not of the production cycle.

Probably the most controversial issue involving this 2 hypotheses is the relative significance of the existence of retention areas and of larval drift to nursery areas [Townsend, 1992]. Again, studies on herring are behind this contention. Recently, Townsend [1992] and Heath [1992] have reviewed the ecology and dispersal of Atlantic herring larvae and have discussed this issue. Herring larvae in the northeast Atlantic and North Sea have been shown to exhibit a larval drift period and utilize both inshore and offshore nursery areas. With the exception of some regions around the British Iles, which present some overlap in the distribution of spawning and juveniles, all other regions present larval drift to nursery areas (see Heath [1992] for review). Here, the drift occurs in the larval stage, and the inter-annual variability in the drift pattern may be an important factor for recruitment variability [Bartsch *et al.*, 1989]. It is also thought that the advective transport route of the larvae in the North Sea may be the result of spawning strategies of herring in offshore spawning areas [Heath and Richardson, 1989].

In the northwest Atlantic, however, larvae seem to be retained in tidally mixed waters. In the George's Bank area, larvae are entrained by the anticyclonic circulation [Lough *et al.*, 1985], producing considerable overlap between the distribution of young and late larvae Larvae hatching from the eastern Maine–Grand Manan area,

as well as from smaller spawning units along the coast, are believed to rely on the residual circulation, as well as selective tidal transport, to move along the coast and eventually enter the numerous inshore nursery areas in estuaries and embayments [Graham, 1972; Graham *et al.*, 1990; Graham and Townsend, 1985; Stevenson *et al.*, 1989]. However, Chenoweth [1989] showed that a significant portion of the larval population in this region may be retained in the vicinity of the spawning grounds until late October, and that their retention was incomplete. There is no doubt that the majority of herring larvae on the Scotian Shelf are in fact retained for several months [Stephenson and Power, 1988].

The strongest evidence for retention of larvae in tidally mixed areas in the Gulf of Maine is presented by Townsend [1992]. Results from winter cruises show significant numbers of larvae overwintering offshore rather than in the inshore nursery areas. He also suggests that the possibility that larvae retained in the eastern Maine–Grand Manan area, or even on the Nova Scotian Shelf have contributed to springtime inshore samples could not be ruled out. He points out that, as proposed by Sinclair and Iles [1985], this influx of larvae into the inshore areas during the spring would assume dispersion from the retention areas of late-larvae that are near metamorphosis.

The "member/vagrant" hypothesis emphasizes that continued membership to a population in the oceans is what determines population regulation. Spatial processes, *e.g.* displacement from a distributional area appropriate for continued membership in the population, are sufficient for population regulation. Density-dependent energetic processes, *e.g.* predation, disease and starvation, are not necessarily required for population regulation. The existence of optimal conditions for the larvae is of secondary importance. One of the examples used to illustrate success of a population in spite of the lack of optimal conditions was low food availability for the larvae in SW Nova Scotia. They based their argument on the observation that primary production was low in the well mixed area, and that there was some evidence that zooplankton abundance was also low. The long larval phase and slow

growth rate shown by these fall spawners also supported such an interpretation [Sinclair and Tremblay, 1984].

The independence between larval fish distribution and its food as proposed by Sinclair and Iles [1985] was a challenge to the traditional food based hypotheses, and stimulated further studies in larval fish dynamics. Cushing [1986; 1990] pointed out that herring larvae in the Eastern Atlantic did not have a "retention" area. Rather, they were transported to nursery areas where food was abundant. Frank [1988] reported a strong onshore-offshore positive gradient in microzooplankton for the well mixed regions off SW Nova Scotia . He argued that bias in the sampling method and in the data presentation of Sinclair and Iles' [1985] zooplankton abundance invalidated their interpretation. However, studies in other tidally-driven frontal systems indicate that waters which are, or have become, stratified have higher concentrations of microzooplankton than well mixed regions [Holligan *et al.*, 1984; Scrope-Howe and Jones, 1985; Thompson and Harrop, 1991].

In this thesis, I intend to contribute to this discussion by carefully examining the feeding environment of herring larvae. This is done by considering not only the distribution of larval abundance and their prey, but by studying physical processes that are considered important to characterize the feeding environment of the larvae. Furthermore, the condition of the larvae in the different regions is evaluated in order to assess the direct effect of feeding . This study is conducted with the herring larval population off southwest Nova Scotia, which has been at the center of this controversy.

The herring (*Clupea harengus* L.) population off southwest Nova Scotia (NAFO Div. 4WX) supports the largest herring fishery in the western Atlantic [Stephenson *et al.*, 1987; Stephenson *et al.*, in press], and recent estimates indicate a stock size in the order of 600,000 to 1,000,000 t [Stephenson and Power, 1989a]. Like many other late summer and fall spawning populations of Atlantic herring, it spawns close to or in unstratified regions with strong tidal mixing [Lough *et al.*, 1985; Townsend *et al.*, 1986; Chenoweth *et al.*, 1989]. The herring larvae that result from the spawning in

this region form a large and well defined aggregation [Stephenson and Power, 1988] that emerges at the end of summer, persists during the winter months [Townsend, 1992], and is still present in March surveys [Stephenson and Power, pers. comm.].

In the next chapter, I characterize the spatial distribution of herring larvae in two different oceanographic regions off southwest Nova Scotia – an inshore well mixed area, and an offshore stratified region. The determination of the spatial distribution of the larvae is important to assure that the feeding environment being studied is that of the larvae. The results of two research vessel surveys conducted in the fall of 1989 and 1990 to collect data on the horizontal and vertical distribution of larvae are analyzed and discussed with respect to current understanding of herring larval dynamics. An alternative hypothesis, which relates food availability to the existence of the larval aggregation in areas of tidally well mixed waters, is presented. This hypothesis states that the average food availability is the same in the well mixed areas and in stratified waters.

With this hypothesis in mind, the microzooplankton distribution off SW Nova Scotia from previous studies is re-evaluated in Chapter 3. Available data sets in the literature and data collected here in a new survey are used to test this hypothesis. If stratified waters have the same, or more food available for the larvae, it suggests that larval aggregation is independent of food availability, and the hypothesis rejected. This chapter also evaluates the vertical distribution of the microzooplankton in the area of larval aggregation.

An alternative is that the feeding environment of the larvae is not completely characterized by measuring food abundance alone. Recent evidence suggests that small scale turbulence could enhance growth of fish larvae by increasing predator-prey encounter rates [Rothschild and Osborn, 1988; MacKenzie and Leggett, 1991], and it has been suggested that future research in larval fish dynamics should give more attention to this process [Heath, 1992]. This proposed enhancement in feeding success should be clearly evident in turbulent, tidally-mixed areas. In Chapter 4, dimensional analysis, coupled with relevant biological parameters describing herring

life history and field data from the previous chapters, is used to evaluate whether variations in small scale turbulence can influence their feeding success. The hypothesis that turbulent, tidally well mixed regions provide a preferential feeding environment for herring larvae is explored, and its implications discussed.

Finally, in Chapter 5, the physiological condition of herring larvae in the well mixed and stratified water is investigated using the RNA/DNA ratio. The condition index should reflect the time-integrated feeding conditions the larvae have been exposed to. If feeding success is the same in both, well mixed and stratified areas, the RNA/DNA ratio should be the same. If food is more abundant, or if small scale turbulence enhances feeding success, the RNA/DNA ratio of the larvae in the well mixed region should be higher. The distribution of the larval condition with respect to depth and period of the day is also investigated.

The thesis concludes with a summary of principal results from the previous chapters, and provides directions for fruitful future work.

Chapter 2

Distribution of herring larvae in well mixed and stratified waters

2.1 Introduction

Many late summer and autumn spawning populations of Atlantic herring (*Clupea harengus*) spawn in regions of tidally-induced well mixed water. In the Gulf of Maine/Bay of Fundy region, Boyar *et al.* [1973] identified 3 areas of larval distribution: Georges Bank, coastal Gulf of Maine, and Nova Scotia. Their observation was based on composite data from 8 years of survey (1962–1970); and they ascribed variations in larval aggregation in these areas to the surface circulation. This spatial coincidence – between spawning, larval distribution and well mixed waters – occurs throughout coastal areas of most of the North Atlantic. Iles and Sinclair [1982] showed that the size and location of these spawning areas correspond closely to physical features (well mixed areas bordered by fronts) that can be predicted by the Simpson and Hunter stratification parameter [Simpson and Hunter, 1974].

For some populations, a significant proportion of the larvae remain in these tidally well mixed areas for several months. This happens in the Gulf of Maine/Bay of Fundy region, where larval aggregations in four spawning areas (Southwest Nova Scotia, Eastern Maine-Grand Manan, Georges Bank, and Nantucket Shoals) occur

to a larger degree within vertically well mixed areas bordered by frontal zones [Iles and Sinclair, 1982].

In the SW Nova Scotia region, the spawning season extends from late July to early November [Das, 1968; Power and Stephenson, 1990; Power and Stephenson, 1991]. Herring eggs are incubated on the bottom for a period of 1 to 3 weeks [Blaxter, 1963]; hatching produces larvae between 5 and 10 mm [Das, 1968]. The duration of the larval phase is long for populations spawning in the autumn, with metamorphosis occurring in the early spring (see Sinclair and Tremblay [1984] for review). Thus growth (and feeding rate) is low compared to spring spawning herring populations [Sinclair and Tremblay, 1984].

The herring larvae resulting from spawning in this region form a large and well defined aggregation [Stephenson and Power, 1988]. This larval aggregation has been documented in annual autumn surveys since 1972 [Sinclair and Iles, 1985]. It appears at the end of summer/early fall and it persists during winter months [Townsend, 1992], and in early spring [Stephenson and Power, unpublished results]. These larvae remain in the well mixed area despite a residual current of approximately 18 $km\,d^{-1}$ in a NW direction [Stephenson and Power, 1988]. It would be expected that with residual flows of this magnitude, any passively drifting organism in the area would be displaced several hundreds of kilometers during their larval phase, a prediction that is not borne out in observation.

Sinclair and Iles [1985] inferred that these larval aggregations may be maintained through active vertical migration, in relation to the tidal currents to offset their horizontal displacement, in a manner similar to that used by herring larvae in tidal estuarine regions [Graham, 1972; Fortier and Leggett, 1983]. However, studies on the vertical migration off SW Nova Scotia have found that the timing of vertical movement conforms better with a diel pattern than a semi-diurnal tidal pattern [Stephenson and Power, 1988; Stephenson and Power, 1989b]. In shallow well mixed areas, larvae are found throughout the whole water column, and there is evidence of accumulation right near the bottom [Stephenson and Sochasky, 1991]. In deeper

stratified regions, larvae tend to concentrate at or above the pycnocline [Stephenson and Power, 1989b; Heath *et al.*, 1988].

The objective of this chapter is to analyze the spatial distribution of herring larvae in the well mixed and stratified waters off Southwest Nova Scotia. The proper characterization of the larval distribution is important to assure that the feeding environment, investigated in the remainder of this thesis, is that of the larvae. Also, the spatial analysis of the larvae combined with a new understanding of the physical forcing of the region may help to better understand the processes involved in larval retention off SW Nova Scotia. The results of two research surveys conducted in the region to examine the horizontal and vertical distribution patterns of the larvae are presented. These results are discussed in the light of the current understanding of herring larvae dynamics, and in relation to current theories of fisheries oceanography. An alternative hypothesis is presented to interpret the existence of the larval aggregation in areas of tidally well mixed waters. This hypothesis incorporates the effect of differential food availability to the existence of the larval aggregation.

2.2 Material and Methods

2.2.1 Horizontal distribution

In October 1989, two transects were conducted off SW Nova Scotia to study larval herring abundance and distribution (Figure 2.1). These transects were designed to cross the well mixed area off SW Nova Scotia along and cross-shore, enabling the determination of the size and location of the aggregation of herring larvae. The stations overlaid a larger spatial survey of 226 stations occupied in the area by the Department of Fisheries and Oceans. Transect I crossed the well mixed region alongshore; it was 181 km long and contained 12 stations. Transect II ran cross-shore; it was 109 km long and contained 10 stations.

At each station, herring larvae were sampled with a 61 cm Bongo frame mounted with a 505 μm-mesh net and flowmeters. The net was towed obliquely with ship's

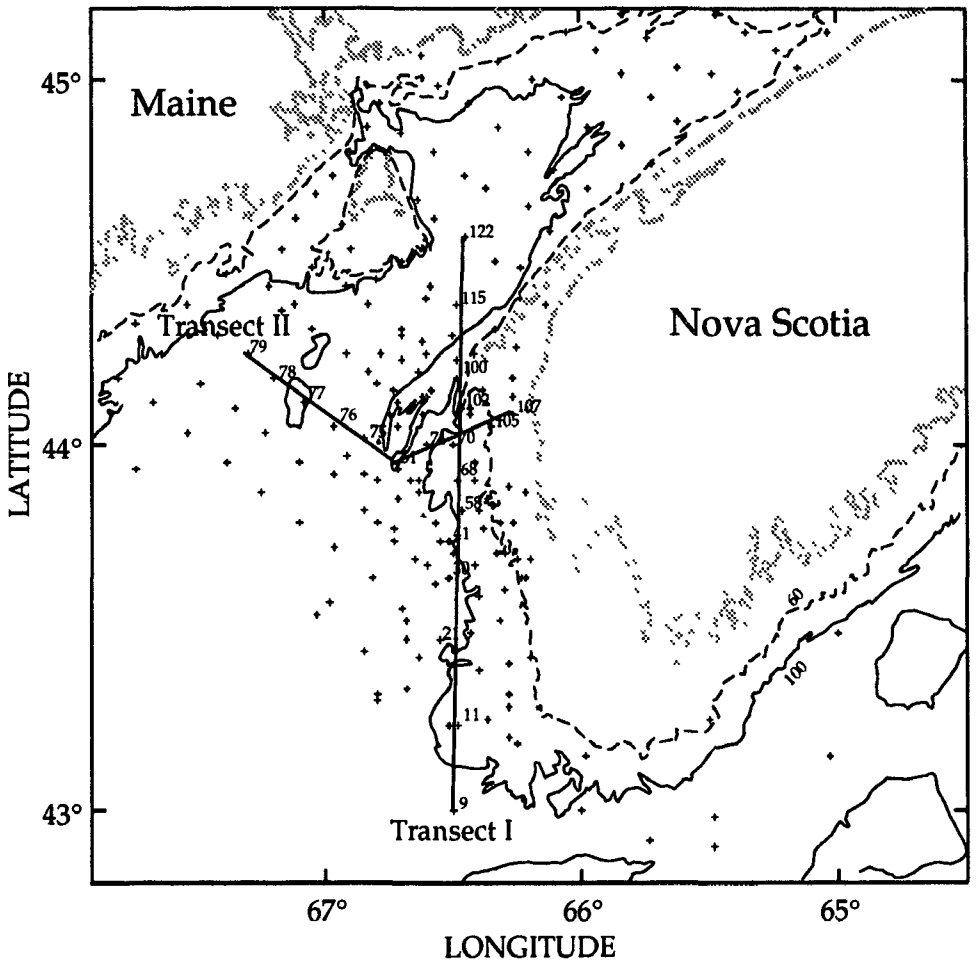

Figure 2.1: Map of the study area. The two transects are indicated along with their respective station numbers. Stations occupied every year by the DFO for the larval herring survey are indicated as (+).

speed maintained at 1.8 $\mathrm{m\,s^{-1}}$ and each tow had a minimum retrieval time of 10 minutes. Samples were taken from 5 m off the bottom to the surface, and up to 200 m in areas where depths were greater than 200 m. A Seabird CTD was used to measure temperature, salinity and density of the water column.

In the laboratory, herring larvae were sorted from the remainder of the zooplankton and their abundance estimated. Larval abundance is expressed as number per meter square ($\mathrm{larvae\,m^{-2}}$). This is the number of larvae sampled per unit of volume filtered integrated over the depth sampled by the net. Standard length, measured to the nearest millimeter, was taken of up to 80 larvae per sample whenever possible.

To characterize horizontal distribution of the herring larvae with respect to different oceanographic conditions, their abundance and size are expressed as a function of the stability of the water column. Delta Sigma-t ($\Delta\sigma_t$, in $\mathrm{kg\,m^{-3}}$), defined as the difference between the density of the bottom and the surface waters, is used to represent the water column stability. Garrett *et al.* [1978] showed this parameter to be a good indicator of stratification of the water column, when tidal mixing and thermal stratification are the dominant buoyancy forcing. They demonstrated that in tidally mixed regions off SW Nova Scotia, well mixed water columns are defined by $\Delta\sigma_t \leq 0.5$; higher $\Delta\sigma_t$ corresponds to an increase in stratification. This parameter is also correlated with the depth of the water column ($r = .69$, $p < .0001$), and the difference in potential energy (ΔPE) between the bottom and the top of the water column ($r = .92$, $p < .0001$) (Figure 2.2). ΔPE ($\mathrm{J\,kg^{-1}}$) required in mixing a linearly stratified fluid was calculated for each station as:

$$\Delta PE = \frac{1}{12} N^2 h^2 \tag{2.1}$$

where N^2 ($\mathrm{s^{-2}}$), the buoyancy frequency for the water column, is:

$$N^2 = -\frac{g}{\rho_m}\frac{\rho_s - \rho_b}{h} \tag{2.2}$$

and ρ_m is the mean density ($\mathrm{kg\,m^{-3}}$) for the water column, ρ_s and ρ_m are the density ($\mathrm{kg\,m^{-3}}$) of the surface and bottom water, and h is the depth of the water column

(m). Figure 2.2 shows that more coastal shallower waters are well mixed, and that at depth greater than approximately 90 m the water column becomes stratified.

2.2.2 Vertical distribution

A "semi-fixed" station was occupied during 28-31 October, 1990, in the well mixed area off SW Nova Scotia, and 11 sets of plankton tows were taken to collect herring larvae during a 48h time series (Figure 2.3). The strategy was to sample the same water parcel during the study period, matching the sampling activity with the horizontal displacement of the water column due to tidal forcing. Earlier work showed that the path of drifters in the same area is consistent with the narrow tidal ellipse predicted from Greenberg's [1983] model [Stephenson and Power, 1988]. The mean tidal current velocities estimated from Greenberg's model [Greenberg, 1983] for that period were used to determine the position of each consecutive set. Although it was not possible to follow completely this strategy, the sets were successfully taken within the limits of the calculated tidal excursion, ensuring that the same parcel of water was sampled. Figure 2.3 shows the position of the sets, and one tidal ellipse calculated using Greenberg's model for the initial sampling period.

An opening and closing Mininess [Reid *et al.*, 1987] plankton net frame (0.5 x 0.5 m mouth opening), mounted with eight 333 μm-mesh Nitex nets fitted with codend buckets, was used to sample the larvae. A Guildline CTD was attached to the frame and General Oceanics electronic flowmeters were mounted in the mouth opening and outside of the net. Samples were taken at regular depth intervals at 50, 40, 30 20, 10 and 5 m. Tow durations were approximately 8.5 minutes at each depth interval at a speed of 1.8 $m\,s^{-1}$ (3.5 kt). An average of 196 m^3 was sampled at each depth strata. At the end of each tow, all nets were removed and washed to prevent clogging. Filtration efficiency of the net was controlled by dividing the the readout of the internal flowmeter by that of the outside flowmeter. The mean filtration efficiency of the nets over the sampling period was 95 %. Samples were preserved in 5 % formalin in seawater buffered with a few marble chips. Prior to

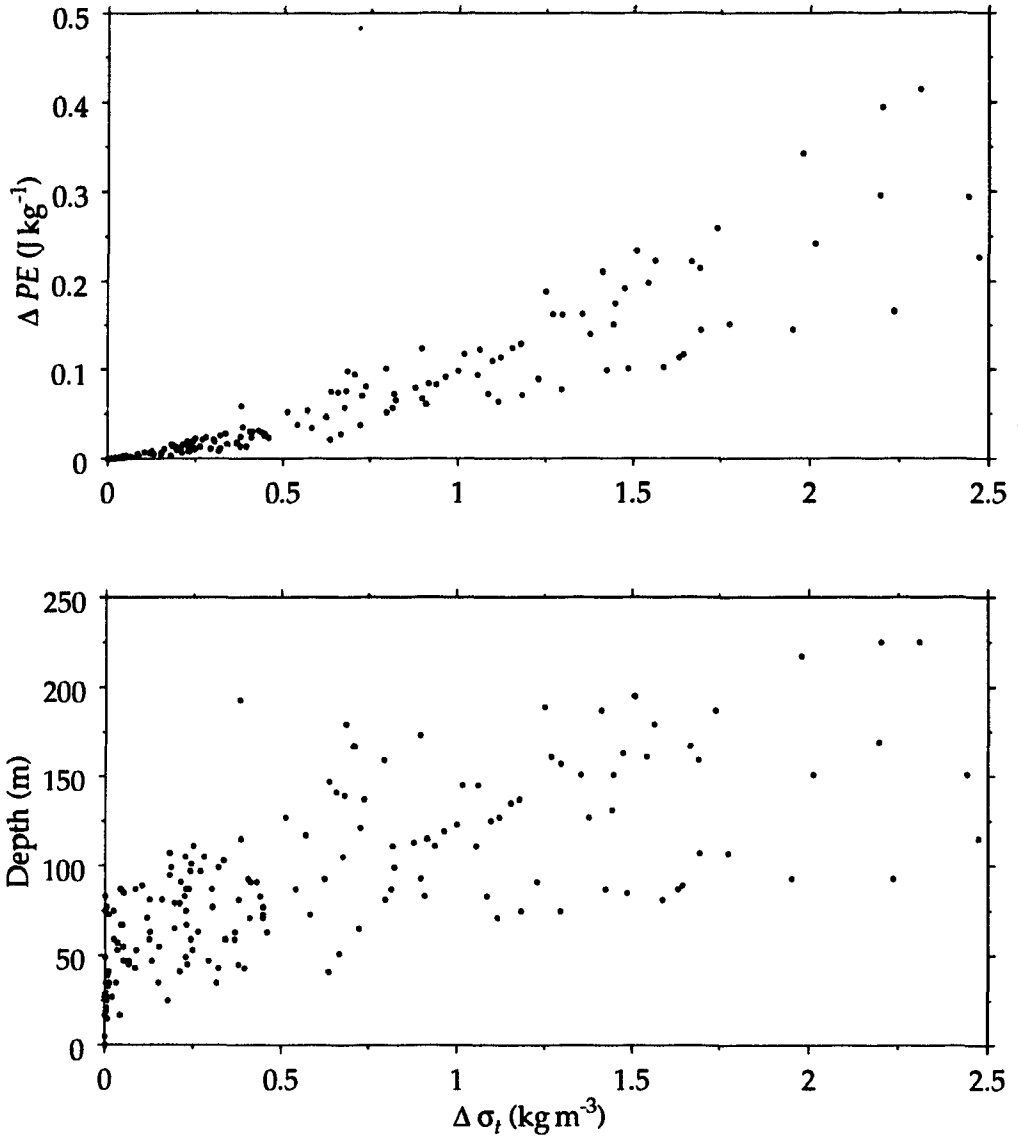

Figure 2.2: Scatterplots showing the correlation between depth and the stratification of the water column ($\Delta\sigma_t$, kg m^{-3}), and between the difference in potential energy (ΔPE, J kg^{-1}) between the bottom and top of the water column and $\Delta\sigma_t$.

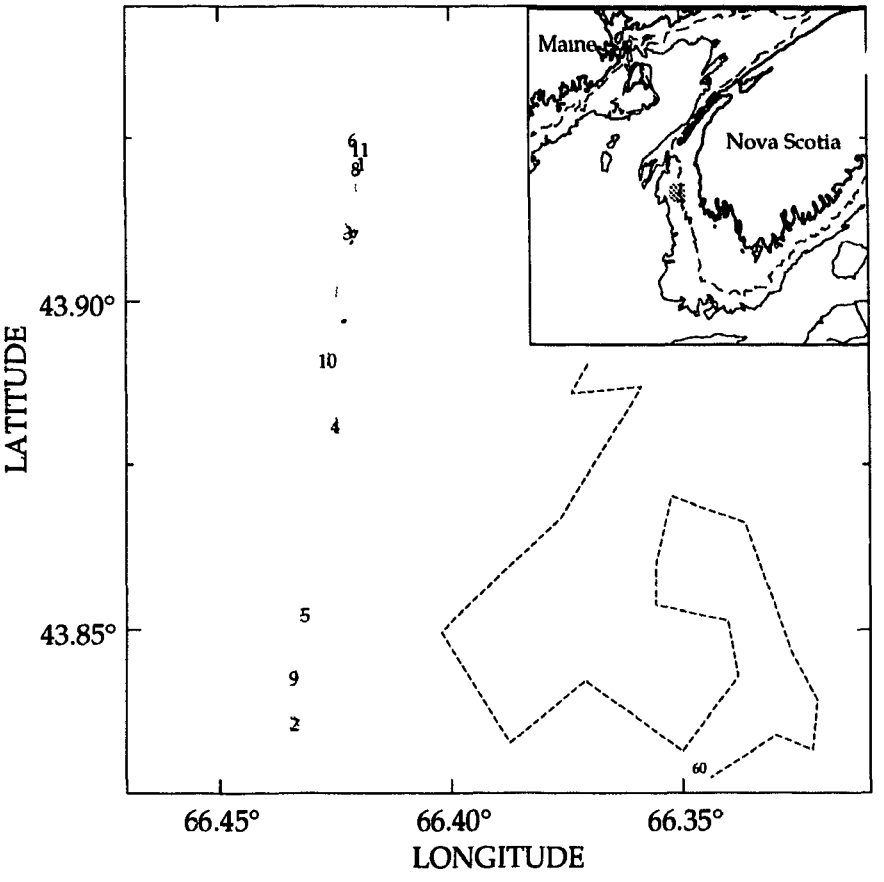

Figure 2.3: Location of the semi-fixed station used during the 48 h sampling. One tidal ellipse for this period is shown. The numbers on the ellipse correspond to the location where sampling was started at each set. The 60 m isobath is shown for reference.

each larval sample, information on the vertical distribution of temperature, salinity and density was taken using a Seabird CTD.

In the laboratory, all the larvae were counted. The counts were standardized to a volume unit (m^{-3}) using the volume filtered at each depth strata corrected for its filtration efficiency. Larvae were measured for standard length (tip of snout to end of notocord) with a dissecting microscope to the nearest 0.1 mm. A sub-sample of randomly selected 30 larvae was taken from collections with greater then 30 larvae, otherwise all individuals were measured. A total of 1173 Atlantic herring larvae were measured. A large proportion of larvae collected could not be measured due to net damage.

Two statistics of location and dispersion are used to analyze the vertical distribution of the larvae during the sampling period. The mean depth distribution ($\bar{Z}$) is calculated as:

$$\bar{Z} = \frac{1}{n}\sum_{i=1}^{6} n_i z_i \tag{2.3}$$

where n = the total number of larvae (m^{-3}) in a set, n_i = number of larvae (m^{-3}) occurring at stratum i, and z_i is the strata depth (m). This is the weighted depth average of the larvae, and it is equivalent to the mean center of mass (ZCM) used by Fortier and Leggett [1983] and others recently [Stephenson and Power, 1988; Munk *et al.*, 1989; Heath *et al.*, 1991]. The standard deviation (SD) of the mean depth distribution ($\bar{Z}$) is calculated as:

$$SD = \sqrt{\frac{1}{n}\sum_{i=1}^{6}(z_i - \bar{Z})^2 n_i} \tag{2.4}$$

For vertically migrating populations, it would be expected that the organisms would move either to the top or to the bottom of the water column. In this case, their distribution around a mean depth value would not be symmetrical and $\bar{Z}$ and SD would not be an appropriate indicator of vertical displacement. To avoid this bias, the median depth Z_M (m) was calculated. Z_M is the depth which divides the distribution in half, *i.e.*, 50% of the larvae are above and 50% are below this depth. It is estimated by identifying the depth which corresponds to the 50% cumulative

frequency of larvae at each set. Since the data are discretely distributed, linear interpolation between the 2 depth strata surrounding the $n/2$ th larvae is used to calculate the exact value of Z_M. The vertical dispersion of the larvae in the water column is evaluated using Z_{25} and Z_{75}, the depth above which 25% and 75% of the larvae lie, respectively. This criteria is similar to that used by Heath *et al.* [1988].

These parameters are also compared to the mean tidal velocities estimated using Greenberg's model [Greenberg, 1983]. Some modulation between the frequency of the tidal oscillation and of the vertical migration is expected if larvae use the tides to maintain their horizontal position.

2.3 Results and Discussion

2.3.1 Horizontal distribution

Hydrographic conditions

The study area is located on the continental shelf off southwest Nova Scotia. Its boundaries are the Gulf of Maine to the west, the Bay of Fundy to the north and Brown's Bank to the south. This region is characterized by strong tidal mixing [Garrett *et al.*, 1978; Loder and Greenberg, 1986], and by an upwelling circulation off Cape Sable [Lauzier, 1967; Smith, 1983]. It is currently believed that this upwelling is induced by a tidal rectification process resulting from tidal currents flowing over complex bottom topography [Tee *et al.*, 1993]. Deep, cold, saline and nutrient-rich water upwells on the eastern flank of Cape Sable and downwells on the western flank. While in the shallower region, the water is strongly mixed and carried northwest, producing the cold water anomaly observed over most of the study area.

Figure 2.4 shows the density fields along the two transects for the study area. The southern stations of Transect I (9–30) are characterized by some degree of stratification. Stratification is more developed on the most offshore station (9), and

the gyre-like feature on station 11 represents the crossing over a shallower region, which is influenced by the well mixed cooler waters resulting from the upwelling off Cape Sable [Tee *et al.*, 1993]. Stations 21–30 are on the margin of the shelf and show the influence of deeper water on the bottom, resulting in some degree of stratification. Stations 41 to 100 are located on the shelf and are characterized by well mixed waters. Stratification develops again in the northern stations (115–122), located in the deeper waters at the entrance of the Bay of Fundy.

Transect II shows the clear, well-defined onshore-offshore stratification pattern. Well mixed waters are found from stations 107 to 71, at approximately 100 m. At this point, stratification quickly develops, resulting in a well defined stratified water column.

Herring larvae abundance and size distribution

Das [1968] observed that spawning was from late July – early August and continued into October and early November in an area covering Trinity Ledge and Lurcher shoals at the south of St. Mary Bay. This area is roughly coincident with the center of the distribution of larval abundance shown in Figure 2.5. To the south, Logbook analysis of the 1989 and 1990 purse seine catch and effort distribution for the roe fishery reveals the important contribution of German Bank and Seal Island as spawning areas from August, September and the first half of October [Power and Stephenson 1990, Power and Stephenson 1991].

As has been shown previously, herring larvae abundance was always higher in the well mixed waters, with an abrupt decrease in the stratified region (Figure 2.5). This is particularly evident for transect II, where the mean larval density decreased from 258 larvae m^{-2} in the well mixed region to 4.4 larvae m^{-2} in the adjacent stratified waters (Figure 2.6). Along transect I, mean densities decreased from 254 larvae m^{-2} to 1.5 larvae m^{-2} from the well mixed to the stratified waters (Figure 2.6). In general, there was a significant negative correlation ($r = .84, p < .0001$) between larval density and the stratification parameter ($\Delta\sigma_t$) reflecting the existence of the

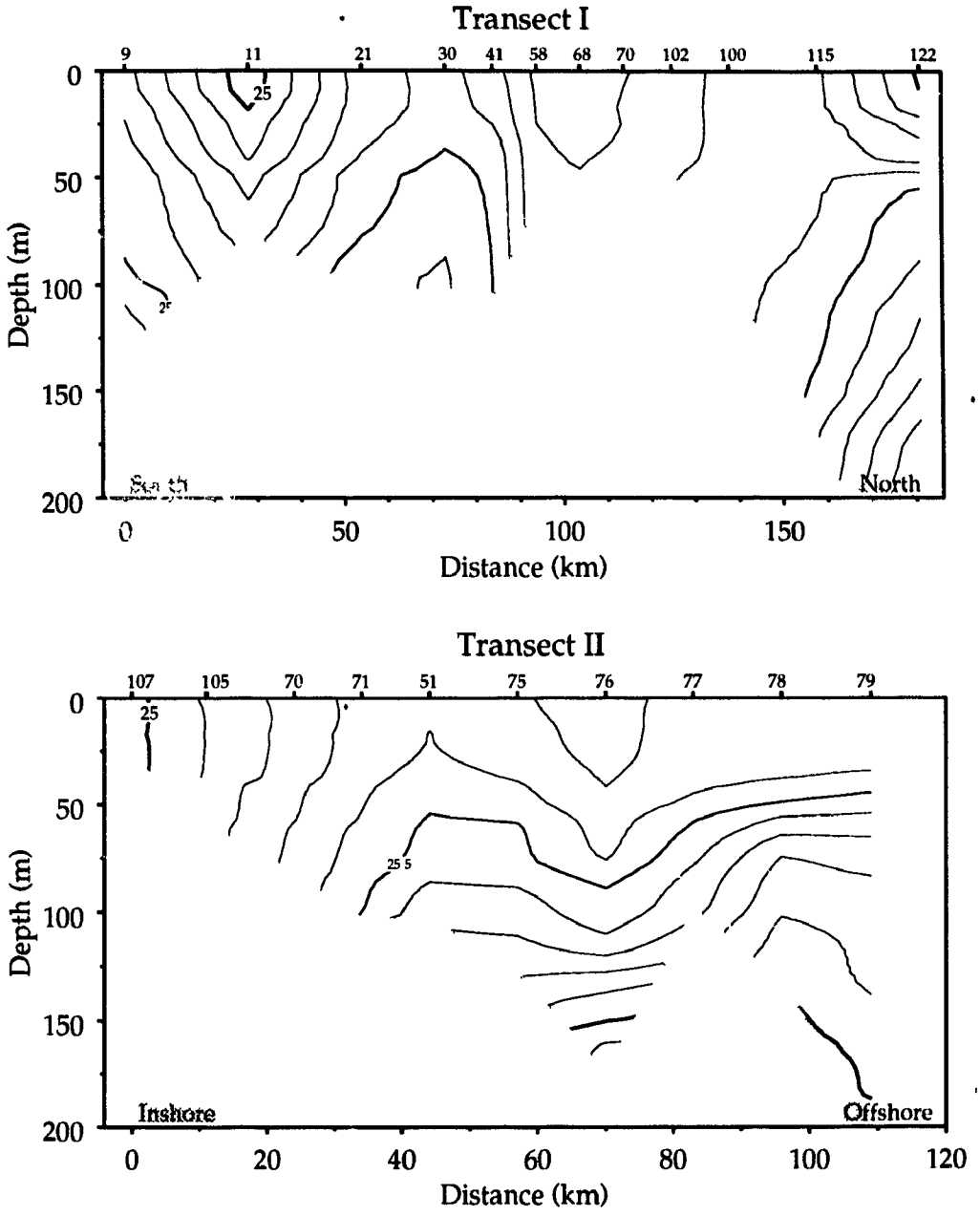

Figure 2.4: Density contour plots along the two transects.

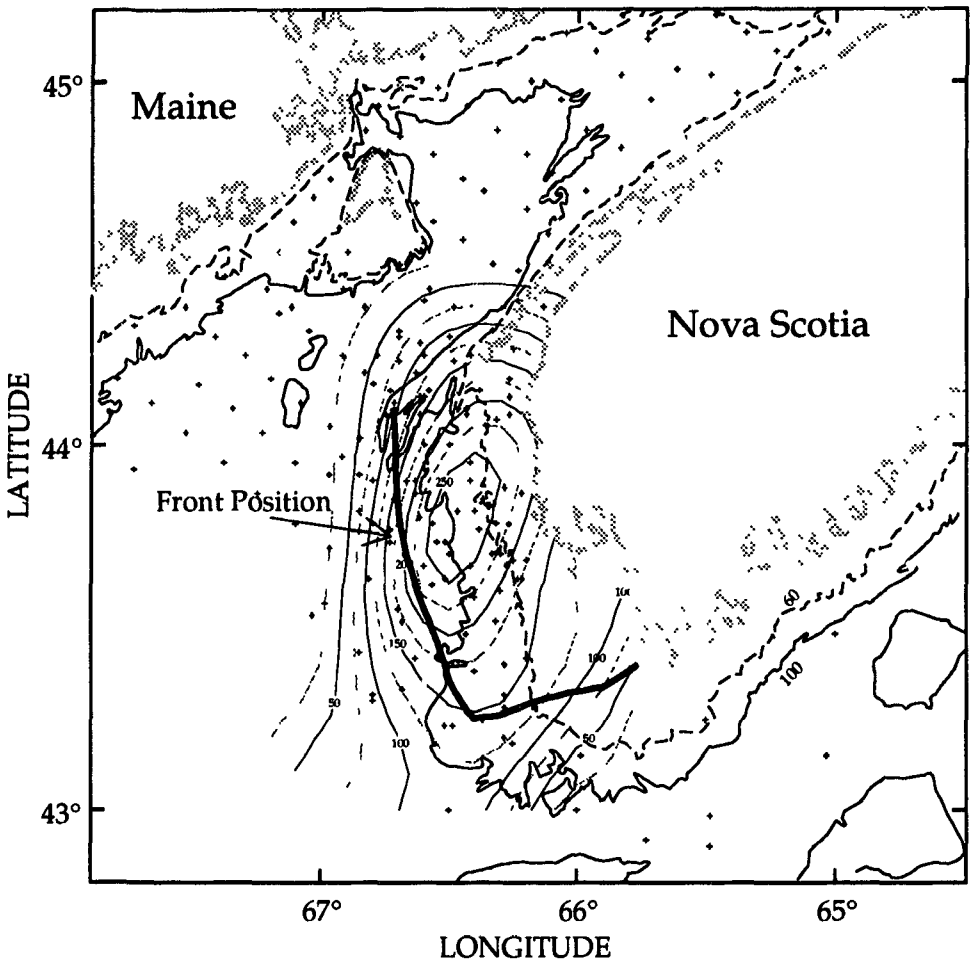

Figure 2.5: Distribution of herring larvae off southwest Nova Scotia and estimated position of the front (isoline of $\Delta\sigma_t = 0.5\ \mathrm{kg\,m^{-3}}$). Larval contours are in larvae $\mathrm{m^{-2}}$. Contours are drawn using stations inside of a box defined by 65.7° W 44.5° N and 68° W 43° N. Larval density contours are smoothed by 0.3° in latitude and longitude.

larval aggregation in shallower well mixed waters (Figure 2.7).

The size of the larvae sampled during this study varied from 6 to 27 mm (Figure 2.8). About 80 % of the larvae were between 6 and 10 mm, and approximate 35 % of them were between 8.5 and 9.5 mm long. These are small, newly hatched larvae originating from the main spawning grounds located in the sampling area. Using growth rates of approximately 0.24 mm day^{-1} for these larvae [Chenoweth *et al.*, 1989], a mean hatching size of 7 mm, and an incubation period of 15 days [Blaxter, 1963], it can be inferred that these larvae spawned early in October. The 15 mm larvae were probably spawned early in September; the largest larvae in the sample were from late July.

Although smaller larvae occurred in both well mixed and stratified waters, they were more confined to the well mixed region (mean length around 9 mm). This would correspond to the regions between stations 21 and 100 for transect I, and stations 107 to 71 for transect II (Figure 2.4 and 2.9). Stations 51 to 75 (Transect I) and 11 and 9 (Transect II) have intermediate stratification values and present a mixture of small and larger larvae. The location of these stations coincides with the approximate position of the tidal front, and with the edge of the larval aggregation [Stephenson and Power, 1991]. Larger larvae, with mean length around 18 mm, are found mostly at the more offshore stations, where stratification is well developed. These are stations 115 and 122 in Transect I and 77 to 79 in transect II (Figure 2.4 and 2.9). It is important to notice also that smaller larvae do not occur at these stations. The exception to this pattern is station 76, which is the station with the most stratified water column, but also with small larvae.

This larval distribution pattern is consistent with that found in previous years, reflecting the existence of the larval aggregations in the well mixed area off SW Nova Scotia. The existence of spawning, followed by the large larval aggregation coincident with well mixed waters, led Iles and Sinclair [1982] to formulate their "herring stock hypothesis". According to this hypothesis, the number, location and extent of geographically predictable larval "retention" areas define the number of

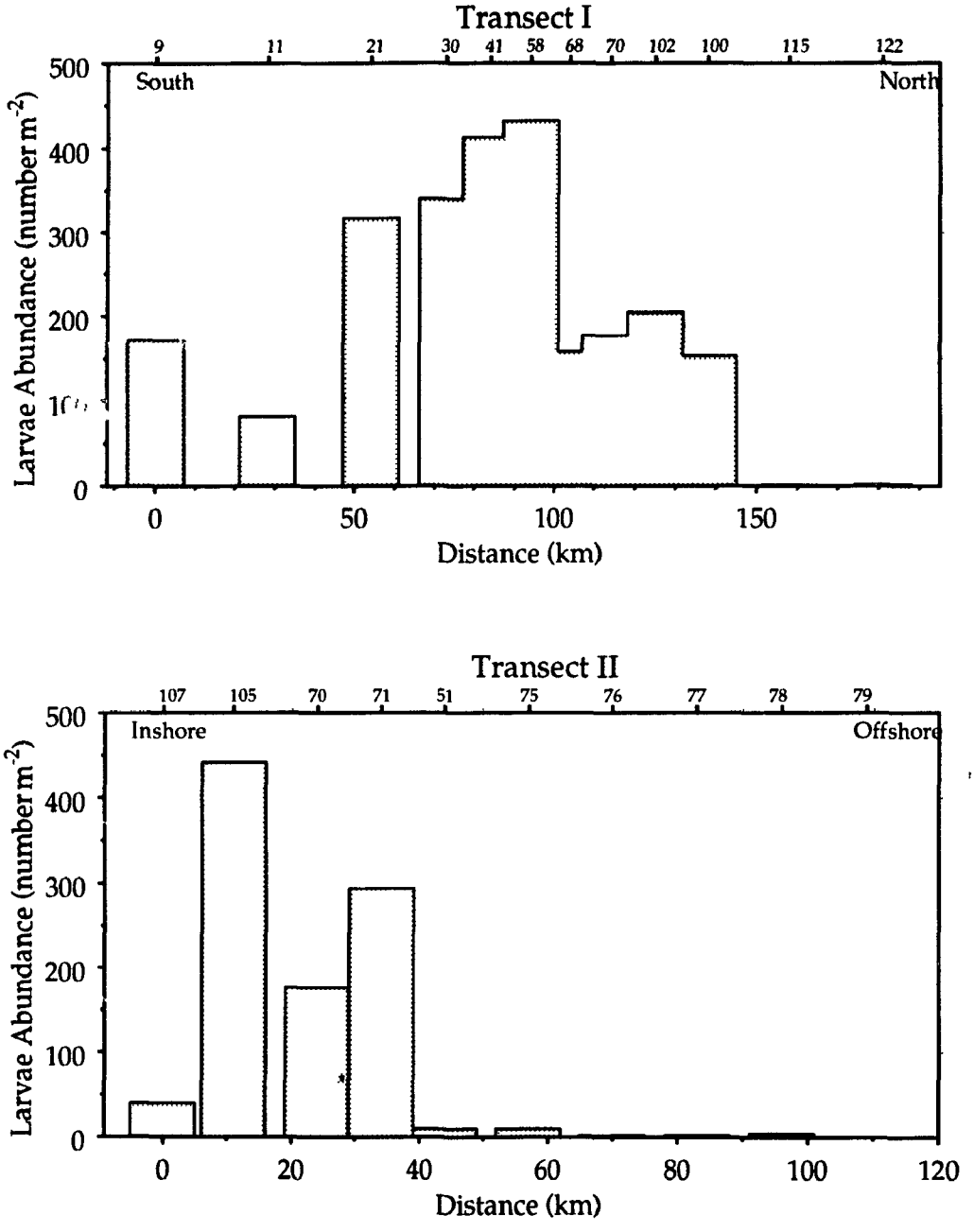

Figure 2.6: Distribution of herring larvae along the two transects.

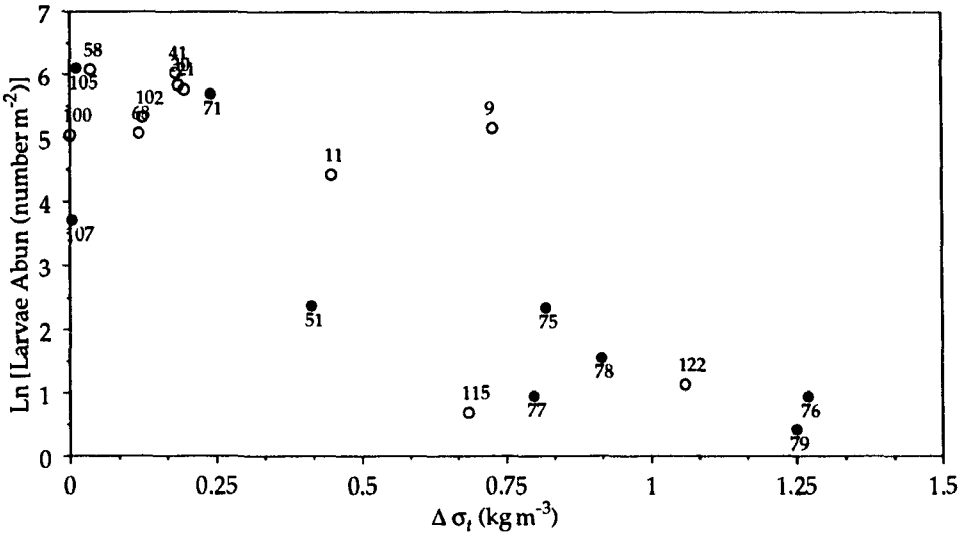

Figure 2.7: Plot of the relationship between the natural logarithm of herring larvae abundance [ln(larvae m^{-2})] and the stratification of the water column ($\Delta\sigma_t$, kg m^{-3}). The station numbers are shown with each data point. (o) transect I; (•) transect II.

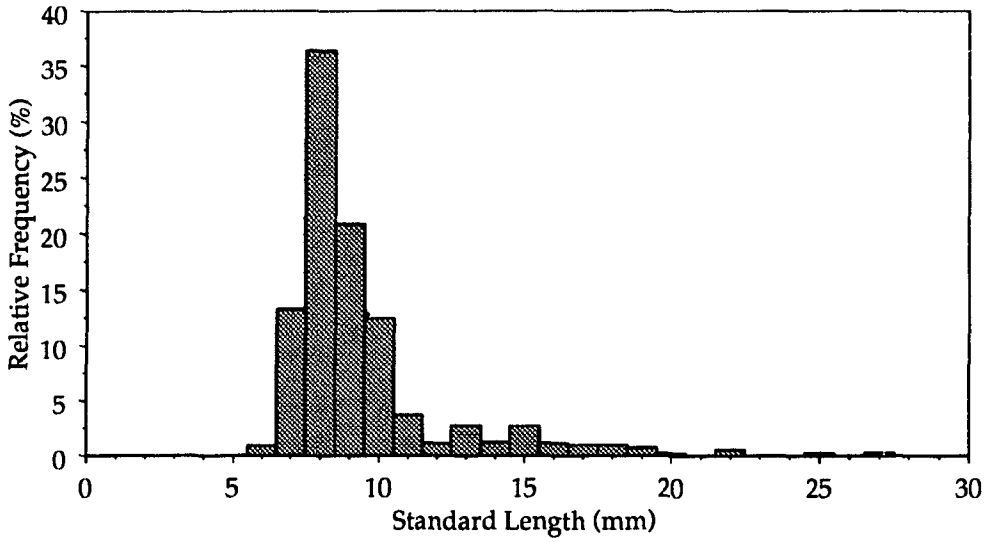

Figure 2.8: Length frequency distribution of all the herring larvae sampled during the 1989 study.

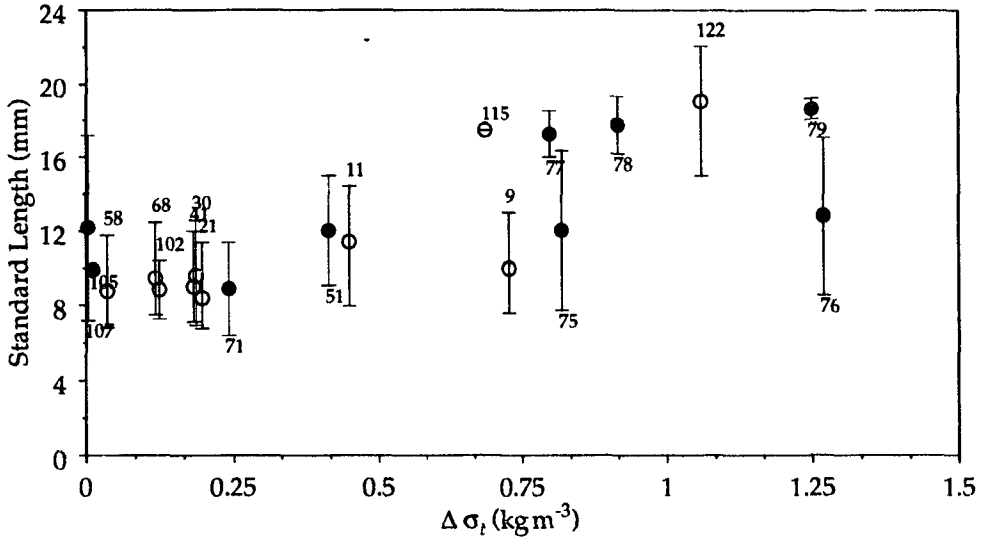

Figure 2.9: Variation of the mean standard length (mm) of herring larvae along the two transects as a function of the stratification of the water column ($\Delta\sigma_t$, kg m^{-3}). Bars are 1 standard deviation of the mean. (o) transect I; (•) transect II.

herring stocks and the location of their respective spawning sites. Sinclair and Iles [1985] emphasized that the larvae may not be retained passively by the circulation in these areas, and inferred that an active behavioural response to the physical regime may account for the retention. They also pointed out that this coexistence was to guarantee the maintenance of a reproductive unit, and not necessarily because of optimal conditions for the larvae. In the light of the "member/vagrant" hypothesis [Sinclair, 1988], these are areas where membership to the population would ensure closure of the life cycle.

This hypothesis better accounts for the distribution of the early life history of herring larvae than other hypotheses. First, the "Stable Ocean hypothesis" of Lasker [1975] does not seem to apply in this case. This hypothesis states that stratification and vertical stability of the water column allows for the concentration of food items, thus enhancing the survival of fish larvae. The waters in the aggregational area lack stratification and do not provide the required vertical stability needed by the larvae to improve their feeding. Second, the early life history of herring does not seem to be affected by a temporal "match or mismatch" [Cushing, 1975] with the food supply. Herring spawning period is long, and not confined to a temporally defined source of food. Third, the herring larval distribution patterns reported here are not in agreement with the general theory of fish migration [Harden-Jones, 1968], since there is no apparent larval drift to a nursery area. In fact, the general broad spatial distribution off SW Nova Scotia resembles that of a single source diffusion process superimposed on a tidal advection component (Figure 2.5). In this case, some individuals remain in this area and become "members"; others are dispersed and become "vagrants", which will not contribute to the population.

The lack of a larval drift period and the maintenance of these aggregations for such a long time are probably the most intriguing feature in the distribution of herring larvae. It is well established that off SW Nova Scotia, there is a residual flow of 10-20 km day^{-1} to the northwest into the Bay of Fundy [Sinclair and Iles, 1985; Stephenson and Power, 1989b]. Such a current would displace the larval center

of aggregation by several hundred kilometers over a 3 month period. However, the larvae are still found in this area after this period. In a recent review, Townsend [1992] showed that for most of the major herring spawning in the Gulf of Maine–Bay of Fundy region, the majority of the larvae remained in the vicinity of their spawning grounds well into the winter. Furthermore, the aggregation off SW Nova Scotia is still present on the spring of the subsequent year, 6 months after spawning has occurred (Stephenson and Power, unpublished results]. If the dispersion process of the larvae were mainly diffusive, it would be expected that larvae would be more homogeneously distributed after some time, and not retain the same relative level of abundance in the same area as it had earlier in the year.

2.3.2 Vertical distribution

Hydrographic conditions

During the 48 h survey, no major changes were observed in the vertical structure of the water column. Figure 2.10 shows the vertical profiles for temperature, salinity and density. During the sampling period, the water-column remained well mixed, with average temperatures of 10.5 °C, salinities of 33 ppt and densities of 1025.5 $kg\,m^{-3}$. Figure 2.11 shows the alongshore velocity component of the tidal (M_2) current calculated using Greenberg's model [Greenberg, 1983]. This is the most important component of the M_2 tides, and current speeds of up to 70 $cm\,s^{-1}$ reflect the strong influence of the tides in this region.

Herring larvae abundance and size distribution

Although the water column is fully well mixed (Figure 2.10), herring larvae are not uniformly distributed throughout the water column (Figure 2.12). The vertical distribution of the larvae follows a diel pattern, with higher concentration in surface waters during day time and closer to the bottom at night. This indicates that the larvae are able to determine their position in the water column, independent of the

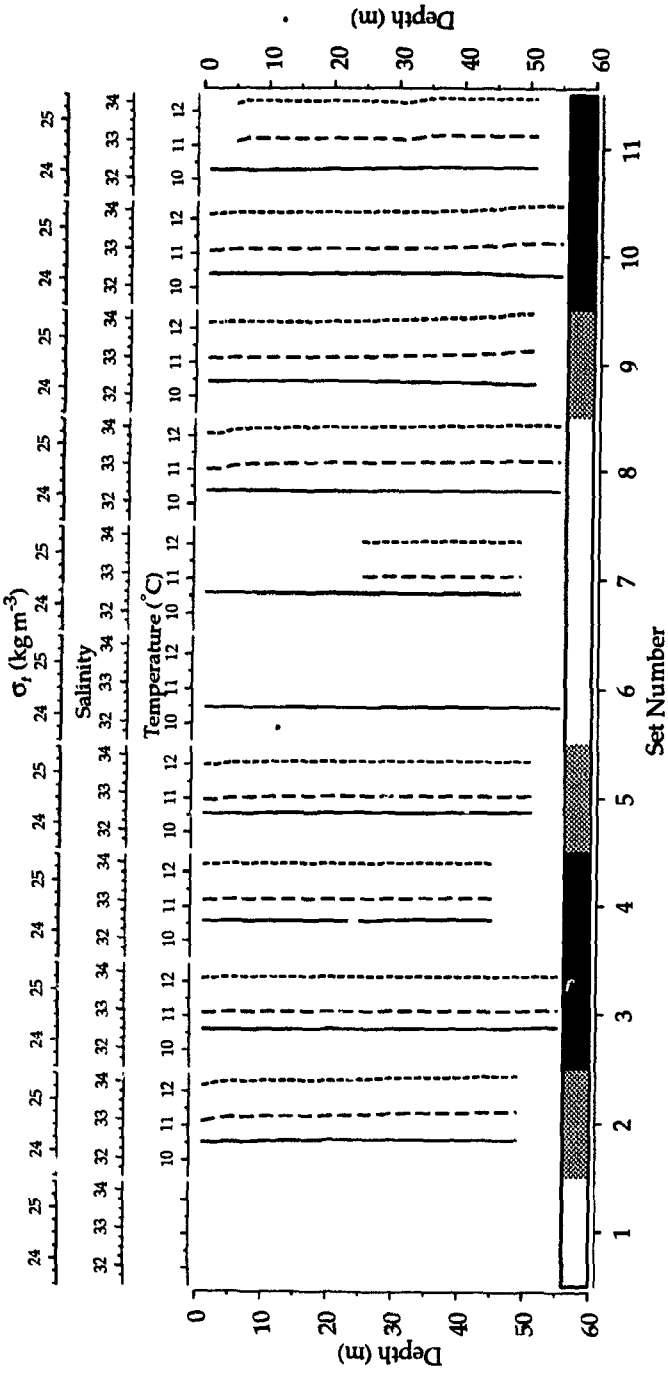

Figure 2.10: Vertical distribution of temperature (solid line), salinity (larger dashed line), and Sigma-*t* (smaller dashed line) over the sampling period. Horizontal bars indicate period of the day: solid bars are night; shaded bars are crepuscule; open bars are day time.

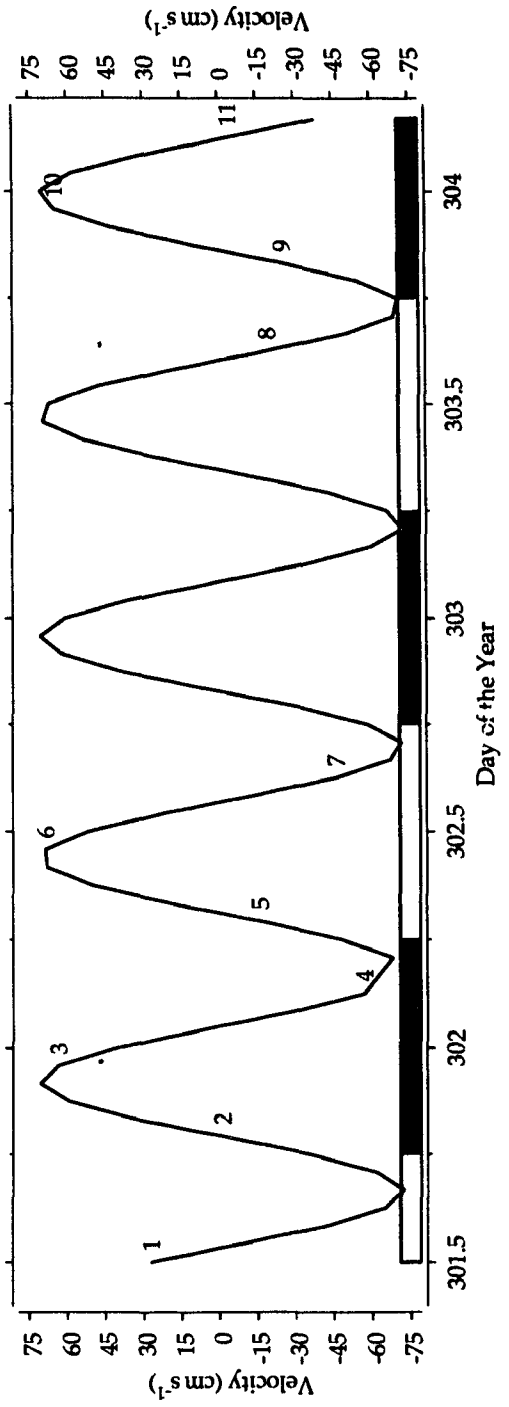

Figure 2.11: The alongshore velocity ($cm\,s^{-1}$) component of the tidal (M_2) current during the sampling period. Horizontal bars indicate period of the day: solid bars are night; shaded bars are crepuscule; open bars are day time.

strong vertical tidal mixing in the region. A vertical diel migration seems to be the general pattern for larvae of this species in this region, and the results of this study are in agreement with a 7.5 day study conducted by Stephenson and Power [1989a] in 1987, and with a 3 day study conducted by the same authors in 1989 [Stephenson and Power, 1991]. It has long been recognized that light plays an important role in directing the migratory behaviour of larvae [Wood, 1971], although probably not being the main motivating factor [Heath, 1992].

This pattern is expressed by both the mean (and its standard deviation), and by the median (and the 25 and 75% quartiles) (Figure 2.12). As mentioned earlier, the median is a better indicator of the vertical distribution of the larvae, since a skewed distribution is expected. For example, at set 5, the median indicates that 50% of the larvae are above 28 m, and 50% are below it. In fact, 75% of the larvae occupy most of the water column (8 to 42 m). In contrast, the interpretation of the mean depth distribution would be that most of the larvae are centered at 30 m, and that 1 standard deviation of this distribution would be between 22 and 39 m. The use of this measure can bias the interpretation of vertical migration studies.

The vertical distribution of the size structure of the larvae, however, does not change throughout the water column (Figure 2.13). Mean larval size during the study is approximately 9 mm. These are newly hatched larvae, and indicate that sampling was carried in the vicinity of the spawning grounds. The uniformity of the standard deviation of the mean larval size with depth suggests that there is no differential distribution between larger and smaller larvae. Stephenson and Power [1988] showed that larvae of small (< 9 mm but pos' yolk sac) and intermediate (9 to 14 mm) sizes follow the same vertical migration pattern; larvae of the largest group (> 14 mm) were few in number, and appeared to be taken mostly in deeper samples or at night. Their results suggested that differential capture was responsible for the different pattern showed by larger larvae. It has been shown that herring larvae can avoid plankton nets, and that significant differences are found between day/night catches of larger larvae suggesting visual avoidance [Brander and Thompson, 1989].

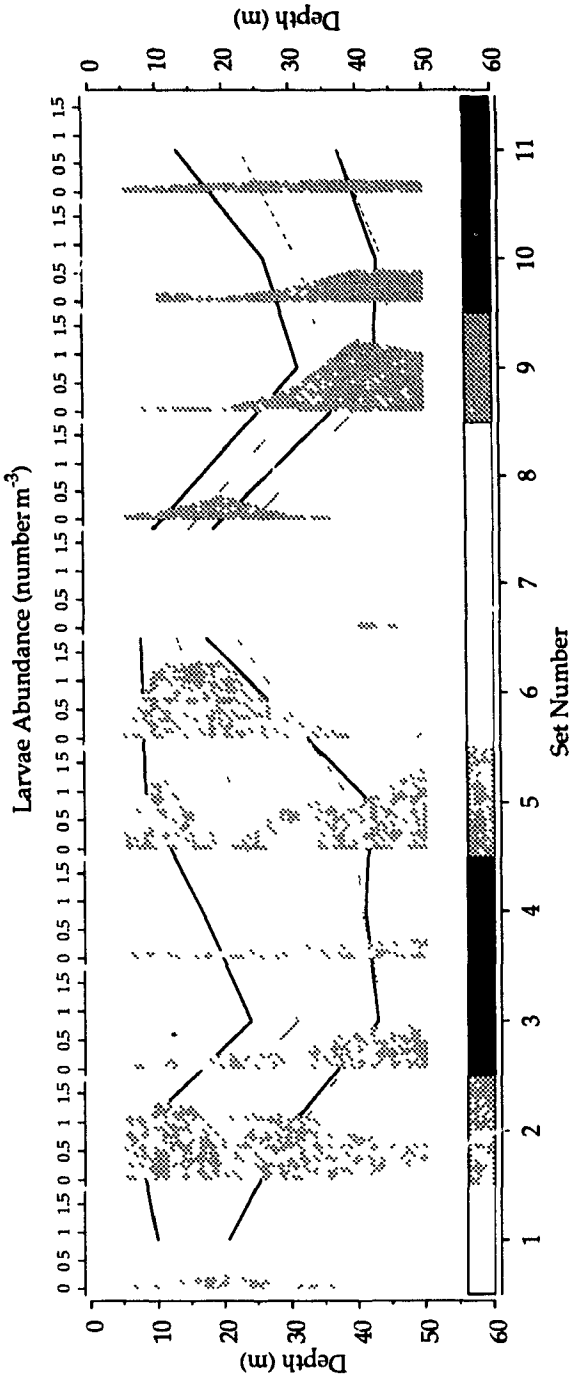

Figure 2.12: Vertical distribution of herring larval abundance (number m^{-3} during the sampling period. Solid lines represent Z_{25} and Z_{75}. Dotted lines surround the 1 standard deviation of the mean vertical distribution. Horizontal bars indicate period of the day: solid bars are night; shaded bars are crepuscule; open bars are day time.

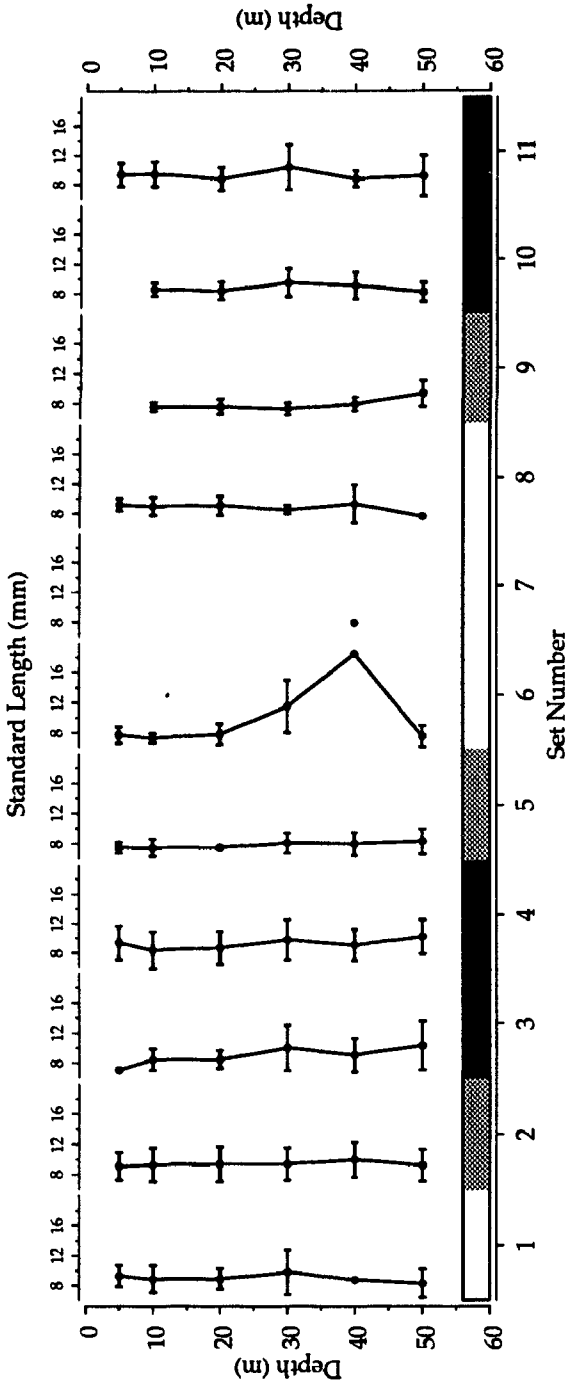

Figure 2.13: Vertical distribution of the mean larval size (mm) and 1 standard deviation of the mean. Horizontal bars indicate period of the day: solid bars are night; shaded bars are crepuscule; open bars are day time.

However, it can be argued that the uniformity in the mean and standard deviation of larval size found in this thesis is the result of a source of small larvae in the region. Sampling was conducted in the proximity of a spawning ground (Trinity Ledge), and probably at a time when hatching was taking place (October 28 to 31, 1990). Sephenson and Power [1988] took their samples between November 8 and 13, 1985. At a growth rate of 0.24 mm day^{-1} [Chenoweth *et al.*, 1989], for a period of 10 days, the larvae I collected would have a mean size of approximately 11.5 mm and the larger larvae would be around 15 mm. The mean larval length of Stephenson and Power [1988] was approximately 14 mm during daytime and 16 mm at night.

Three observations indicate that avoidance was not a problem in the present study: a) the magnitude of the catches seem to be the same at day and night time, and at the surface and bottom (Figure 2.12); b) the absence of an increase in the variability of the mean size of larvae with depth, and between day/night samples; and, c) when larger larvae were present, they were sampled (set 6, 40 m in Figure 2.13). Furthermore, the "semi-fixed" sampling strategy adopted allowed for plankton collections to be taken from approximate the same water parcel during the study. Stephenson and Power [1991] showed that horizontal variability increased in scales greater than 1 km. If a different strategy had been used, different larval populations would have been sampled, probably resulting in a different larval size structure. This suggests that the uniformity in the size distribution is due to the spatial and temporal match between a source of small larvae and the sampling activity.

Other factors influencing the vertical distribution of herring larvae are their food distribution, light, tidal currents and wind-induced mixing [Graham, 1972; Fortier and Leggett, 1983; Heath *et al.*, 1988; Munk *et al.*, 1989; Heath, 1992]. Generally, a combination of some of these factors is used to explain the observed pattern of vertical migration. Heath *et al.* [1988] showed that although larvae aggregated during the day and dispersed at night, the mean depth of the population was strongly influenced by wind-driven turbulence. This mechanism would not

necessarily apply to explain the vertical distribution found in the present study. The effect of wind mixing is mostly to disrupt any stratification in the water column. The shelf off SW Nova Scotia is a shallower region, with no stratification and is already very well mixed. It is estimated that a wind of 22 $m.s^{-1}$ would be required to generate the amount of turbulence equivalent to that of tidally mixed regions [Rothschild and Osborn, 1988]. The larvae here seem to be capable to vertically migrate, in spite of a large degree of turbulent mixing.

Munk *et al.* [1989] found that in calm weather, the larvae move to depths where light is sufficient for feeding, and that an adjustment within that zone is made according to a compromise between optimal light conditions for feeding and optimal prey densities. This strategy also would not account for the vertical distribution of larvae in well mixed regions. There is no vertical variation either in the physical properties of the water column, nor in the food distribution. Microzooplankton, the main food item of these larvae, are uniformly distributed in well mixed waters off SW Nova Scotia [Stephenson and Power, 1991]. The relationship between food and larvae distribution will be further discussed in the next chapter of this study.

The relation between tidal currents and vertical distribution of larvae are well established for estuarine regions [Graham, 1972, Fortier and Leggett, 1983]. In these areas, vertical migration through vertical shear is thought to be an adaptation to maintenance of horizontal position and transport into nursery areas. During periods of flood, the larvae are closer to the surface and are displaced inland; at ebb tide they are found closer to the bottom, and their displacement away from the nursery is reduced. Since herring larvae are not displaced by the residual northerly flow into the Bay of Fundy, Sinclair and Iles [1985] postulated that a similar vertical migration strategy would be used by herring larvae off SW Nova Scotia to reduce their horizontal transport. This would allow the population to maintain a discrete distribution in a relatively fixed geographic location.

Stephenson and Power [1988, 1989b] tested this hypothesis and found that, although the larvae showed a semi-diel periodicity in one year (1985), a diel pattern

was found in two other years (1987, 1989). The diel pattern is the same pattern found in this study. These findings coupled with those in the present study do not support the view that the larvae are actively migrating in relation solely to the tides as was proposed by Sinclair and Iles [1985]. Hill [1991] has shown that the interaction between vertical migration and tidal currents plays no effective role in the net horizontal displacement of organisms. He noticed that only migration interaction with the residual flow affects horizontal transport. Stephenson and Power [1989b], also pointed out that a diel migration would reduce the northerly transport due to the residual flow, although not as efficiently as if the migration patterns were tidal. The northerly transport is minimized if the upward migration of the larvae is in phase with the southerly flow of the tides.

An inspection of the broad-scale distribution of the larvae (Figure 2.5) indicates that the main axis of dispersion is coincident to that of the tidal ellipses for this region (Figure 2.3). The symmetry of the larval abundance contour lines around this axis indicates that larvae are not preferentially advected northwards, and that large concentrations of larvae are found to the south of the main larval source. This seems to support the idea that a diel migration may be sufficient to minimize advection of the population to the Bay of Fundy. If the larvae remain in the surface for 24 h, and are subjected to a residual current of 10 km day^{-1} for a period of 10 days, they will be displaced by 100 km. However, if the larvae are at the surface for only 12 h, the displacement would be 50 km. This calculation assumes the simplest possible scenario of a constant residual current at the surface and a linear sheared water column, with a residual current of zero at the bottom. The larvae are not allowed to remain in the water column, where they would be subjected to a weaker residual flow. It appears that a combination of this migration period with the complex circulation patterns on the shelf off SW Nova Scotia [Tee *et al.*, 1993] could explain the retention of herring larvae. This is currently being considered in a modelling study [Stephenson, pers. comm.].

However, this explanation would account only for the maintenance of the aggregation in the well mixed area with respect to the alongshore horizontal transport due to the northerly residual current. It remains to be understood why larvae are not found in more numbers in the adjacent stratified waters. Figure 2.5 shows that larvae do leave the well mixed region and occupy the adjacent stratified waters. This suggests that an onshore–offshore displacement also occurs. If it is assumed that larvae at the edge of the aggregation, with mean length of 13 mm (*e.g.*, station 76), were originated at its center, with approximately 9 mm (*e.g.*, station 58), the speed of this displacement can be estimated. If the larvae grow at 0.24 mm day^{-1} [Chenoweth *et al.*, 1989], they are approximately 16 days old. This suggests that they have traveled about 3 km day^{-1}. After a period of several months, a larger concentration of larvae should be found in the adjacent stratified waters. But they are not.

A possible explanation for the low concentration of larvae observed in the stratified regions is the existence of a better feeding environment in the well mixed water. It can be argued that if the well mixed area feeding environment is better, larvae in the stratified region would not encounter the same favorable growth conditions. It can be predicted that these larvae would have an enhancement in mortality induced by starvation. This would indicate that the existence of larval aggregations would not only be a function of the physical features associated with "larval retention", but they would also be the result of differential mortality acting upon larvae distributed throughout the region. This interpretation is supported by some of the observations in this chapter. Herring spawn in favorable well mixed sites and are dispersed offshore (Figure 2.7). The negative slope of Figure 2.7 reflects the differential mortality and a dispersal rate of the larvae. The fact that there are no small larvae offshore (Figure 2.9) suggests that these larger larvae are the survivors of larvae hatched in the well mixed regions. The result is that "vagrants" lost by spatial processes are now subjected to energetic processes too. In the next chapter, I examine this hypothesis based on the availability of the principle food source for

larval herring.

Chapter 3

Abundance and distribution of the microzooplankton: herring larva and its food

3.1 Introduction

Plankton dynamics in tidally well mixed areas are different than in stratified waters. On average, the net primary production in well mixed waters is restricted by a low photosynthesis to respiration ratio due to low mean light levels [Holligan *et al.*, 1984; Foog *et al.*, 1985]. In this situation diatoms appear to survive through resuspension by tidal mixing. The metabolic activity of the microheterotroph community is also low [Holligan *et al.*, 1984], and allows the plant biomass to be higher than in the stratified waters, but lower than in the active front. Fournier *et. al* [1984a; 1984b] showed that phytoplankton biomass in the well mixed area off Southwest Nova Scotia during the summer and the fall is relatively high in the well mixed waters when compared to the stratified region, and that the highest values were associated with fronts.

In stratified waters, phytoplankton biomass in the surface mixed layer becomes nutrient limited. When there is sufficient light, and nutrients are available in the

thermocline, a chlorophyll maximum develops. Under these conditions, a very active microheterotroph population is found [Holligan *et al.*, 1984]. This activity leads to an increase in secondary production relative to well mixed waters, and microzooplankton and larger zooplankton are generally more abundant [Holligan *et al.*, 1984; Scrope-Howe and Jones, 1985; Thompson and Harrop, 1991]. The concentration of microzooplankton (20 to 200 μm) has been reported to be highest at the frontal region [Scrope-Howe and Jones, 1985; Kiøboe and Johansen, 1986]. This is important, because this is the size fraction of the plankton used as food resource by herring larvae [Cohen and Lough, 1983].

Off Southwest Nova Scotia, there is a coincidence between herring larvae spawning, distribution of larvae and tidally well mixed waters. Iles and Sinclair [1982] and Sinclair and Iles [1985] argued that food availability was not the most important factor in determining the location of spawning of this herring population. They based their argument on the observation that primary production was low in the well mixed area, and that there was some evidence that zooplankton abundance (of larger size categories) was also low in this area. The long larval phase and slow growth rate shown by this fall spawners [Sinclair and Tremblay, 1984] also supported such an interpretation.

Frank [1988] argued that bias in the sampling method and in the data presentation of Sinclair and Iles' [1985] zooplankton abundance invalidated this interpretation. He reported a strong onshore-offshore gradient for the microzooplankton. He also showed that when the zooplankton size category most relevant to young larvae was used there was a positive correlation between the distribution of food and larvae abundance. Furthermore, he stated that other sampling in this area [Sameoto, 1977] reported higher biomass levels of copepods within the well mixed area.

Frank's data, however, did not cover adequately the distributional range of the herring and were for the spring rather than for the fall. There are thus several complicating factors in the controversy:

1. The sampling method and presentation of results. The appropriate size of the larval food has to be sampled. Furthermore, the results must take into account differences in the vertical distribution of the food items when comparing shallow, well mixed water columns to deep, stratified columns;

2. The observations must be at the appropriate larval distributional area and period, in order to reflect the food abundance that is actually available for the larvae;

3. Seasonal differences in the food size that is required and available to the larvae have to be taken into account (*e.g.* the relevant size category for the larger herring larvae in the spring is the larger fraction, while that for the smaller larvae in the fall is the smaller one);

4. The quality of the samples, because in tidally well mixed waters an increase in inorganic particulate matter in suspension can contaminate samples collected with fine mesh sizes, and produce erroneous abundance estimates of the smaller size fraction of the plankton.

The aim of this chapter is to re-evaluate the microzooplankton distribution off southwest Nova Scotia, and to examine the influence of these complicating factors in the inferences about food availability for herring larvae. This will allow a better characterization of the food availability for herring larvae, which is important if one wishes to properly test hypotheses related to larval feeding in tidally well mixed and stratified waters. The data sets used in this analysis are those available in the literature [Subba Rao, 1975; Sameoto, 1977; Dugas, 1984; Frank, 1988] as well as data collected in this study.

It is hypothesized that the well mixed and the stratified areas provide the same food availability for young herring larvae. If the hypothesis is not rejected, it would support the interpretation that herring larvae aggregations occur "in spite of" the food characteristics of these areas as suggested by Sinclair and Iles [1985]. This interpretation is also supported if the hypothesis is rejected, but food abundance

is greater in the stratified waters. The implication is that food availability for the larvae by itself is not an important factor in the determination of the location of spawning, *i.e.* other factors dominate in the decision with respect to spawning – and eventual distribution of larvae. However, if the hypothesis is rejected, and with the well mixed regions having more food available, it would suggest that larvae may be found in these aggregations because of the food resources available, supporting Frank's [1988] argument. In this case, it can be predicted that larvae found in the stratified region will encounter unfavorable growth conditions and an enhancement in mortality induced by starvation. This would indicate that the existence of larval aggregation in these well mixed areas is not only a function of the location of physical features and behaviour associated with "larval retention", but it may be due to differential mortality acting upon larvae distributed in different areas throughout the region, contributing to an "apparent" retention.

This chapter also evaluates the vertical distribution of the microzooplankton in the area of larval aggregation. Despite changes in concentration over time, microzooplankton are generally evenly distributed in the water column in tidally well mixed regions [Holligan *et al.*, 1984; Scrope-Howe and Jones, 1985; Buckley and Lough, 1987; Stephenson and Power, 1991], while the larvae undergo vertical migration [Stephenson and Power, 1988, 1989b, and previous chapter]. If it is expected that larvae remain in this region because of their food resources, it is reasonable to expected that changes in the vertical structure of the food items would also be encountered. Stephenson and Power [1991] tested this hypothesis and found no support for it. They showed that food items were available in equivalent numbers throughout the water column and did not show the same type of aggregation or movement demonstrated by the larvae. They also found that herring larvae were feeding specifically and that calanoid copepods appeared to be the preferred item. This suggest that vertical changes in total abundance of the whole microzooplankton community may not be a good indicator to study herring larval migration with respect to feeding. In this study, I hypothesized that there is a change in the vertical

size structure of the microzooplankton community, that reflects a pattern similar to the larvae vertical migration, and that indicates that the larvae may be moving vertically to feed.

3.2 Material and Methods

3.2.1 Horizontal distribution

Microzooplankton were sampled at the same stations used to collect herring larvae in October 1989 (Figure 3.1). These stations were distributed in two transects that crossed the larval distribution. Microzooplankton were collected using a vertically hauled 40 cm Bongo frame with a 53 μm-mesh. Samples were taken from 5 m off the bottom to the surface. A 4 mm-mesh sieve was used to remove all large macrozooplankton and detritus. Samples were washed off the net with seawater and preserved with 5 % formalin buffered with marble chips.

In the laboratory, a Motoda box-type splitter was used to subsample the microzooplankton. This aliquot was filtered through a 602 μm sieve to remove the large aggregates and marble chips. A Coulter-Counter TA II was used to determine the particle size composition of the sample. The procedure used is that described in Taggart and Leggett [1987], with the counter fitted with a 800 μm aperture tube and calibrated using 94.6 μm polystyrene beads. The particle counts were corrected for dilution and fractionation of the original samples. The results for each sample were standardized by the volume filtered by the net. Microzooplankton abundance is expressed in number of particles at each size class per litre (number ℓ^{-1}), and as integrated wet weight biomass (g m^{-2}) of each size class. The biomass was obtained by multiplying the particle count in each size class by its spherical volume. A density of 1 g cm^{-3} is assumed for the microzooplankton. The integrated biomass for each sample was obtained by multiplying the biomass concentration by the sampling depth.

At the size range found for herring larvae (7–29 mm) (Figure 2.8, Chapter 2),

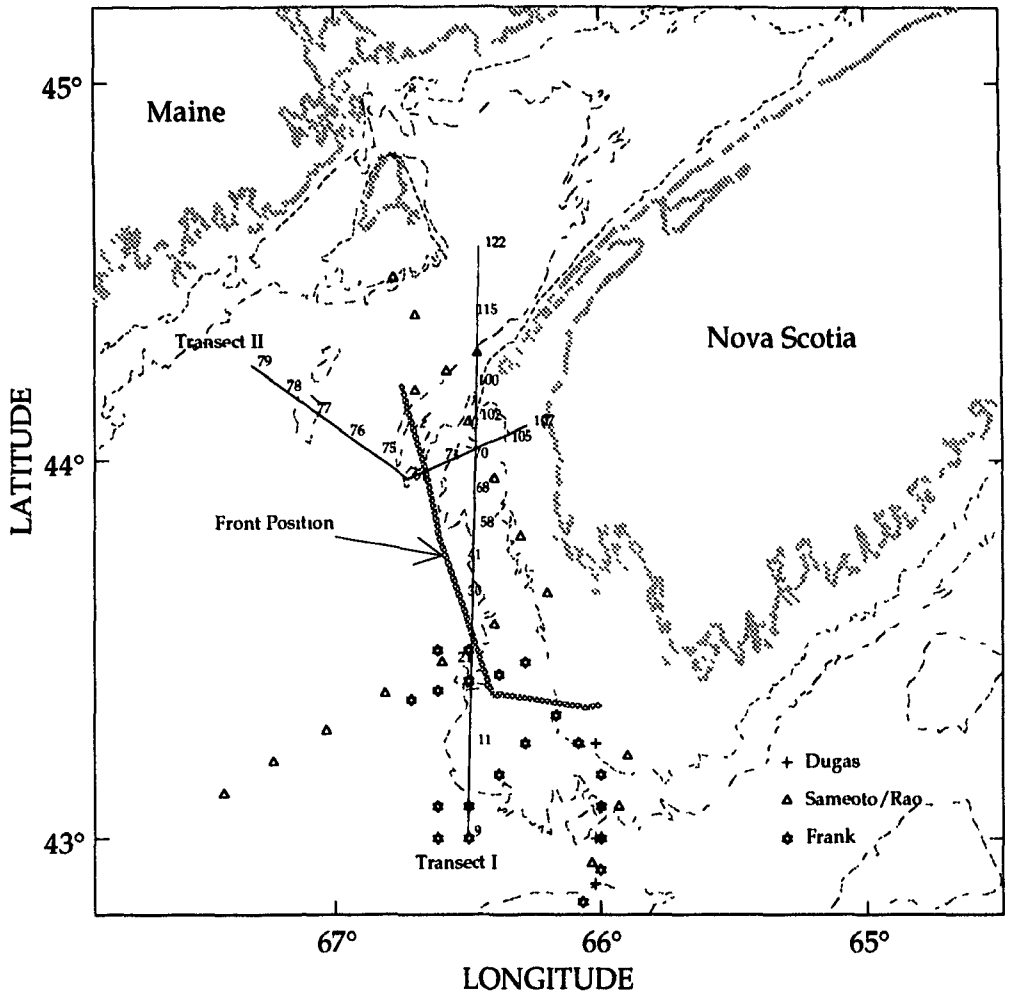

Figure 3.1: Map showing the position of the stations used for the study of microzooplankton off SW Nova Scotia.

the size of prey items ranges from 10–600 μm [Cohen and Lough, 1983] (Table 3.1). Based on this information, the plankton samples were classified into 10 sizes: 50–64, 64–80, 80–101, 101–128, 128–161, 161–203, 203–256, 256–322, 322–406, and > 406 μm. Throughout this thesis, I will refer to these size classes as microzooplankton, and for brevity, only the lower limit will be used when referring to a determined class size. The choice of this size range was based on sampling and processing limitations, and because it incorporates the 50 to 200 μm size classes. These are the most important prey sizes for herring larvae [Checkley, 1982; Cohen and Lough, 1983; Stephenson and Power, 1991].

Another subsample was used to determine the microzooplankton dry weight and ash-free weight. Samples were fractionated by passing them through sieves with a gentle flow of water. Three size classes were used: 53–158, 158–350, and > 350 μm. The content of each size class was then vacuum filtered through a precombusted glass microfiber filter (Whatman GF/F). For the determination of dry weight, samples were dried to constant weight in a 70 °C oven for 24 hours. Samples were cooled in a desiccator and weighted to the nearest 0.1 mg. The samples were then combusted in a muffle furnace at 500 °C for 6 hours, cooled in a desiccator and weighed, yielding the ash weight. The difference between the dry weight and the ash weight yields the ash-free or carbon weight.

To characterize the horizontal distribution of microzooplankton with respect to different oceanographic conditions, its biomass and concentration are expressed with respect to the stability of the water column. Correlation analysis was performed between microzooplankton abundance and Delta Sigma-t ($\Delta\sigma_t$). A positive or negative significant correlation would indicate differences in food availability between the different oceanographic conditions. A lack of correlation would demonstrate that food availability is equal for both areas. Correlation analysis is also performed between larval abundance and abundance of prey, and among the different size classes. The level of significance used in all analysis is 0.05, unless otherwise indicated.

Data were also selected from the studies of Subba Rao [1975], Sameoto [1977],

Larval size	Prey size (μm)		
(mm)	1974	1975	1976
< 10	20–180	10–220	–
10–14.9	50–400	50–310	100–220
15–19.9	50–520	60–310	150–350
20–24.9	100–750	60–500	180–400
25–29.9	50–650	50–500	210–380

Table 3.1: Approximate prey sizes (μm) for different size classes (mm) of herring larvae extracted from Cohen and Lough [1983] Figure 5. (–) no data available.

Dugas [1984] and Frank [1988]. The criteria for this selection were the spatial coincidence of the stations with the herring larvae aggregation and its adjacent stratified waters. Data that are not coincident with the period of larval distribution, but are pertinent to the discussion related to the inshore versus offshore food availability, are also included. Although these data are not directly relevant to the feeding of herring larvae, their analysis is important if the complicating factors enumerated earlier are to be addressed.

Subba Rao [1975] and Sameoto [1977]

Subba Rao [1975] and Sameoto [1977] sampled the southwest portion of the Scotian Shelf during August, 1974. 18 of the 47 stations sampled, varying in depth from 30 to 190 m, were selected to be re-analyzed in this study (Figure 3.1). Microzooplankton were collected from 5 m depth with a 30 ℓ Niskin bottle. Twenty milliliters of the sea water samples were preserved with Lugol, sedimented in a settling chamber and identified and counted with an inverted plankton microscope. The categories included were: copepodite, nauplius, tintinid and veliger [Subba Rao, 1975]. A 75 cm diameter octagonal 243 μm-mesh net towed obliquely from within about 2 m of the bottom to the surface was used to sample the zooplankton. All samples were preserved in 5 % formalin and large forms of zooplankton were removed. The remaining sample, consisting primarily of copepods, was vaccumed over a 30 μm filter until the water ceased to drip and then weighed for a wet biomass estimate [Sameoto, 1977]. Only the data on copepod biomass and *Pseudocalanus* sp. were re-analyzed.

Dugas [1984]

Dugas [1984] collected samples off SW Nova Scotia during the months of February, April, May, June and November of 1983. Seven stations were sampled along a transect from within the well mixed area to the Northeast Channel (Figure 3.1). Stations 7-4 and 7-6 (40 and 125 m, respectively) are in our area of interest and

are used in this study. With the exception of the February cruise, all other cruises used a 75 cm plankton net with 80 μm-mesh, which was vertically hauled from 50 m to collect the samples. During the February cruise, a 60 cm Bongo with 333 and 80 μm-mesh obliquely towed from near bottom to surface was used. The zooplankton were identified and abundance was estimated by counts of each species. The information on total nauplii, and larval fish food is used. Larval fish food is the sum of all *M. norvegica, O. similis, L. retroversa* (Sm), and nauplii.

Frank [1988]

Frank [1988] sampled the microzooplankton during May, 1985 and 1986. A 75 cm diameter, 80 μm-mesh, ring net was used to sample at discrete depths from the surface to 20 m, 20-40 m, and, where total depth permitted, 40-60 m. Data were reviewed from 20 stations sampled in 1985 (Figure 3.1). The data from these stations, which were more complete [K. Frank, pers. comm.], were sampled close to, or in, the area of herring larvae distribution, and presented the most striking contrast between concentrations onshore and offshore. Three size categories where processed using standing screens: 80–153, 153–308, > 308 μm. Samples were subsampled using a Motoda box plankton splitter, thoroughly rinsed with a steady stream of tap water, resuspended, and filtered by aspiration through a preweighed glass microfiber filter. The filters were oven dried at 70 °C and weighed. The mass of the size-specific zooplankton fractions at each station was expressed as the mean of the multiple depth strata.

Data representation: concentration versus integrated density

Whenever possible, microzooplankton abundance is expressed as concentration and as integrated density. Concentration represents a measure of abundance (biomass or number) in unit volume (ℓ or m^3). Integrated density is a measure of abundance within the water column and it is expressed per unit area (m^2). The integrated density is obtained by multiplying the concentration by the sampling depth. The

integrated density is more appropriate for comparisons between shallow well mixed and deep stratified regions when vertical and oblique hauls are used. Vertical and oblique hauls sample in an integrated way, and to express data collected by these methods in a per volume basis (concentration) would require "*ad hoc*" assumptions about the vertical distribution of the plankton. When concentration is used, the results are averaged and represent a mean plankton abundance in a unit of volume. For the mean to be the appropriate abundance representation for the whole water column, the plankton has to be either uniformly or normally distributed with depth. This is certainly not the case with microzooplankton or most fish larvae, including herring. Microzooplankton are even. distributed throughout the water column in well mixed areas [Buckley and Lough, 1987]; in deeper stratified waters, they tend to be concentrated at or above the pycnocline [Townsend *et al.*, 1984; Buckley and Lough, 1987; Incze *et al.*, 1990]. This same pattern is observed for herring larvae [Heath *et al.*, 1988; Stephenson and Power, 1988; Munk *et al.*, 1989; Stephenson and Power, 1989a]. The use of concentration as an indicator of abundance would systematically underestimate food availability for the larvae in the deeper stratified water column when compared to the shallower well mixed region [Peterson and Miller, 1977; Scrope-Howe and Jones, 1985].

Undoubtedly, the best way to characterize and present information on food availability for herring larvae would be the concentration of prey (*e.g.* number m^{-3} or number ℓ^{-}) at different depth strata. Unfortunately, this type of data is only available from Dugas [1984] and Frank [1988]. When information on the vertical distribution of the larvae and their prey is lacking, both representations (concentration and integrated density) of the data are useful in attempting to describe and compare the feeding environment as realistically as possible. Therefore, in order to summarize the information on the abundance of microzooplankton off SW Nova Scotia, the results of this study and the results of the studies available in the literature are expressed as standardized integrated density and concentration. These datasets are different expressions of abundance (counts, dry weight, wet weight),

and were collected and processed in different ways. For this analysis, the interest is on the trends these data may present with respect to the the stability of the water column. Thus, they are standardized by subtracting the mean value of a each set from each individual value of the set, and dividing by the mean of its set. In this way the abundances become dimensionless and only the trends are maintained. The standardized microzooplankton abundance is expressed with respect to depth of the water column, since information on the stratification parameter is not available for all studies. Depth is highly correlated with $\Delta\sigma_t$ (r=0.7, $p < 0.0001$).

3.2.2 Vertical distribution

The same sampling strategy outlined in Chapter 2 was used to collect information on the vertical distribution of herring larval food. Microzooplankton were collected immediately after the Mininess tows. A pump system was used to sample the microzooplankton. This system consisted of an electrical centrifugal pump (FLYGT model 2051), 6 cm suction hose, and an in-line paddlewheel flowsensor and readout (SIGNET MK515). The hose was attached to a rosette sampler and a Guildline CTD was used to monitor sample depth. Samples were taken at 5, 10, 20, 30, 40, and 50 m. Approximately 1500 ℓ of water were sieved first through a 333 μm mesh-net to remove larger organisms and then through a 53 μm mesh-net. Samples were then washed off the net with seawater and preserved with 5 % formalin buffered with marble chips.

In the laboratory, samples were prepared to be analyzed by a Coulter Counter Multisizer II. Samples were gently mixed and sieved onto a 602 μm nitex screen to remove large aggregates and marble chips. The entire sample was then placed into a plankton splitter and diluted to an appropriate concentration. Typically, 1/16 of the original sample was sufficient to generate an accurate size frequency distribution. A 293 mℓ aliquot was aspired through a 1000 μm aperture tube previously calibrated with 220 μm polystyrene beads.

The counts were standardized by the volume filtered (1500 ℓ) and are expressed

as number of particles per liter. The total microzooplankton concentration is the integration of all the concentrations between 50 and 400 μm. The size spectra of each sample is the relative frequency (%) of the biomass concentration for a given size. The original particle counts were converted to biomass by multiplying the count in each class by its spherical volume assuming a plankton density of 1 $g\,cm^{-3}$. The original size spectra was smoothed using a running mean filter with width of 10 μm.

3.3 Results and Discussion

3.3.1 Horizontal distribution

Quantitative Analysis

Figure 3.2 shows the relation between the different size classes of microzooplankton and the stratification of the water column ($\Delta\sigma_t$) for the combined transects. The closed circles represent the integrated wet weight biomass ($g\,m^{-2}$), while the open circles represent the concentration (number ℓ^{-1}) of each size class. There seems to be a negative trend between the integrated microzooplankton biomass and the stratification of the water column for the smaller size classes (Table 3.2). The 161, 203, 322 and 406 μm size classes differ from this pattern, showing a positive correlation with $\Delta\sigma_t$. However, only the 322 μm size class presents a significant trend. Overall, there is no statistically significant difference in the integrated biomass of the different prey sizes between the inshore well mixed and the offshore stratified waters.

When food availability is expressed in terms of microzooplankton concentration (number ℓ^{-1}), all size classes show a negative correlation with the stratification of the water column (Figure 3.2, Table 3.2). Furthermore, for three of the 10 size classes, 80, 101 and 256 μm, this correlation is statistically significant. That is, when food availability for herring larvae is expressed in terms of mean concentration, there is

	50–64	64–80	80–101	101–128	128–161	161–203	203–256	256–322	322–406	> 406	$\Delta\sigma_t$
50–64	–	0.99**	0.94**	0.94**	0.86**	0.42	0.28	0.14	-0.08	-0.27	-0.12
64–80	0.99**	–	0.98**	0.98**	0.87**	0.44	0.27	0.16	-0.12	-0.28	-0.17
80–101	0.95**	0.97**	–	0.98**	0.85**	0.43	0.22	0.18	-0.18	-0.26	-0.26
101–128	0.93**	0.96**	0.99**	–	0.92**	0.54*	0.34	0.27	-0.06	-0.27	-0.20
128–161	0.90**	0.94**	0.96**	0.99**	–	0.80**	0.63**	0.53*	0.17	-0.25	-0.08
161–203	0.77**	0.81**	0.84**	0.88**	0.92**	–	0.90**	0.82**	0.46*	-0.17	0.09
203–256	0.58**	0.62**	0.61**	0.65**	0.67**	0.87**	–	0.76**	0.69**	0.11	0.36
256–322	0.44	0.46*	0.49*	0.47*	0.47*	0.68**	0.82**	–	0.45*	-0.19	-0.21
322–406	0.13	0.11	0.08	0.07	0.03	0.22	0.50*	0.57**	–	0.28	0.48*
> 406	-0.10	-0.11	-0.12	-0.16	-0.20	-0.21	-0.22	-0.11	0.37	–	0.06
$\Delta\sigma_t{}^1$	-0.42	-0.44	-0.53*	-0.46*	-0.43	-0.35	-0.18	-0.50*	-0.03	-0.18	–

Table 3.2: Correlation coefficients for the different size classes (μm) of microzooplankton and for the stratification parameter ($\Delta\sigma_t$). $\Delta\sigma_t{}^1$ indicates the correlacion coefficients when concentration (numberl^{-1}) was used. * $p \leq 0.05$, ** $p \leq 0.01$.

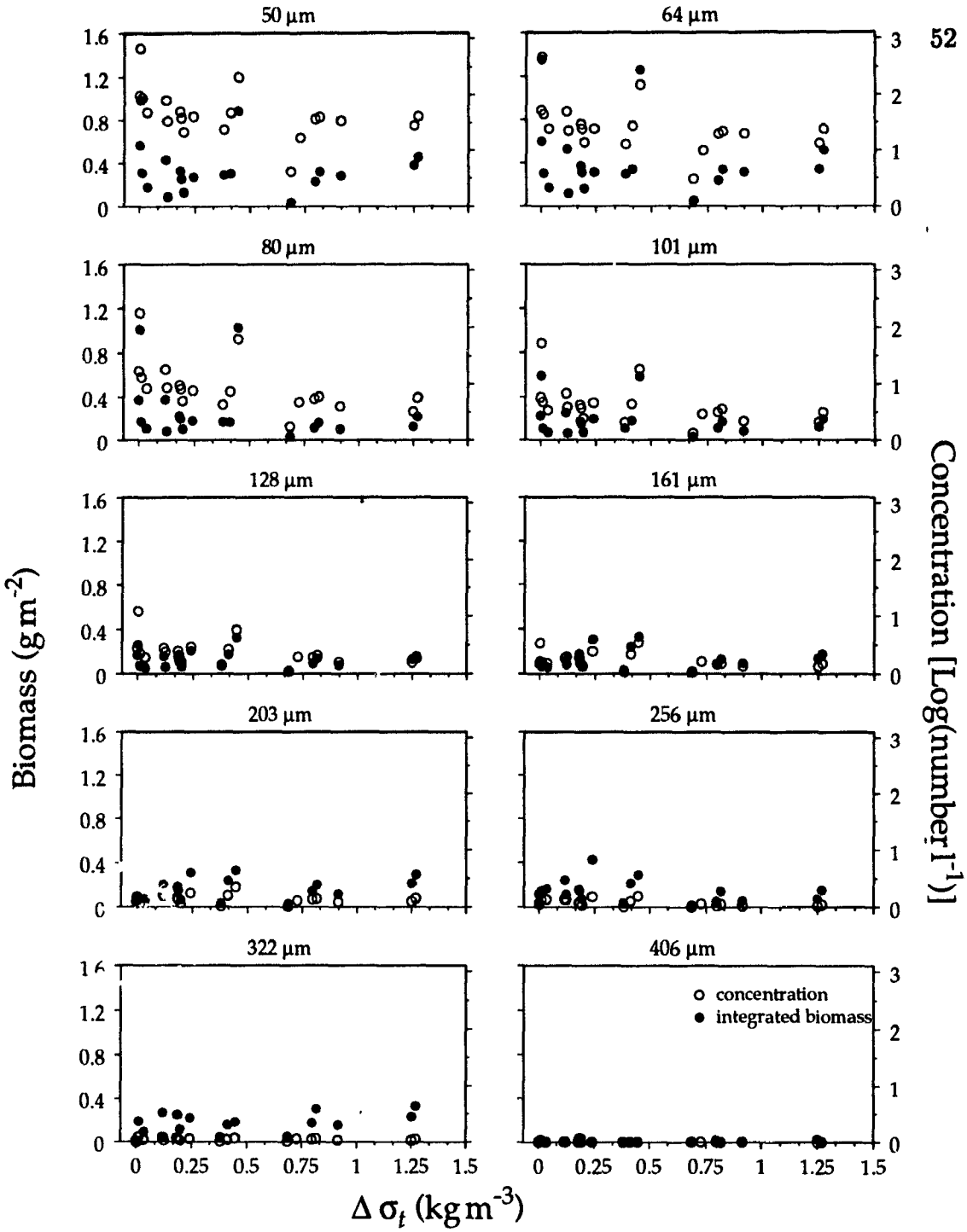

Figure 3.2: Plot of the relation between the integrated biomass of microzooplankton ($g\,m^{-2}$) and the logarithm of the concentration (number ℓ^{-1}) for each size class and $\Delta\sigma_t$ ($kg\,m^{-3}$) for the combined transects. (•) integrated biomass; (○) concentration.

an indication of higher food availability in the well mixed waters.

Another interesting result is the association that results when the different size classes are expressed in different units. When the integrated biomass data set is used, the smaller size classes, between 50 and 128 μm, are highly correlated among themselves (Table 3.2). From the 128 μm class size on, the correlations are only significant among adjacent size classes. The larger size class, 406 μm, is not significantly correlated to any of the other sizes. A different picture emerges, though, when the data is expressed in terms of concentration. There is a significant positive correlation among all size classes smaller than 322 μm. Although not significant, the larger size class (406 μm) is negatively correlated with this association of smaller sizes.

Figure 3.3 shows the distribution of the integrated biomass, expressed as wet weight in $g\,m^{-2}$, and of the concentration, expressed as number ℓ^{-1}, for the combined microzooplankton size classes (50–406 μm) with respect to the stratification of the water column. Biomass values vary between 0.3 and 5.2 $g\,m^{-2}$, while concentration varied from 6.5 to 1393 particles per litre. The concentration of microzooplankton in transect II and in the combined transects has a significant negative correlation with the stratification parameter (Table 3.3). It is interesting to notice that when food availability is expressed in terms of integrated biomass, none of these correlations are significant.

These results indicate that one has to proceed with care when testing hypotheses concerning food availability for fish larvae in different environments. Generally, abundance of food for fish larvae is expressed in concentration, since this would represent the amount of prey available in an amount of volume of the environment. However, this measure is not always the most adequate, since it assumes that two populations have the same distribution with depth. This is clearly not the case in environments such as those off SW Nova Scotia. Microzooplankton are uniformly distributed in shallow well mixed waters [Holligan *et al.*, 1984; Scrope-Howe and Jones, 1985; Buckley and Lough, 1987; Stephenson and Power, 1991], while their

	Biomass	Concentration
All data	0.19**	-0.07
Without dry weight data	0.45**	0.09

Table 3.3: Correlation coefficients for the standardized integrated biomass and concentration of microzooplankton and depth (m). ** $p \leq 0.01$.

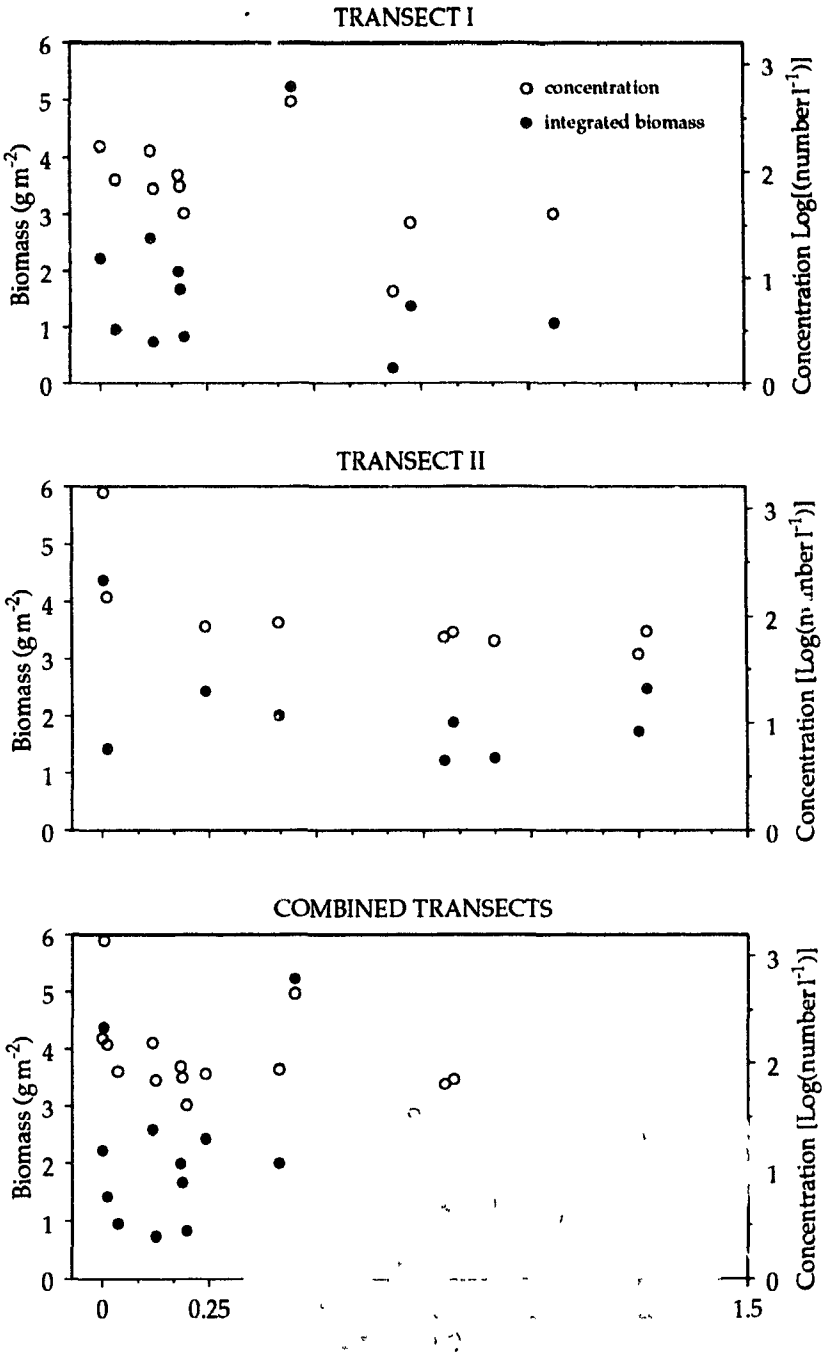

Figure 3.3: Plot of the relation between [illegible] integrated biomass ($g\,m^{-2}$) and logarithm of the concentration ([illegible] ℓ^{-1}) for the combined size classes versus the stratification of the water column ($\Delta\sigma_t$, $kg\,m^{-3}$) for each transect and the combined transects. (•) integrated biomass; (o) concentration.

distribution is skewed to the surface in deeper stratified waters [Townsend *et al.*, 1984; Holligan *et al.*, 1984; Scrope-Howe and Jones, 1985; Buckley and Lough, 1987; Incze *et al.*, 1990].

The results of the distribution of integrated biomass show that there are no significant differences in food availability between well mixed and stratified waters off SW Nova Scotia. With the exception of the 322 μm size class, all other individual size classes and the combined size class support this conclusion. This result is not in agreement with recent studies on the microzooplankton distribution in tidally well mixed waters. Off the western English channel, Holligan *et al.* [1984] reported the largest densities of copepod nauplii and organic carbon of microzooplankton in the stratified waters. Scrope-Howe and Jones [1985] show that in the tidal system of the western Irish Sea, the largest concentration of copepod nauplii and copepodites were coincident with the frontal region. Scrope-Howe and Jones [1985] and Thompson and Harrop [1991] also show an increase in the abundance of copepods in waters which are, or have become stratified.

Off SW Nova Scotia, Frank [1988] found an inverse correlation between the concentration of microzooplankton dry weight and the distance from the coast. Although volumetric concentration is used, samples were all from less than 60 m depth, and the results are not affected by the dilution problem discussed above. The discrepancy between his result and the results of this study may be accounted for by spatial and temporal differences in the sampling. His samples were from the southeastern portion of the region (Figure 3.1) and from the spring, while this study is conducted throughout the whole larval distributional region and during the fall.

The continental shelf off SW Nova Scotia is very dynamic, and it is influenced by four factors in addition to the normal seasonal stratification-mixing regime: tidal mixing, upwelling, input from alongshore residual circulation, and episodic incursions by warm-core eddies [Fournier *et al.*, 1984a]. It has recently been shown that topographic upwelling and downwelling characterize the southeastern portion of this region [Tee *et al.*, 1993]. The combination of upwelling and strong tidal mixing is

the mechanism that produces the observed cold water anomaly off Cape Sable. Off this region, Fournier *et al.* [1984a] found that the summer season had the highest concentrations of chlorophyll, and the greatest frontal extent. This could indicate that this portion of the shelf is indeed more productive during spring and summer, and an onshore/offshore gradient in microzooplankton biomass is observed.

For the rest of the shelf, the highest chlorophyll concentrations were generally observed in the frontal region [Fournier *et al.*, 1984a]. However, Fournier *et al.* [1984a] and Denman and Herman [1978] report that some stations presented higher concentrations which were not coincident with the position of the front. They both attributed this anomalous enrichment to some form of localized topographically induced upwelling. The results of the numerical model of Tee *et al.* [1993] predict several areas of strong upwelling and downwelling off SW Nova Scotia, and they suggest that this process is expected to be important in other coastal areas where strong tidal currents and significant variations of the bottom topography exist. It would not be expected then, that in a region with such dynamic features, which could enhance localized biological activity, a strong onshore/offshore gradient in biological production be present. The existence of localized areas of enrichment would tend to offset any significant trend. For example, station 9 is coincident with downwelling, while station 11 is an area of upwelling (Figure 3.4). Microzooplankton concentration and integrated biomass are maximum at station 11, and sharply declined in the adjacent stations (Figure 3.5).

The fact that the surveys were conducted at different times of the year could also account for some of the differences between the results of this work and that of Frank [1988]. It would be expected that during fall, biological activity over the continental shelf would decrease following the decrease of available light. This was found by Fournier *et al.* [1984b] in December 1978, and it is in agreement with the general trend of biological production in temperate regions of the Northern Hemisphere. However, in November 1979, the same authors report that both inshore and offshore waters were stratified, and chlorophyll levels were, in some places, 5 times above

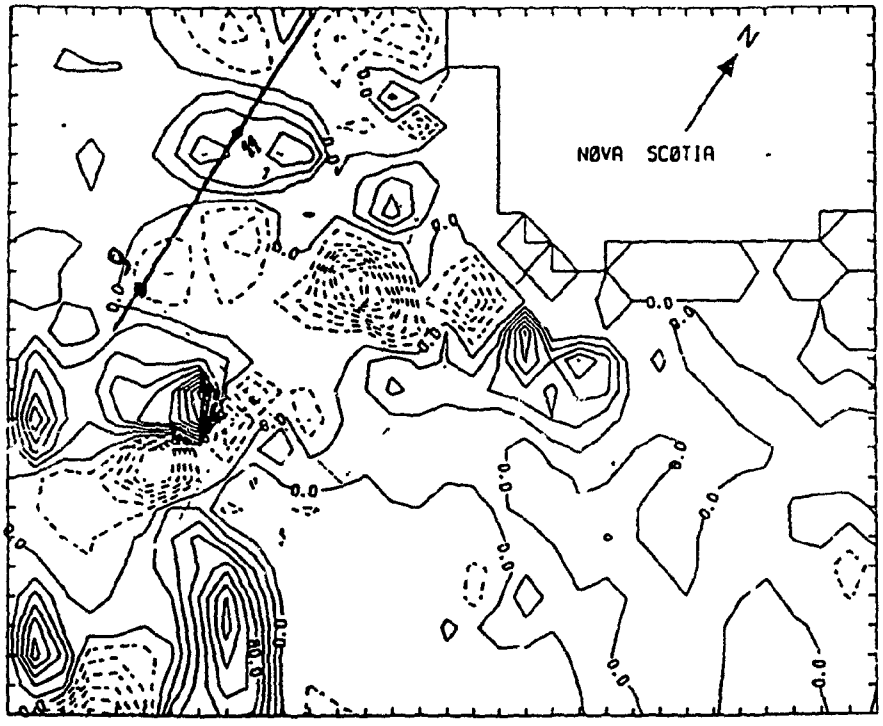

Figure 3.4: The spatial distribution of the vertical velocity induced by the depth-averaged cross-isobath residual currents (10^5 m s^{-1}). Solid curve indicates upwelling; dashed curves indicate downwelling. The distance between two tick marks on the boundaries is 7.047 km. Note the position of stations 9 and 11 from transect I. Modified from Tee *et al.* [1993].

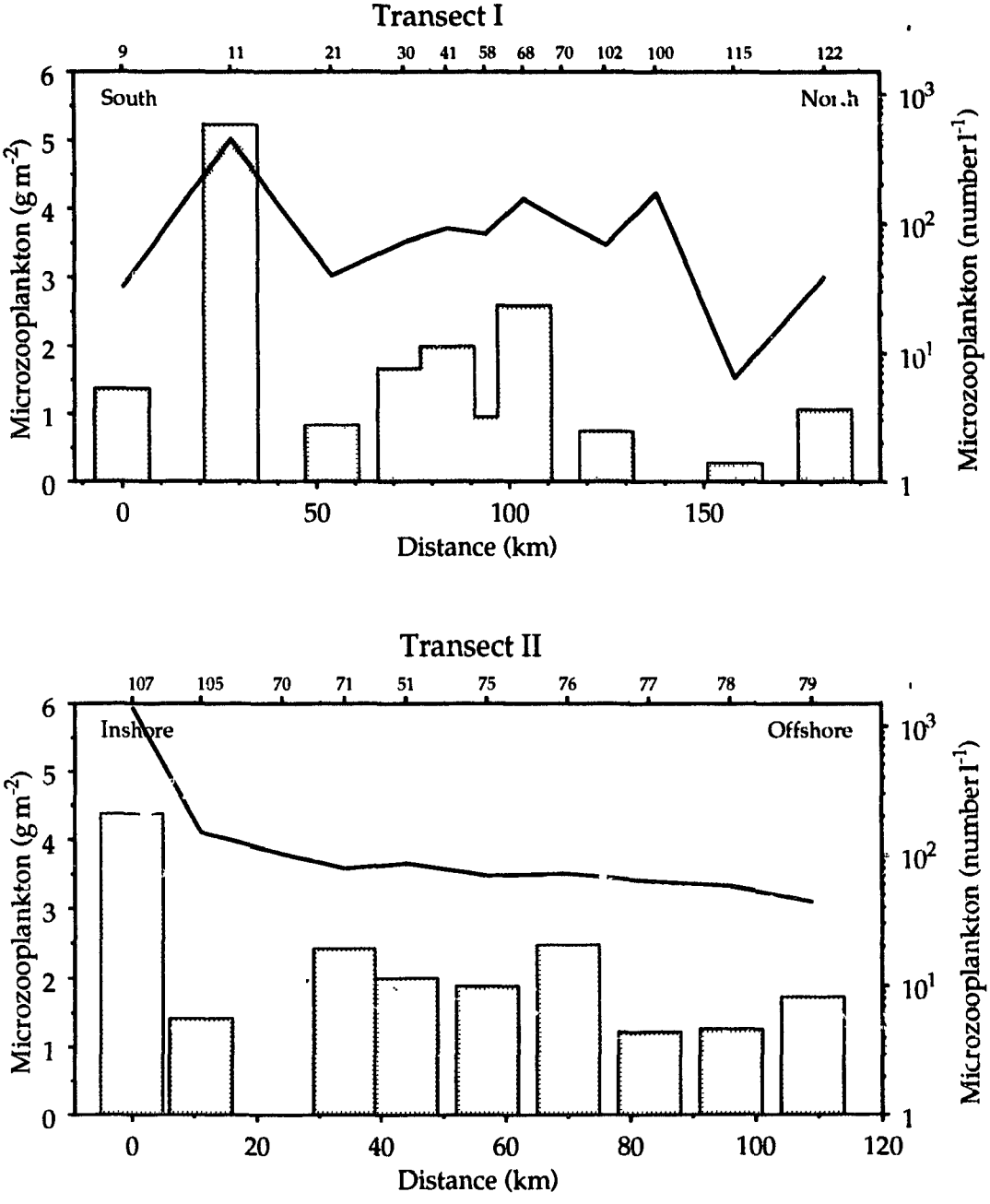

Figure 3.5: Distribution of microzooplankton abundance along the two transects. Bars are the integrated biomass ($g\,m^{-2}$); solid lines are the logarithm of the concentration (number ℓ^{-1}).

background. Offshore, warm saline water from either the slope or the Gulf of Maine may have caused the stratification. Inshore, stratification could result from the influx of a shallow layer of relatively low-salinity water carried by the Nova Scotia current. These temporary conditions resulted in a bimodal spatial distribution of chlorophyll. This example not only illustrates the variability of oceanographic conditions off SW Nova Scotia, but also that these conditions change at different times of the year. That is, the oceanographic environment sampled by Frank [1988] in the spring may have been different than the one sampled in this study during the fall.

Qualitative Analysis

Another important aspect to consider is the quality of the samples. Figure 3.6 shows the carbon content of three size classes in relation to the stratification of the water column. It is clear that the finest mesh size retained a great amount of inorganic material. The 53-158 μm size class samples was less than 50 % carbon. This was enhanced in the shallower well mixed waters (*i.e.* low values of $\Delta\sigma_t$). The amount of organic material in the samples increases in the larger size classes. For the 158-350 μm class, most of the samples are between 85-100 % carbon, while some of the samples in the well-mixed waters still have less than 60 % of organic material. For the largest size class, the majority of the samples have between 80-100 % of carbon.

Qualitative microscopic analysis confirms this trend, and reveals that the smaller size class samples contain fine sand particles. Samples in the shallower, well mixed waters were dominated by these fine particles, while in more stratified waters their relative amount decreases significantly. In deeper waters, the samples were generally dominated by large diatoms, dinoflagelates, copepod nauplii and copepodites. The proportion of these sand particles decreased also in the larger size classes. The 158-350 μm class was generally dominated by copepodites and small copepods. The larger group, $>$ 350 μm, was constituted by copepods, mostly *Pseudocalanus* sp., and in the stratified waters there was also an increase in the presence of euphausiids

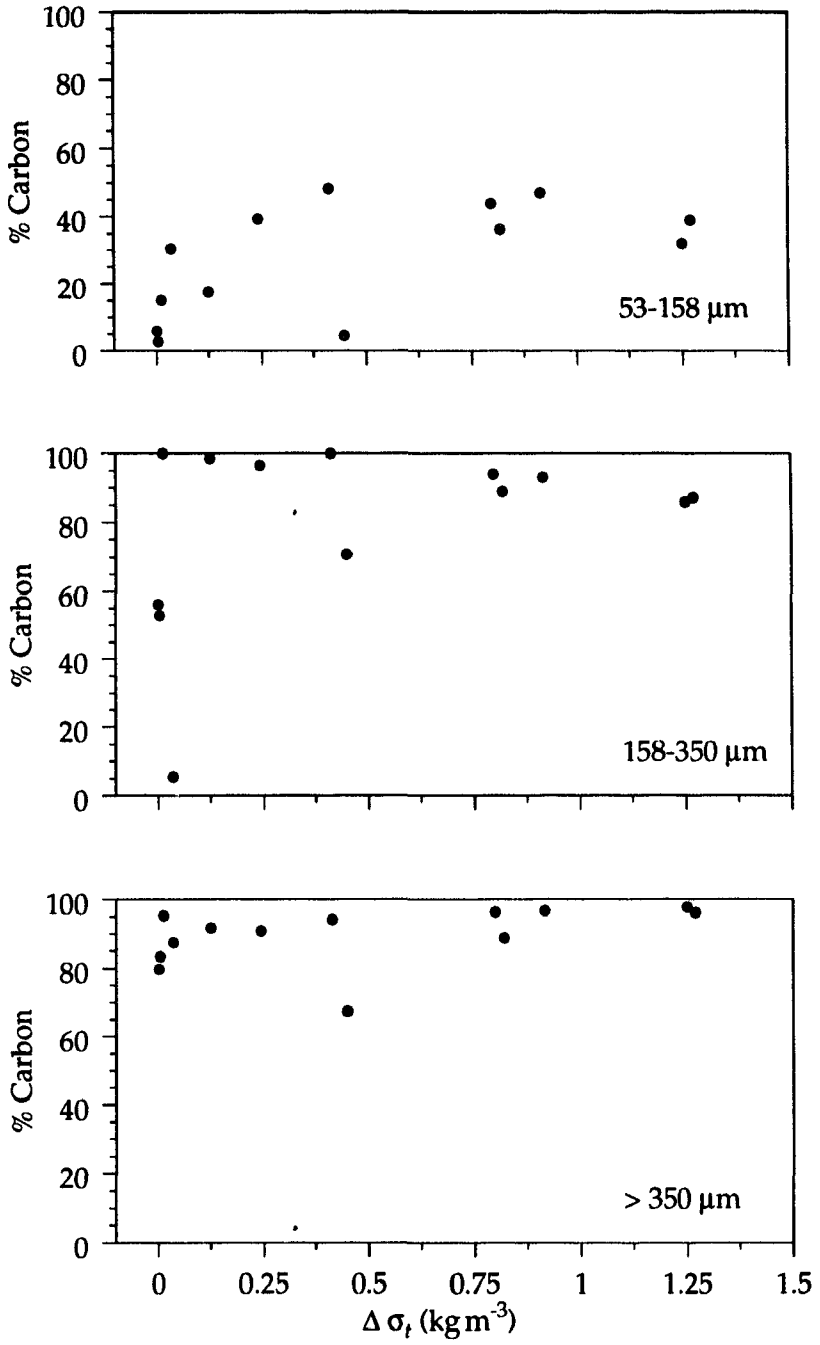

Figure 3.6: Plot of the relation between the microzooplankton carbon content (%) and the stratification of the water column ($\Delta\sigma_t$, kg m^{-3}).

and chaetognaths.

The differential composition of the samples have a direct effect on the way food availability is represented. Figure 3.7 shows the relation between dry-weight, ash and ash-free weight and the stratification of the water column for the 53-158 μm size class. The closed circles represent the integrated biomass ($mg\,m^{-2}$), and the open circles are the microzooplankton concentration ($mg\,m^{-3}$). When concentration is expressed as dry weight, there is a significant negative correlation with the stratification of the water column. However, when the dry weight results are corrected for the amount of inorganic material in the samples, and the results are expressed as ash-free biomass, this correlation is no longer significant. This is very important, since the smaller size classes are the ones most affected and are also the relevant size classes of prey for herring larvae [Cohen and Lough, 1983]. As the mesh size increases, the amount of contamination by these particles decreases, and this correction does not seem to affect any existing trends between food availability and stratification of the water column (Figure 3.8). However, it is interesting to notice that just a small adjustment in the larger size class reveals a positive significant trend between the microzooplankton concentration and the stratification of the water column (Figure 3.9).

The correction for the amount of inorganic material in the samples does not significantly affect the correlation results when food availability is expressed as integrated biomass. For the 2 smaller size classes (53-158, and 158-350 μm), although the correlation is strengthened, and becomes positive when the correction is applied, this change is not statistically significant (Figure 3.7 and 3.8). The larger size class is not affected by the correction.

Figure 3.10 shows a modified Hjulstrom diagram [Hjulstrom, 1939]. This diagram displays the mean current velocities at which different grain sizes are affected by erosion, transport, and deposition. Off SW Nova Scotia, tidal currents vary between 10 and 100 $cm\,s^{-1}$. The sedimentary coverage off SW Nova Scotia can be roughly categorized according to the bathymetry. Areas shallower than 50 m off

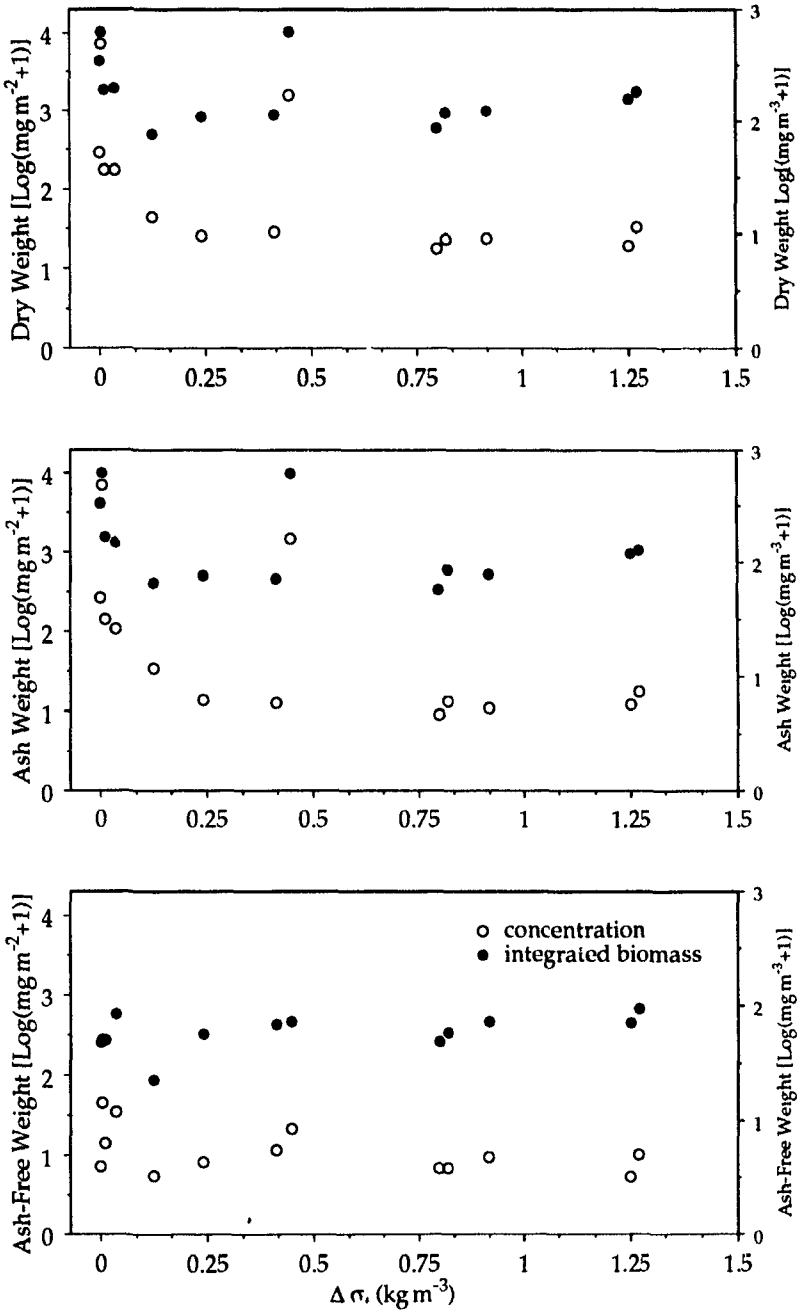

Figure 3.7: Plot of the relation between the microzooplankton dry weight, ash weight and ash-free weight versus the stratification of the water column ($\Delta\sigma_t$, $kg\,m^{-3}$) for the 53–158 μm size class. (•) integrated biomass ($mg\,m^{-2}$); (○) concentration ($mg\,m^{-3}$).

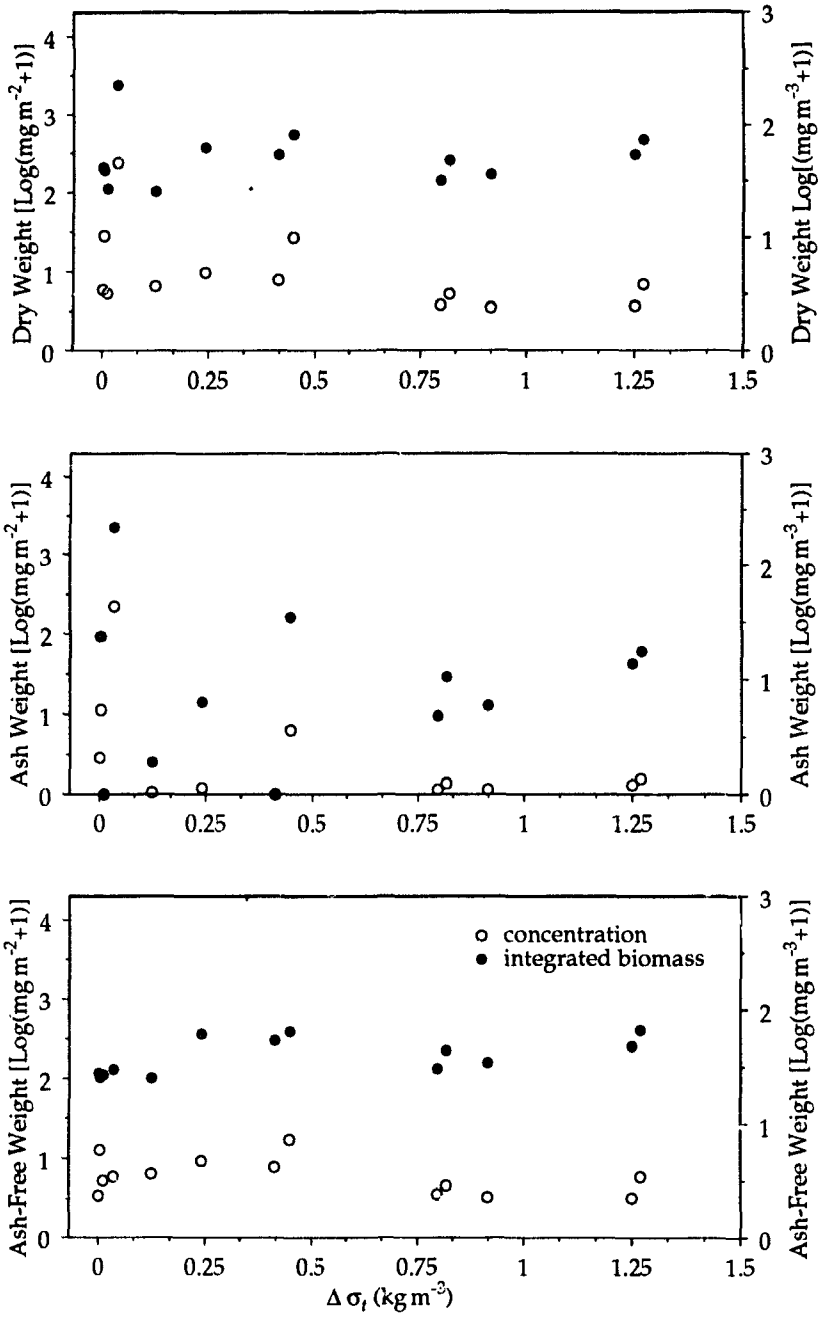

Figure 3.8: Plot of the relation between the microzooplankton dry weight, ash weight and ash-free weight versus the stratification of the water column ($\Delta\sigma_t$, $kg\,m^{-3}$) for the 158–350 μm size class. (•) integrated biomass ($mg\,m^{-2}$); (o) concentration ($mg\,m^{-3}$).

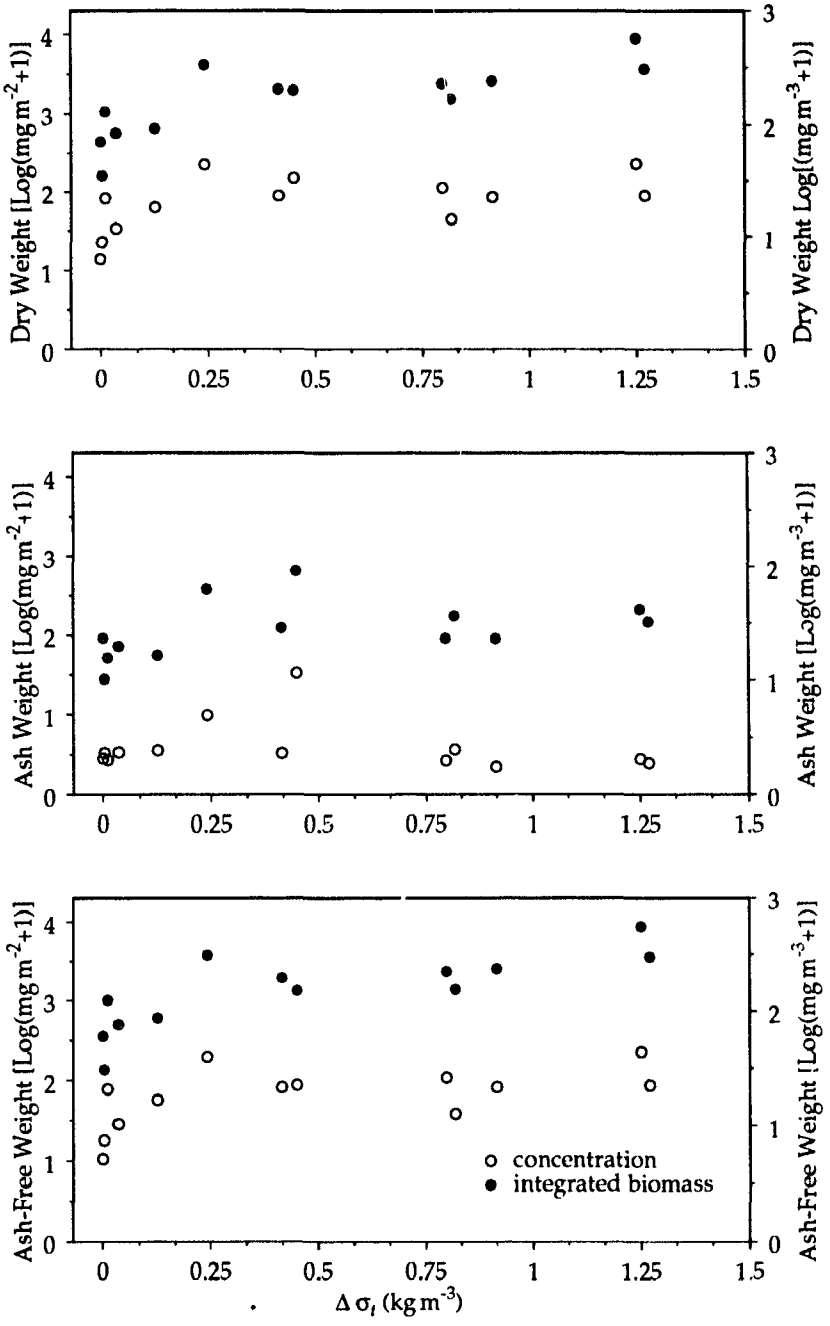

Figure 3.9: Plot of the relation between the microzooplankton dry weight, ash weight and ash-free weight versus the stratification of the water column ($\Delta\sigma_t$, $kg\,m^{-3}$) for the > 350 μm size class. (•) integrated biomass ($mg\,m^{-2}$); (o) concentration ($mg\,m^{-3}$).

Yarmouth are composed with a mixture of gravel with less than 50 % sand, and sand with less than 50 % gravel. Most of the shelf of SW Nova Scotia and the regions between 50 and 80 m off Yarmouth are composed of mainly silty and clayey sand with less than 10 % gravel (grain sizes between 200 and 2000 μm). The deeper areas, between 80 and 100 m, present Scotian Shelf Drift sediments, which are a mixture of quartz and feldspar ranging from 180 to 1500 μm [Fader *et al.*, 1977].

The availability of small sand particles, the presence of strong tidal currents to keep these particles in suspension, and the use of fine mesh size to sample, lead to some contamination of the plankton samples. This contamination cannot be easily detected by naked eye. It is also more evident in the finer mesh size and in shallower waters. Since a mesh-size of 53 μm was used, it is expected that sand contamination will be high in the smaller sizes, and decrease for the larger sizes, since that at these sizes the sand tends to deposit when the tidal currents are lower.

The bias induced by sand contamination is more pronounced when the results are expressed as dry weight. Fine sands have on average a density of 2.5 g cm^{-3}. This is about 2.5 times greater than the density of the microzooplankton, and even a small amount of sand can account for a large overestimation of the dry weight. Frank [1988] did not correct his results for the presence of inorganic material, and it can be observed that his highest values are concentrated around the shallower depth. Samples from this study that have dry weight values of the same order as those reported by Frank [1988] had a high content of sand. Furthermore, examination of the vertical distribution of Frank's data (unpublished), reveals that the highest dry weight values are always associated with the deeper strata. Deeper strata are closer to the bottom boundary layer, where shear stress keeps sediments in suspension.

3.3.2 Vertical distribution

Figure 3.11 shows the vertical distribution of the combined microzooplankton size classes (50–400 μm) over the study period at the well mixed "semi-fixed" station. Microzooplankton were uniformly distributed in the water column, and did not

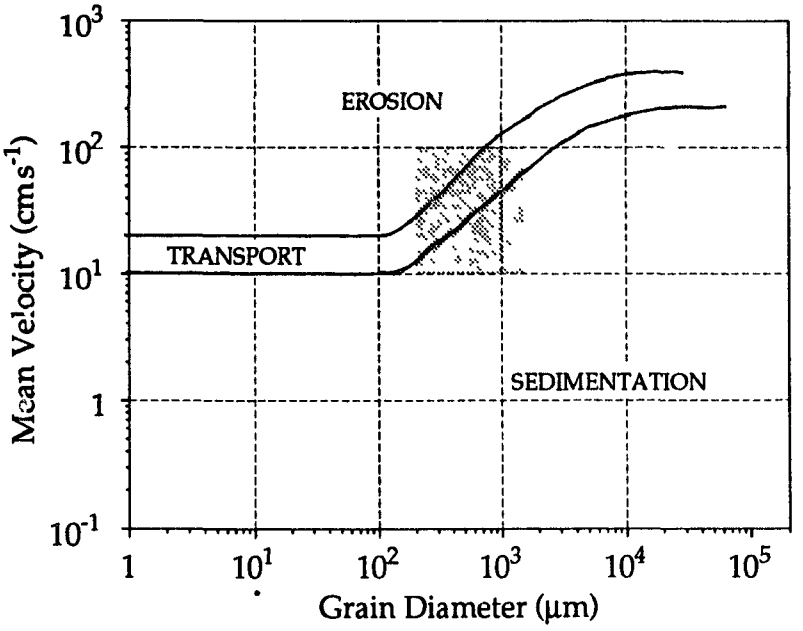

Figure 3.10: Modified Hjulstrom diagram showing the mean velocities ($cm\,s^{-a}$) at which sediments of different sizes (μm) are affected by erosion, transport and sedimentation. The shaded area encompasses values for mean tidal velocity and grain diameter characteristic for the continental shelf off SW Nova Scotia.

show any particular trend with respect to day and night, or tidal oscillation. The intense tidal mixing at this station prevents microzooplankton aggregation. Uniform vertical distribution of microzooplankton has been reported for the same region by Stephenson and Power [1991]. It has also been observed for copepod species in other tidally mixed waters such as Georges Bank [Turner and Dagg, 1983; Buckley and Lough, 1987], and for scallop larvae [Tremblay and Sinclair, 1990]. Off the frontal system of the western Irish Sea, Scrope-Howe and Jones [1986] sampling during slack tides report some diel vertical displacement of copepods. However, the observed distributions were much more uniform when compared to that of stratified waters. Off the English channel, Holligan *et al.* [1984] showed that the vertical distribution of total microzooplankton was relatively uniform, although some groups showed consistent trends with depth.

The size class structure also does not vary substantially over the time of the study (Figure 3.12). The solid curves are relative frequency of microzooplankton biomass concentration at each depth for each set. The shape of the spectra is relatively constant, with most of the biomass being concentrated around the 75 μm size class. There are occasionally peaks at higher size classes, for example at 10 m in set 5, and 30 and 40 m in set 10. However, these peaks don't seem to follow any specific pattern.

Visual inspection of the samples of this study reveals that the size class between 53 and 118 μm was composed mainly of small nauplii, diatoms, dinoflagellates, fragments of phytoplankton and some sand granules. The 118–202 μm class is a mixture of copepodites and copepod nauplii stages, and large diatoms. The size class between 202 and 253 μm contains about 25 % adult copepods and 75 % copepodites. For the next class, 253–315 μm, this proportion is inverted and adult copepods start to dominate the sample. Samples greater than 400 μm have mainly adult copepods.

Stephenson and Power [1991] noted some temporal changes throughout the water column, with no clear evidence of vertical structure or vertical movement for four

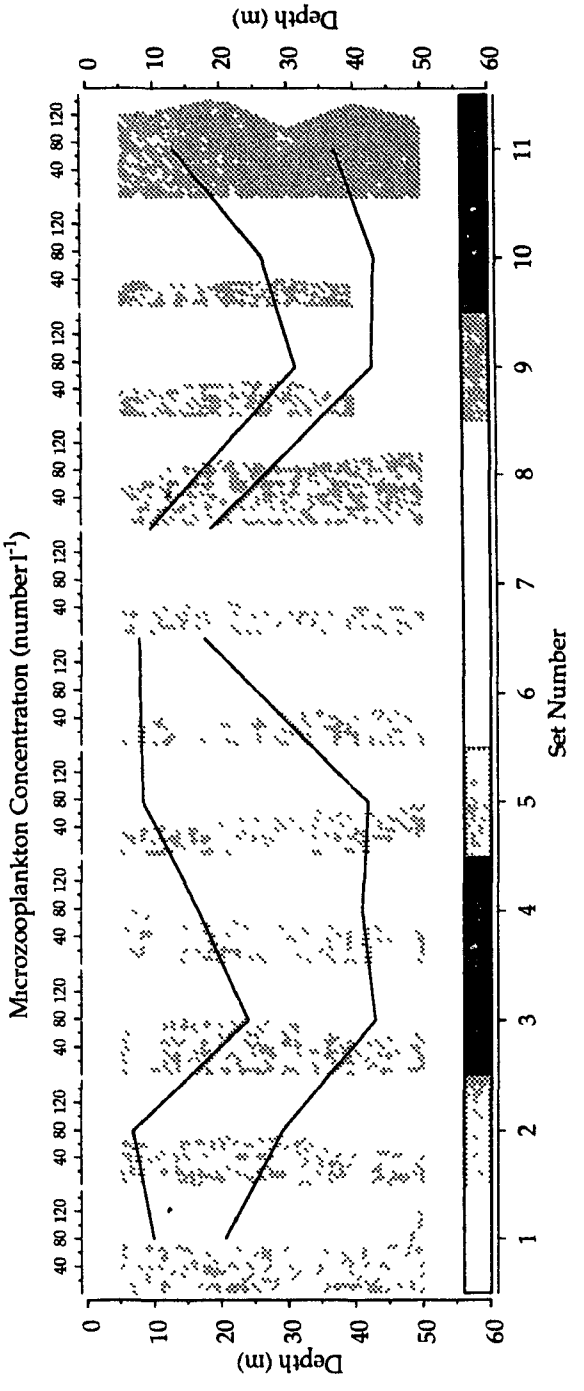

Figure 3.11: Vertical distribution of microzooplankton abundance (number ℓ^{-1}) during the sampling period. Solid lines represent Z_{25} and Z_{75} for the herring larvae (see Chapter 2). Horizontal bars indicate period of the day; solid bars are night; shaded bars are crepuscule; open bars are day time.

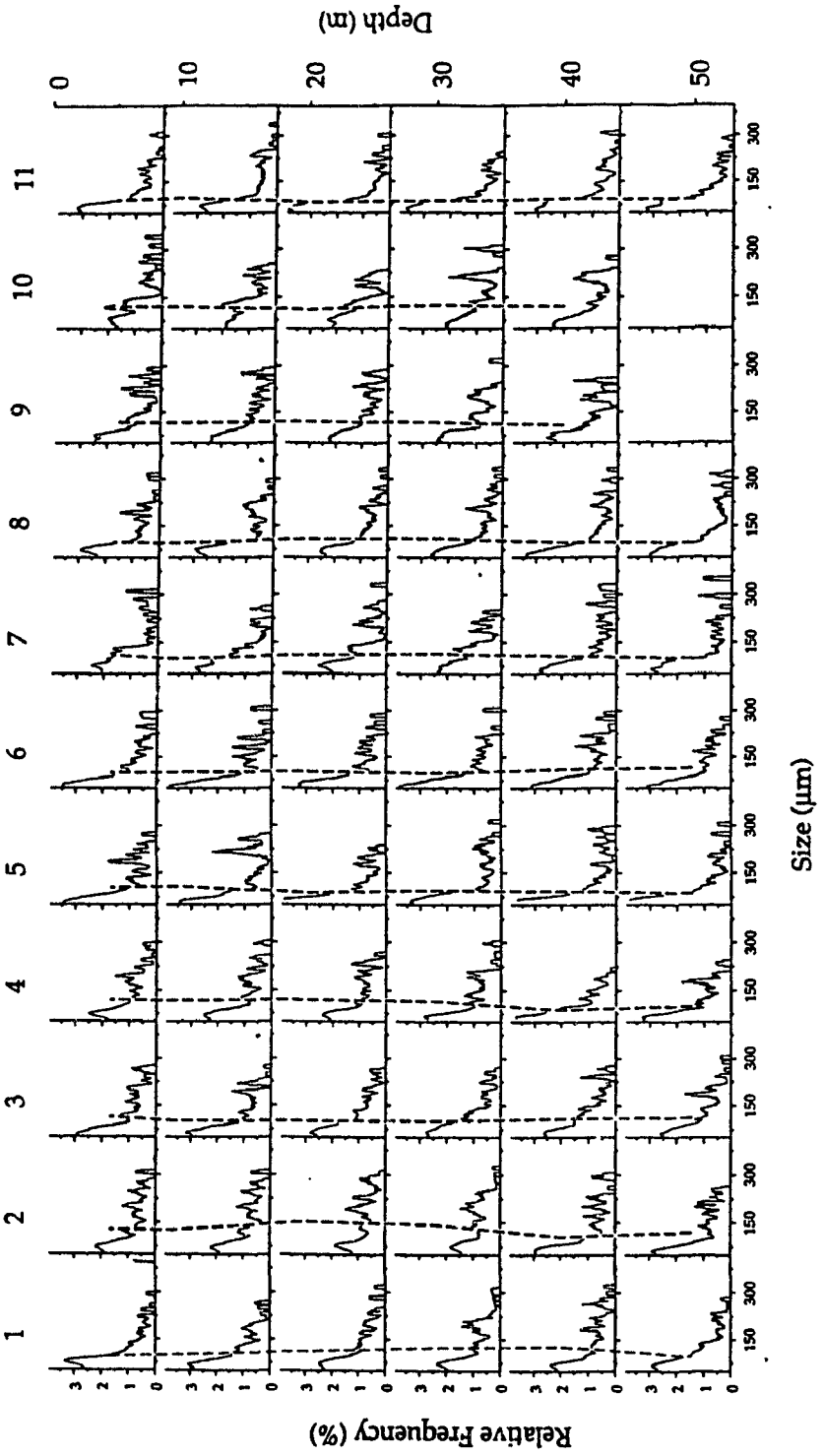

Figure 3.12: Microzooplankton size (μm) spectra at each depth for the different sets. Abundance is the relative frequency (%) of the biomass concentration ($mg\,m^{-3}$). Vertical dashed lines unite the 50 % cumulative frequency size class for each depth.

major larval food items. These corresponded to copepod nauplii, invertebrate eggs, *Oithona* copepods and calanoid copepods. This appears to happen in this study also. Different size classes are present at certain sets, throughout the water column, and decreasing in abundance in the next set. For example, during set 2 there is a noticeable peak at the 300 μm size class, which disappears in set 3, and returns in set 4 (Figure 3.12). This size class corresponds to adult copepods and copepodites.

Microzooplankton concentrations varied between 32 and 145 ℓ^{-1} (Figure 3.11), which is in agreement with the results found for this area in the horizontal study. Stephenson and Power [1991] report concentrations ranging from 0.1 to 20 ℓ^{-1} for each of the following groups calanoid copepods, *Oithona* copepods, and invertebrate eggs for this region. Together with copepod nauplii, these were the dominant groups collected using the same methodology as this study. They were also the dominant prey types in herring larvae's gut [Stephenson and Power, 1991]. Using a 35 μm mesh net to collect copepods, Thompson and Harrop [1991] report nauplii and copepodite concentration ranging from 0 to 89 and 0 to 29 ℓ^{-1} for the western Irish Sea. However, reports of zooplankton concentrations in tidally well mixed waters vary considerably. Turner and Dagg [1983] present concentrations that oscillate between 0.01 and 0.6 ℓ^{-1} for different groups and sizes of copepods at Georges Bank in October using a 102 μm mesh size. In coastal waters of Eastern Maine and Southwestern New Brunswick, Chenoweth *et al.* [1989] reported concentrations of small copepods varying between 0.001 and 0.006 ℓ^{-1}. They collected their samples using a 333 μm mesh size. It seems like that the lowest concentrations are associated with the largest mesh sizes used to collect the plankton samples.

The dashed line on Figure 3.12 represents the 50 % accumulated frequency point of biomass concentration for each depth. It can be noticed that this point is generally around 90 μm, with a small increase to 125 μm in set 2. When number of particles is used, the 50 % cumulative frequency size class is generally between 60 and 75 μm. This indicates that when sampling small prey items to study fish larvae food abundances, adequate mesh size has to be used, otherwise these items will be

underestimated. In fact, Stephenson and Power [1991] noted that when they used an 85 μm mesh size they only found few invertebrate eggs, which were abundant in herring larvae's gut. They mentioned that measurements of these eggs indicated that they could have passed through the mesh used. Frank [1988] has assessed the problem of inadequate sampling methods for fish larvae prey and how it can lead to inappropriate testing of hypothesis in fisheries biology. The above results show that proper evaluation of food availability for herring larvae requires a very fine mesh size.

Food Available for Herring Larvae

Although there is a significant positive correlation between the standardized integrated zooplankton density and depth of the water column, there is no correlation, however, between microzooplankton concentration and depth (Figure 3.13, Table 3.3). It can be observed that in both cases the results originated from studies that used dry weight data have clear outliers in the shallower region. When these are removed, the correlation coefficient becomes stronger for the standardized integrated density, and the direction of the trend for the standardized concentration is reversed, although the correlation remains insignificant.

This general description of the microzooplankton distribution across the study area indicates that, after appropriate corrections, the available data suggests an increase in food abundance with water depth. This is in agreement with the results found in other tidally well mixed areas, and supports the argument of Sinclair and Iles [1985] that food concentration alone is not an important factor in determining the location of the aggregation of herring larvae in the shallow, tidally well mixed waters. However, the association of this trend to larval feeding can be an oversimplification of the patterns that are relevant for the larvae given the large amount of variability. As discussed earlier, this region is very dynamic and marked by areas of topographic upwelling and downwelling that allow for variable areas of production. Furthermore, this general description contains data that are not from the period

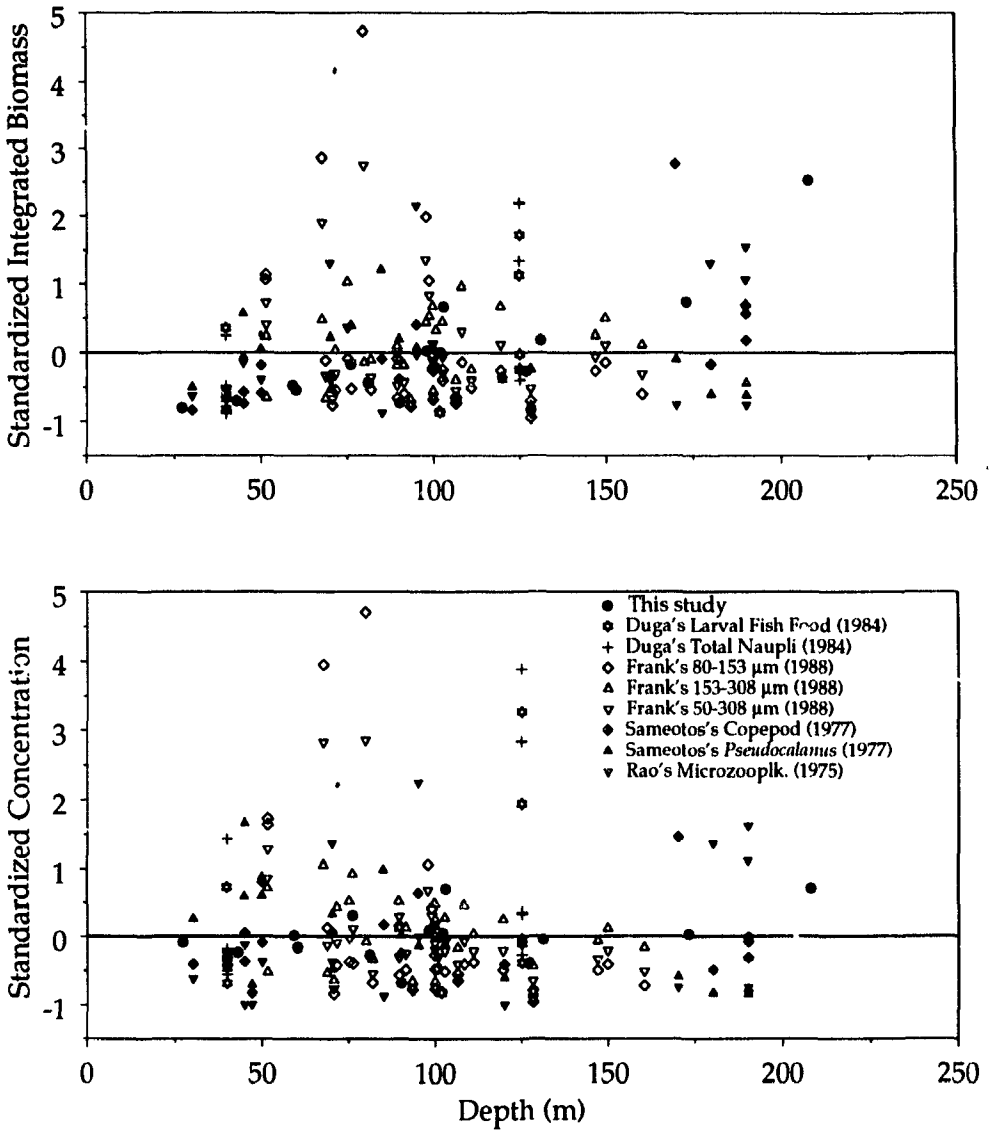

Figure 3.13: Scatterplot of the standardized integrated biomass and the standardized concentration with respect to depth (m) for all the available data on fish larval food for the SW Nova Scotia region.

when larval occur. As shown earlier, during the fall, when larvae are present, there are no significant differences in food abundance between inshore and offshore.

Over the study area, the integrated ash free microzooplankton biomass demonstrates that the largest abundances of larvae are found in areas of lower food abundance (Figure 3.14). This seems to be a paradox, it would be expected that the larvae would match their distribution to that of their food. Why would the larvae concentrate in areas with less food? The greater availability offshore, combined with higher temperatures could be used by the larvae to enhance their growth and survival. However, larvae remain in large aggregations in the well mixed area. According to Frank [1988], the independent distribution between the larvae and their food may be an indication of the influence of an environmental factor important in regulating population abundance. Sinclair and Iles [1985] have argued that larvae start off in this area because of the location of spawning banks, and they remain in this area to enable the maintenance of a reproductive unit, and not necessarily because conditions are optimal. The results of this study seem to support this view, and that of the "member/vagrant" hypothesis, that biological interactions (*e.g.* food availability) are not required for the definition of absolute population abundance. Clearly, the information about microzooplankton abundance alone it is not sufficient to explain the aggregation of the larvae in this areas.

The analysis of food availability based solely on food abundance may further be confounded by the fact that larvae offshore are larger and have different feeding requirements, and by the fact that the density of food per larvae is different in the well mixed and stratified regions. As shown earlier, herring larvae between 9 and 20 mm eat prey that vary in size from 50 to 400 μm (Table 3.1). If a minimum food requirement of 4 % of the dry weight of the larvae per day is used [Checkley, 1984], the number of food items required can be calculated. Larvae between 9 and 20 mm weigh 100 and 1000 μg, respectively [Gamble *et al.*, 1985], and for a copepod nauplii dry weight of 0.5 μg (Table 1 in MacKenzie and Leggett [1990]), a range of 8 and 160 nauplii per day would be required. However, this higher requirement

of larger larvae offshore may be compensated by a greater abundance of prey per larvae in stratified waters. It was shown in Chapter 2 that the abundance of larvae decreased from approximately $4{\cdot}10^3$ ℓ^{-1} in the well mixed region to 40 ℓ^{-1} in the stratified region. In this chapter, it is shown that food abundance is on average constant through the region at about 100 ℓ^{-1} (Figure 3.3). This yields a density of $3 \cdot 10^{-2}$ prey items per larvae in the well mixed region, compared to 2.5 prey items per larvae in the adjacent stratified waters.

The abundance of microzooplankton in the well mixed areas seems to be sufficient for the larvae. The concentration found during the study of vertical distribution, between 32 and 145 ℓ^{-1}, are above the level of 30 ℓ^{-1} that saturates feeding in laboratory-reared Atlantic herring larvae [Kiøboe and Munk, 1986]. Stephenson and Power [1991] report that 40 % of the larvae had food items in the gut in 1987, and that 99 % had at least unidentifiable remains in the gut during 1988. Thompson and Harrop [1991] report that the concentrations of nauplii and copepodites found in the western Irish Sea, ranging from 0 to 89 ℓ^{-1} and 0 to 29 ℓ^{-1}, were sufficient to meet the energy requirements of the cod larvae populations. Both, the tidally well mixed and the stratified areas seem to be able to provide sufficient food for the fish larvae during the fall.

Favourable conditions in the stratified region are temporary. It has long been recognized that with an increase in wind mixing and a decrease in solar input the stratification in middle and high latitude seas breaks down and biological production decreases [Sverdrup, 1953]. The disruption of the stratification will also mix the microzooplankton and dilute its concentration. Herring larvae overwinter in this region [Townsend, 1992], when feeding conditions are not appropriate anymore for larval growth. In the shallower region, the food is already well distributed throughout the water column, and an increase in mixing would not cause a dilution of microzooplankton concentration.

Another consideration is that the feeding environment of the larvae is not being properly characterized by measuring only food abundance. Some recent evidence

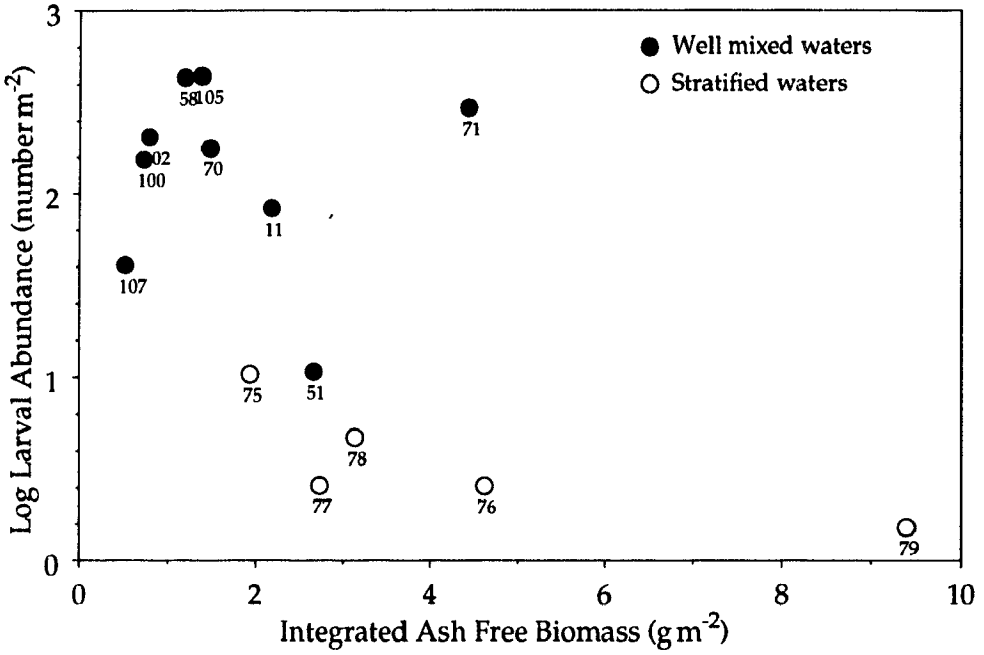

Figure 3.14: Plot of the relation between the integrated larval abundance (number m^{-2}) and the integrated ash-free biomass ($g\,m^{-2}$) for the SW Nova Scotia region.

suggests that small scale turbulence could enhance growth of fish larvae by increasing predator-prey contact rates [Rothschild and Osborn, 1988; Sundby and Fossum, 1990; MacKenzie and Leggett, 1991]. This can be an important factor in tidally mixed waters [Rothschild and Osborn, 1988, MacKenzie and Leggett, 1991], and could be the environmental factor important in regulating population abundance that causes herring larvae to deviate from the general pattern of coincident distribution with high food resources [Frank, 1988]. Furthermore, this variable may provide for the successful establishment of a viable reproductive unit by allowing the maintenance of the larval aggregation off SW Nova Scotia [Sinclair and Iles, 1985]. This will be explored in the next chapter.

Chapter 4

The importance of small scale turbulence in the feeding of herring larvae

4.1 Introduction

Small–scale turbulence influences biological processes in different ways. The vertical distribution of individual species can be modified, resulting in different community structure [Haury *et al.*, 1990]; feeding can be influenced [Marrasé *et al.*, 1990; Saiz *et al.*, 1992], and thus affect development and growth [Saiz and Alcaraz, 1991]; and behaviour responses can be altered [Costello *et al.*, 1990]. One of the main implications of the influence of small-scale turbulence is the impact on the trophodynamics of planktonic organisms. Experiments suggest that at low food concentrations, turbulence is beneficial and enhances feeding; while at high food concentrations, turbulence may be deleterious [Marrasé *et al.*, 1990; Saiz *et al.*, 1992]. Models also suggest that at intermediate levels, physical turbulence causes patch dissipation, and reduces growth; and that at higher levels it would increase encounter rates, thus restoring growth of planktonic consumers [Davis *et al.*, 1991].

Rothschild and Osborn [1988] proposed a mechanism to incorporate small-scale

turbulence into models of planktonic feeding. They added the root–mean–square turbulent velocity, u_W, as a new parameter to an existing predator–prey encounter model [Gerritsen and Strickler, 1977]. It has been suggested that the resulting increase in contact rates between predator and prey due to this mechanism could explain the high ingestion rates observed for fish larvae in regions of relatively low food densities [MacKenzie *et al.*, 1990]. Field observations of gut content of cod larvae indicate a 3-fold increase in predator–prey contact–rates when average wind speed increases from 2 to 6 $\mathrm{m\,s^{-1}}$ [Sundby and Fossum, 1990]. Simulations with different turbulence levels and food concentrations have also shown an enhancement in contact rates [Rothschild and Osborn, 1988; MacKenzie and Leggett, 1991]. This proposed enhancement in feeding success should be clearly evident in turbulent tidally-mixed areas.

As discussed in Chapter 2, many late summer and autumn spawning populations of Atlantic herring (*Clupea harengus*) spawn close to or in regions where the water column is well mixed due to tidal dissipation. This spatial coincidence seems to occur throughout coastal areas of most of the North Atlantic. Off southwest Nova Scotia, herring larvae form a large and well defined aggregate [Stephenson and Power, 1988] that has been documented in annual autumn surveys since 1972 [Sinclair and Iles, 1985]. The aggregate appears at the end of summer/early fall, persists throughout the winter months [Townsend, 1992], and is still present in March [Stephenson and Power, pers. comm.] despite of a northerly residual current of approximately 10 to 18 $\mathrm{km\,d^{-1}}$ [Stephenson and Power, 1988]. In Chapter 2, I suggested that the interaction of the larval diel vertical migration with the complex circulation patterns on the shelf could account for the maintenance of the aggregation with respect to the alongshore transport due to the residual current. It was also suggested that an onshore-offshore displacement occurs, and that more larvae should be found in the adjacent stratified waters.

An alternative hypothesis to explain the existence of these aggregations, and that would account for the lack of larvae in the adjacent stratified waters, is that the

well mixed turbulent regions provide a better feeding environment for the larvae. It would be expected that in tidally energetic areas, predator-prey contact rates would be increased by turbulence, and would result in a more favorable environment for the larvae. Larvae in the stratified region, where encounter rates are lower, would not encounter the same favorable growth conditions and would be subjected to an enhancement in mortality induced by starvation. The existence of larval aggregations would therefore, not only be a function of "larval retention" associated with the northerly residual flow, but also would be the result of differential mortality acting upon larvae distributed outside the aggregation region.

Heath [1992] recently suggested that future research should give more attention to the role of turbulent mixing in structuring plankton communities and influencing encounters between larval fish and their predators and prey. In this chapter, I use dimensional analysis coupled with a relevant biological parameters describing herring life history and field data to evaluate whether micro-scale turbulence can influence their feeding success. The objective is to test the hypothesis that turbulent, tidally well mixed regions constitute a preferential feeding environment for herring larvae, and thus may contribute to an "apparent" retention of larvae in these areas.

4.1.1 Governing Equations

A model describing the interactions between a moving predator and prey in the water-column was proposed by Gerritsen and Strickler [1977]. Z, the predator-prey contact rate (number s^{-1}), can be expressed as:

$$Z = A\pi R^2 N, \tag{4.1}$$

where A is a velocity scale (m s^{-1}), R is a distance scale (m), variously interpreted as encounter radius (Gerritsen and Strickler, 1977), contact radius (Rothschild and Osborn 1988), reactive distance [Wanzenböck and Schiemer, 1989] or perception distance [Blaxter and Staines, 1971] of the predator, and N is the number of prey per unit volume (number m^{-3}). The interpretation of this equation is that the

contact rates are dependent on the interactions between the velocities of predator and prey (A), and on the cross sectional area of a sphere (πR^2) used by the predator to search a volume that contains N prey items.

The speed A is defined by Gerritsen and Strickler [1977] as:

$$A = \frac{(u_P^2 + 3u_L^2)}{3u_L} \quad for\ u_L > u_P, \tag{4.2}$$

where u_P is a root–mean–square (rms) velocity scale of prey movement ($\mathrm{m\,s^{-1}}$), and u_L is a rms velocity scale of predator movement ($\mathrm{m\,s^{-1}}$). They assumed that the animals are randomly distributed and swim in random directions.

Rothschild and Osborn [1988] extended the above formulation, equation 4.2, to include the effect of small–scale turbulence on plankton contact rates:

$$A_t = \frac{(u_P^2 + 3u_L^2 + 4u_W^2)}{3(u_L^2 + u_W^2)^{\frac{1}{2}}} \quad for\ u_L > u_P, \tag{4.3}$$

where A_t is the velocity scale of the contact rate and it incorporates the effects of u_W, the rms turbulent water velocity ($\mathrm{m\,s^{-1}}$).

Evans [1989] further modified the expression of the velocity scale A and A_t. He found that his results differ from equation 4.2 by at most 6 % when $u_L = u_P$. In the present scale analysis the Rothschild and Osborn [1988] modification of the Gerritsen and Strickler [1977] model is used, because for a fish larva preying on copepod nauplii $u_L \gg u_P$, and therefore the difference between the two formulations is negligible. Furthermore, the formulation proposed by Rothschild and Osborn [1988] has been previously used for this problem [Sundby and Fossum, 1990; MacKenzie and Leggett, 1991].

Rothschild and Osborn [1988] assume that at the length scales where plankton contact occurs, turbulence is homogeneous and isotropic [Gargett *et al.*, 1984]. They suggested that, for scales larger than the Kolmogorov scale, u_W can be estimated from:

$$u_W^2 = 3.6(\varepsilon r)^{\frac{2}{3}}, \tag{4.4}$$

where ε = the rate of turbulent kinetic energy (TKE) dissipation ($\mathrm{m^2\,s^{-3}}$) and r

is a decorrelation distance (m), that is, the distance at which fluctuations in u_W become uncorrelated.

4.1.2 Scale Analysis

Equation 4.1 can be divided into two terms: a velocity term, represented by A; and a biological term, represented by the combination of the encounter radius, R, and the number of prey per unit volume, N. These terms were called the velocity and density "components" by Rothschild and Osborn [1988]. A new term can be introduced to identify the importance of turbulence-induced contact rates at the relevant time scale of larval herring feeding. Scale analysis permits a direct assessment of the contribution of each of the parameters in the governing equations for contact rates in specific situations, such as the herring larvae in tidally mixed regions considered here. Although the values used for the biological parameters in this analysis are from the herring literature, the analysis can be readily extended to other organisms.

Velocity Scale

Since R and N are independent of the turbulence level, one way to evaluate the influence of the velocity scale on Z (equation 4.1) is to compare A to A_t, where A_t is subjected to the rms turbulent water velocity (u_W). Let's define A^*, the relative non-dimensional contribution of u_W to the velocity scale of the contact rate equation as:

$$A^* = 1 - \frac{A}{A_t} \tag{4.5}$$

A^* approaches zero when turbulent water velocities are small relative to the swimming speeds of predator and prey, and approaches one when turbulence dominates. The maximum swimming speeds of zooplankton predators and prey are related to body size [Miller *et al.*, 1988], and change slowly relative to changes in turbulent velocity. The rms turbulent velocity (u_W) is a function of ϵ and r (equation 4.4). The TKE dissipation rate can be directly measured [Oakey and

Elliott, 1982; Osborn and Lueck, 1985; Lewis *et al.*, 1986; Veth, 1990], calculated for tidally mixed waters [Garrett *et al.*, 1978], and estimated for the well mixed portion of stratified waters from wind speed [Oakey and Elliott, 1982; MacKenzie and Leggett, 1993]. The decorrelation distance r, a characteristic property of turbulent flows, is independent of the biology. In related studies, r has been approximated either by the mean separation distance of uniformly distributed prey [Sundby and Fossum, 1990; MacKenzie and Leggett, 1991], or has been suggested to be equal to R, the contact radius of the predator [Evans, 1989].

Since the interest is in the influence of turbulence in moving a prey with respect to its predator, I suggest that one way to parameterize r is to approximate it to the size of the smallest turbulent eddy. The smallest eddies with significant shear are larger than the Kolmogorov or viscous length scale [Lazier and Mann, 1989]. This scale is defined by two opposing factors, viscosity and the velocity shear, represented by the kinematic viscosity ν (10^{-6} m^2 s^{-1}), and the rate of turbulent kinetic energy dissipation ϵ as

$$L_v = (\frac{\nu^3}{\epsilon})^{\frac{1}{4}} \tag{4.6}$$

There exists a continuum of eddy sizes with continuous decrease in energy toward smaller sizes. It is therefore difficult to define the magnitude of eddy size related to L_v necessary to retain any biologically meaningful shear (see Lazier and Mann [1989] for discussion on this matter). At eddy sizes a factor of 2π greater than L_v, commonly used in oceanography, (Lazier and Mann, 1989) r must be greater than $\approx 10^{-3}$ to 10^{-1} m for ϵ values ranging from 10^{-4} to 10^{-9} m^2 s^{-3}respectively. From equation 4.4, an order of magnitude change in r corresponds to a 2-fold change in u_W. An r of 10^{-2} m is used as representative for this study.

The change in A^* as a function of changes in u_W when $u_P = 10^{-4}$ m s^{-1} and $u_L' = 10^{-3}$ m s^{-1} (equivalent to the velocities of a fish larva preying on copepod nauplii) is depicted in Figure 4.1. Fish larval velocity of this order of magnitude would correspond to larval sizes between 5 and 10 mm [Miller *et al.*, 1988]. These velocities equate to those used by MacKenzie and Leggett [1991]. The contribution of u_W to

the velocity component of the encounter rate equation begins to become important at approximately 10^{-4} m s^{-1}, and turbulence dominates at $u_W \approx 10^{-2}$ m s^{-1}. The rms turbulent velocity thus enhances encounter rates when its value ranges between the same order of magnitude as the prey velocity and approximately 10 times the velocity of the predator.

Biological Scale

If d is defined to be the distance (m) between prey items, and assume that the prey are uniformly distributed in unit volume, then

$$d \approx N^{-\frac{1}{3}} \tag{4.7}$$

The contact radius R can be scaled relative to the distance between prey and predator by writing

$$R = S^* d, \tag{4.8}$$

where S^* is a nondimensional variable. For a predator to have contact with the prey, $R \geq d$, i.e. $S^* \geq 1$. The influence of turbulence would be negligible in this case, since the predator can "feel" and encounter the prey by its own means. Turbulence would become important when $S^* < 1$. Changes in R are dependent on the development and growth of the predator, and are therefore relatively slow when compared to changes in the ambient food concentrations. The implication is that changes in d (*i.e.* changes in the concentration of food N) determine the contribution of the biological scale to the contact rate. However, a visual predator such as herring may increase its R by migrating vertically to regions of the water column where light intensities are more nearly optimal [Munk *et al.*, 1989].

The importance of the biological scale to the contact rate equation can be evaluated in Figure 4.2. When $S^* \geq 1$ the prey is on average within the predator's contact radius, and it is capable of encountering the prey on its own. In the region below the $S^* = 1$ curve, the prey is too far away on average to be detected by the predator, and the predator has to spend energy to be able to encounter the

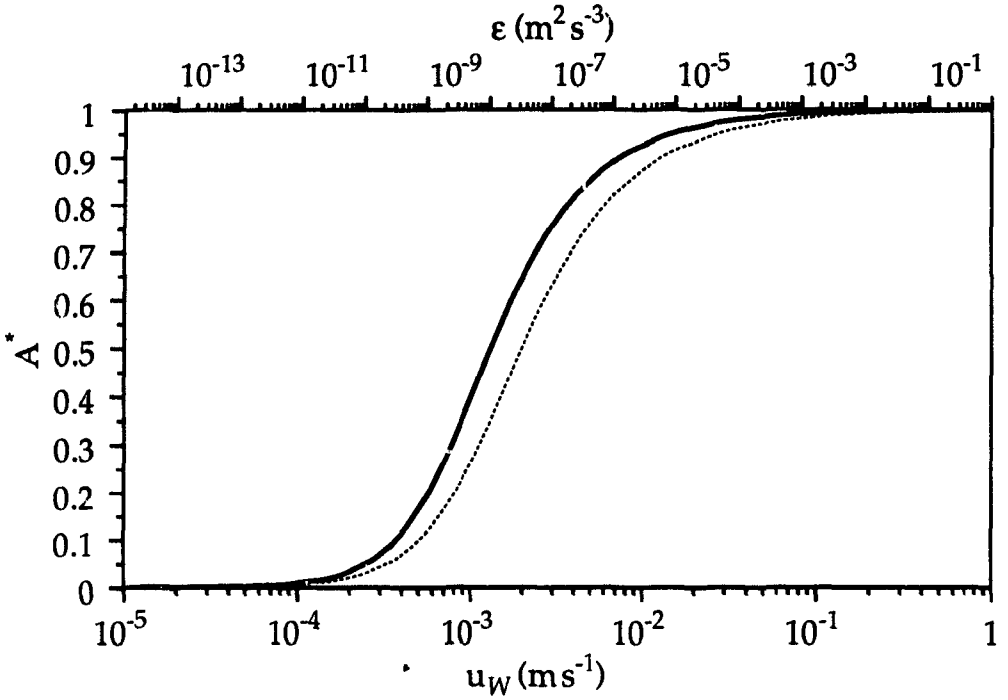

Figure 4.1: The solid line shows the relative contribution of the rms turbulent velocity u_W ($\mathrm{m\,s^{-1}}$) to A^* for fixed values of $u_P = 10^{-4}$ $\mathrm{m\,s^{-1}}$ and $u_L = 10^{-3}$ $\mathrm{m\,s^{-1}}$. The dashed line represents the appropriate dissipation rate ε ($\mathrm{m^2\,s^{-3}}$) for each value of u_W with $r = 10^{-2}$ m assuming equation 4 to relate u_W and ε. When $A^* = 0$, water motion has no effect; when $A^* = 1$, the movement of larvae and food has no effect.

prey. In this case, contact rate can be enhanced by the rms turbulent velocity u_W. This figure also illustrates the range of values found for larval fish contact radius (Table 4.1), and the range of microzooplankton concentrations found in the field (see MacKenzie and Leggett [1990] for review). Contact radius is measured in different ways, but it is generally based on the distance at which the predator reacts to moving food particles (see Miller *et al.* [1988]). It can easily be seen that for the great majority of fish larvae, their food items are far beyond their own capability of encounter. For most marine pelagic species that live in waters with lower food concentrations (about 10 ℓ^{-1}) the contact radius is of the order of $5 \cdot 10^{-3}$ m (Table 4.1). In the case of the herring larvae living off SW Nova Scotia preying on microzooplankton, the contact radius (R) is $\approx 3 \cdot 10^{-3}$ m [Blaxter and Staines, 1971], and the average distance between prey items (d) is $\approx 3 \cdot 10^{-2}$ m ($\simeq 50\ \ell^{-1}$), i.e. $S^* = 10^{-1}$, indicating that on average the prey is 1 order of magnitude away from the predator's reach. In this scenario, turbulence may become important to bring predator and prey together.

Another way that larvae would decrease their relative distance from the prey would be to move into regions where patchiness occurs. In a patch, the prey items are much closer, and S^* would become greater than 1. Using a series of models, Davis *et al.* [1991] showed that fish larval growth rates increase substantially when prey is presented in patches. They also showed that patchiness is disrupted at intermediate turbulence levels, and that growth is only enhanced at higher turbulence. This suggests that patchiness would only be important in less turbulent environments such as the adjacent stratified waters.

In developing the biological scale, I assumed that the prey are uniformly distributed. This is a first order approximation, and it has been suggested that for planktonic particles a probabilistic distribution such as the poisson would be more appropriate [Rothschild and Osborn, 1988]. Chandrasekhar [1943] has shown that for a poisson distribution in three-dimensional space,

$$d = 0.55N^{\frac{-1}{3}} \tag{4.9}$$

This change does not significantly alter the results of the present analysis. For example, in Figure 4.2, the vertical shaded region would be displaced to the left, and be located between $5.5 \cdot 10^{-3}$ and $5.5 \cdot 10^{-2}$. This does not alter significantly the overall results, and may only be important in the stratified region where patchiness may develop. In the tidally well mixed waters prey does not seem to aggregate (Figure 3.11), and patchiness may not develop due to intense turbulence [Davis *et al.*, 1991].

The Time Scale

For turbulence to be efficient in enhancing survivability of a predator, the contact rate must exceed the maximum time interval (t_c) over which the predator can survive between encounters. The number of contacts expected to occur in a given interval, t_c, is:

$$p^* = Z_t t_c, \tag{4.10}$$

where Z_t is the predator–prey contact rate (s^{-1}) generated using the turbulent velocity component (A_t, equation 4.3).

When $p^* = 1$, the amount of food encountered by a predator is equal to that required for maintenance. When $p^* > 1$, the predator is being provided with more food than it requires for maintenance, and thus can invest in growth. On the contrary, when $p^* < 1$, the encounter rates are not sufficient to maintain the predator, and it become vulnerable to starvation. The maximum amount of time an organism survives without eating is dependent on its size, thus t_c changes, but relatively slowly compared to changes in Z_t. Changes in Z_t are mostly influenced by changes in u_W and N. Thus, changes in these parameters will determine the probability of contact between predator-prey.

For herring larvae, energetic studies have estimated the minimum food required to balance metabolic and defecation losses to be 4% of the dry weight of the animal per day [Checkley, 1984]. Larvae between 9 and 12 mm weigh 100 and 1000 μg, respectively [Gamble *et al.*, 1985]. If a copepod nauplii dry weight of 0.5 μg is

Species	Size (mm)	Contact Radius (m)	Reference
Rutilus rutilus	8 - 49	$6 - 25 \cdot 10^{-3}$	Wanzenböck and Schiemer, 1989
Alburnus alburnus	7 - 43	$9 - 40 \cdot 10^{-3}$	Wanzenböck and Schiemer, 1989
Abramis ballerus	10 - 50	$10 - 44 \cdot 10^{-3}$	Wanzenböck and Schiemer, 1989
Amphiprion perideraion	4.2	$3.3 \cdot 10^{-3}$	Coughlin, 1993
Clupea harengus	9 - 20	$3.5 - 5 \cdot 10^{-3}$	Blaxter and Staines, 1971
Clupea harengus	10 - 20	$8 - 40 \cdot 10^{-3}$	Rosenthal and Hempel, 1973
Sardina pilchardus	4.5 - 7	$1 - 2.5 \cdot 10^{-3}$	Blaxter and Staines, 1971
Engraulis mordax	4 - 15	$1.5 - 6 \cdot 10^{-3}$	Hunter, 1972
Pleuronectes platessa	6 - 10	$3.5 - 5.5 \cdot 10^{-3}$	Blaxter and Staines, 1971

Table 4.1: Range of contact radius R (m) for selected species of fish larvae.

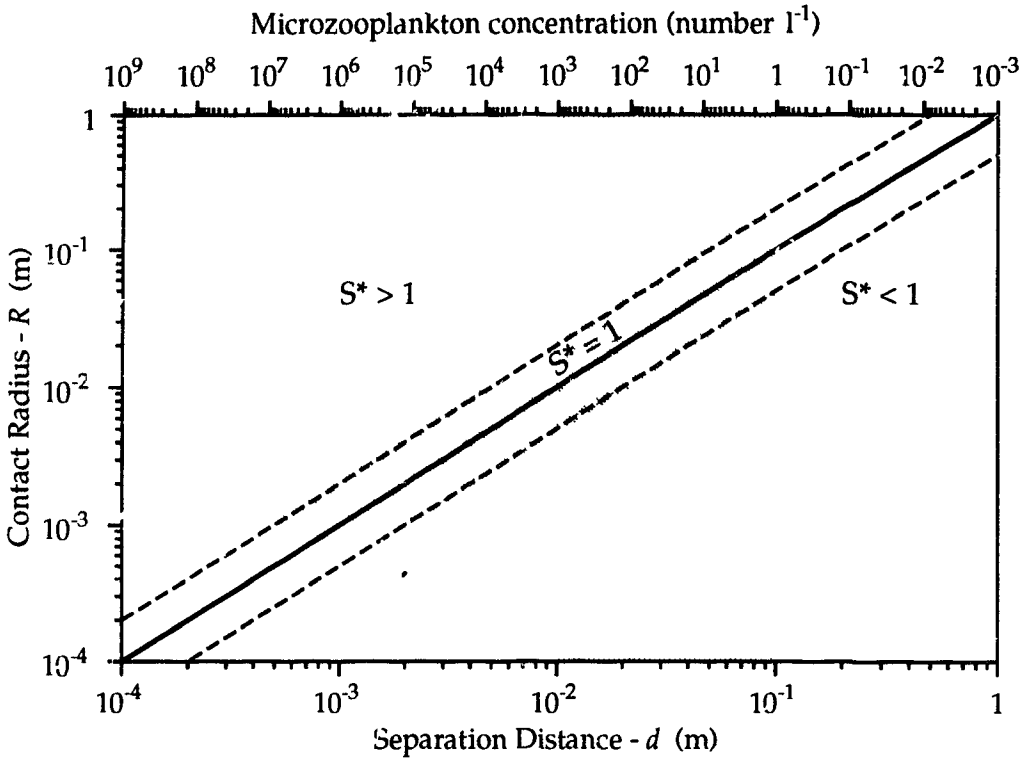

Figure 4.2: The relevant length scales for the predator–prey contact rate problem. The horizontal shaded region represents the range of contact radius R (m) for fish larvae. The vertical shaded region indicates common microzooplankton concentrations (numberℓ^{-1}) found in nature. The intersection of these regions shows that fish larvae and their prey have $S^* < 1$. The dashed lines are for S^* values of 2 and 0.5.

used (Table 1 in MacKenzie and Leggett [1990]) a range of $\approx$ 8 to 80 nauplii per day are required. Herring larvae are visual feeders and like other larval fish have an illumination feeding threshold of about 0.017 μmol photon $m^{-2}s^{-1}$ at the visible light spectrum (0.1 lx, [Blaxter, 1969]). At the latitude of this study, larvae would have more than 10 h per day of surface light intensity above this threshold [Blaxter and Staines, 1971]. If a 10 hour feeding period is assumed per day, t_c is 450 to 4500 seconds for a requirement of 80 and 8 nauplii d^{-1} respectively.

The 10 hour feeding period is just taken as an example to illustrate the importance of the time scale. A decrease in the amount of time the larvae are subjected to this light conditions reduces the amount of time the larvae have to search for food. As it was seen in Chapter 2, herring larvae rarely spend 10 h per day at the surface, and will be subjected to varying conditions of light intensity (see Heath [1992] for review). The implications of a shorter day are non trivial. The present analysis may be under representing the scales at which turbulence becomes relevant, and the magnitude of the effect, as a consequence.

4.2 Results

4.2.1 Required Turbulence

The rate of dissipation of turbulent kinetic energy ϵ can be calculated with equation 4.4 using the values for u_W from Figure 4.1. ϵ on the order of 10^{-11} $m^2 s^{-3}$ begin to influence the contact rates between larval fish and copepod nauplii (Figure 4.1). On the continental shelf off Nova Scotia, dissipation rates of 10^{-8} $m^2 s^{-3}$ generated by winds of $\approx$ 2 $m s^{-1}$ are observed in the top 20 m [Oakey, 1985]. ϵ values of 10^{-7}–10^{-6} $m^2 s^{-3}$ are associated with winds of 10 to 15 $m s^{-1}$. ϵ values of 10^{-7} to 10^{-4} $m^2 s^{-3}$ have been measured on tidally mixed areas similar to SW Nova Scotia, such as Georges Bank [Oakey and Pettipas, 1992] and the Southern Bight of the North Sea (Veth, 1990). Hence small-scale turbulence levels in the ocean are sufficient to enhance the contact rates, as was originally suggested by Rothschild

and Osborn [1988].

The analysis summarized in Figure 4.1 indicate that encounter rates between herring larvae and their food can be increased up to 90 % at a given prey concentration. This is important given that larvae occupy environments where prey is too dispersed, on average, for capture (Figure 4.2, see also MacKenzie and Leggett [1991]). Fish larvae can increase contact rates by swimming faster, or by increasing their contact radius. These changes are partially related to the growth of the larvae and occur at a slower time scale. Thus, at the relevant time scale, turbulence seems to be the only mechanism available to increase the probability of encounter of fish larvae with their prey.

4.3 Discussion

Figure 4.3 summarizes the findings of the scale analysis. The curve represents the minimum number of contacts ($p^* = 1$) expected for herring larvae that require 80 nauplii d^{-1} and have about 450 s to find each nauplius, as a function of changes in S^* and A^*. Thus, this curve divides the non-dimensional parameter space into two regions: one in which the larvae will encounter sufficient food, and would have their survivability enhanced; and another, in which the food encounters will not be sufficient, resulting in an enhancement of mortality. The top horizontal scale is the microzooplankton concentration that corresponds to the values of S^* at the lower x axis, while the vertical scale at the right shows the appropriate TKE dissipation levels corresponding to A^*.

The results show that turbulence levels in the well mixed region enhance the probability of encounter. In the case of herring, a 15 mm individual living in a quiescent stratified water column ($\varepsilon = 10^{-8}$ $m^2 s^{-3}$) would require about 60 nauplii ℓ^{-1} to maintain its minimum feeding requirement. If the same larva were living in an environment with turbulence levels of 10^{-5} $m^2 s^{-3}$, it would only require approximately 6 nauplii ℓ^{-1}. This enhancement becomes more pronounced when turbulence

levels are greater then 10^{-7} $m^2 s^{-3}$. Larvae that require more food benefit from any small increase in turbulence, since they must find food more quickly.

The herring larvae environment off SW Nova Scotia is characterized by concentrations varying between 7 and 1400 ℓ^{-1}, and sixty-seven percent of the stations surveyed had values between 10 and 100 ℓ^{-1}, while 24 % had concentrations between 100 and 1000 ℓ^{-1}. Since there was no significant difference in microzooplankton concentration between stratified and well mixed water (Chapter 3), it is assumed that this distribution pattern of the concentrations is the same for both regions. The tidally well mixed region of SW Nova Scotia can be characterized by ϵ values between $10^{-7} - 10^{-4}$ $m^2 s^{-3}$, similar to other tidal environments [Veth, 1990; Oakey and Pettipas, 1992], while the adjacent stratified waters can be characterized by a wind mixed upper layer with dissipation rates between 10^{-9} to 10^{-6} $m^2 s^{-3}$[Oakey, 1985]. The combination of these characteristics clearly show that tidally well mixed waters constitute a more favorable environment for herring larvae.

Another interpretation of this diagram is that the area to the right of the $p^* = 1$ curve represents "excess" of food resources that can be used for growth. It is easy to observe that larvae in the tidally well mixed waters will always have greater probability of having "excess" resources for growth than their counterparts on the stratified waters. This would be the case even if the well mixed waters had about 1 order of magnitude less food than the stratified region. This interpretation has a very important implication for larval fish ecology. It demonstrates that, when distinct environments are being studied, the use of food concentration "*per se*" is an irrelevant parameter to assess feeding quality of the different regions. It is a combination of the physical and biological characteristics that makes one environment more suitable than another. Thus, the discussion regarding whether herring larvae remain in the well mixed area "*in spite of*" [Sinclair and Iles, 1985] or "*because of*" [Frank, 1988] their food resources is irrelevant. The existence of an aggregation of herring larvae in this region is the result of the physical characteristic (high TKE dissipation rates) that provides the larvae with an environment suitable for feeding

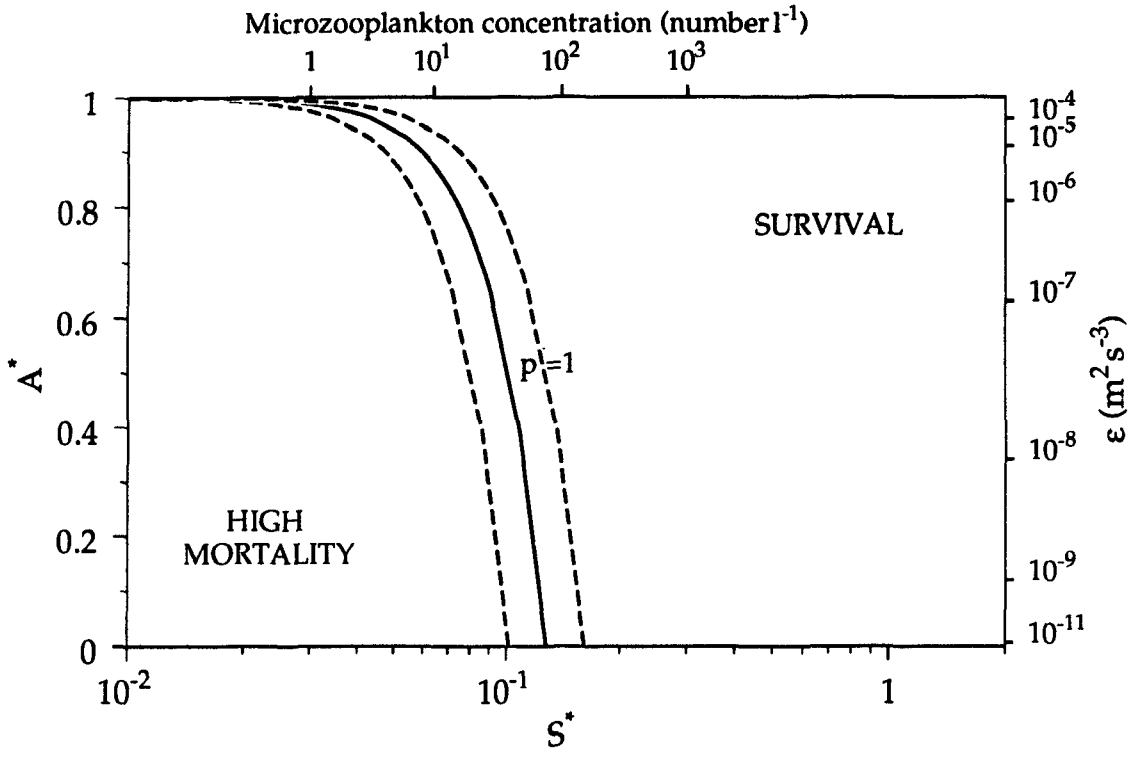

Figure 4.3: The contribution of the velocity (A^*) and the biological (S^*) scale of the contact rate problem. The solid curve is the minimum number of encounters ($p^*= 1$) for herring larvae requiring 80 nauplii d^{-1}. The dashed lines represent ($p^*= 0.5$) and ($p^*= 2$). The top horizontal scale is the microzooplankton concentration (number ℓ^{-1}) that corresponds to the S^* values on the bottom scale. TKE dissipation rates ($m^2 s^{-3}$) corresponding to changes in A^* are indicated on the right axis. Larvae on the right side of the $p^*= 1$ curve would be in the survival region, while larvae on the left side of the curve would be subjected to higher mortality.

and growth.

It appears that herring larvae have evolved to make the best use of this environment. Herring larvae are visual feeders [Blaxter, 1968] and one way to enhance their contact rates would be to increase their contact radius (R) by moving to areas of more light. Herring larvae show a diel migration pattern in this region [Stephenson and Power, 1989b] and they seem to have the ability to regulate their vertical position to match the best combination of optimal light conditions for feeding and optimal prey densities [Munk *et al.*, 1989]. Heath [1988], showed that with increases in wind mixing, herring larvae do not concentrate at the surface and become more dispersed in the water column. As he mentioned, comparison of the vertical distribution of other less mobile organisms (copepod nauplii) with that of herring suggests that the observed change in vertical distribution is not fully accounted for by passive mixing. It appears that herring larvae may respond to the changes in their feeding environment due to mixing. These changes might occur at two levels: first, contact rates are increased as a result of an increase in the rms turbulent velocity deeper in the water column; and second, by changing the vertical distribution of the prey and altering the community structure [Haury *et al.*, 1990]. Thus, larvae would not have to go to shallower waters to feed, and could remain in deeper layers. This mechanism is also discussed by Sundby and Fossum [1990]. They demonstrated that an increase in wind mixing was correlated to an increase in gut content of cod larvae. They showed that this increase could be accounted for by an increase in the velocity component of the contact rate equation, and they also speculated on the possibility that vertical redistribution enhances the accessibility of prey to the larvae.

Herring larvae spawned during the fall have slower growth rates than those spawned during spring, and are characterized by a longer larval phase [Das, 1968; Sinclair and Tremblay, 1984; Gamble *et al.*, 1985]. Growth is a function of temperature and abundance of food [Blaxter and Hunter, 1982], as well as egg size (Gamble *et al.*, 1985). Laboratory studies using temperature ranges from 7 to 14 °C have

shown that herring growth rates can vary between 0.1 and 0.44 $mm\,d^{-1}$, with the highest rate obtained with temperatures between 7 and 11 °C (see Blaxter and Hunter [1982] for review). Temperature may not be an important factor limiting growth off SW Nova Scotia, since the intense tidal mixing coupled with upwelling tends to keep these waters fairly cold all year around [Fournier *et al.*, 1984a; Fournier *et al.*, 1984b]. It is argued that the availability of food is the primary factor controlling growth and thus determines the duration of the larval phase [Sinclair and Tremblay, 1984].

The results of this scale analysis can help in the interpretation of the growth pattern observed for fall spawned herring larvae (Figure 4.4). During the fall, when food is still abundant, larvae are to the right of the $p^* = 1$ curve and they grow relatively fast. During late fall and winter, when food production decreases [Dugas, 1984; Fournier *et al.*, 1984a; Sinclair and Tremblay, 1984; McLaren *et al.*, 1989], the larvae's feeding environment is displaced to the left, becoming closer to the $p^* = 1$ curve, and growth is reduced. At this time turbulence may be the key factor in determining survivability because it allows for the maintenance of contact rates at lower food concentrations. When spring arrives and food is produced, the feeding environment returns to the right of the diagram and growth is resumed. The fate of the larvae in the adjacent stratified region is also illustrated, and it can be seen that the larvae would not be able to find enough food to sustain minimum growth during late fall and winter conditions.

There are other aspects of the physical characteristics to consider. Turbulence in the well mixed region is periodic and of "predictable" magnitude, as it is correlated to the mean tidal velocity [Veth, 1990; Oakey and Pettipas, 1992]. On the contrary, wind mixing is intermittent and of variable intensity. For a species to exploit a physical parameter that would be of ecological value, it would require certain periodicity and "predictability". Second, the source of turbulence by tidal mixing is bottom shear. Hence, higher dissipation rates are found at depth. It is interesting to note that high concentrations of herring larvae are found within

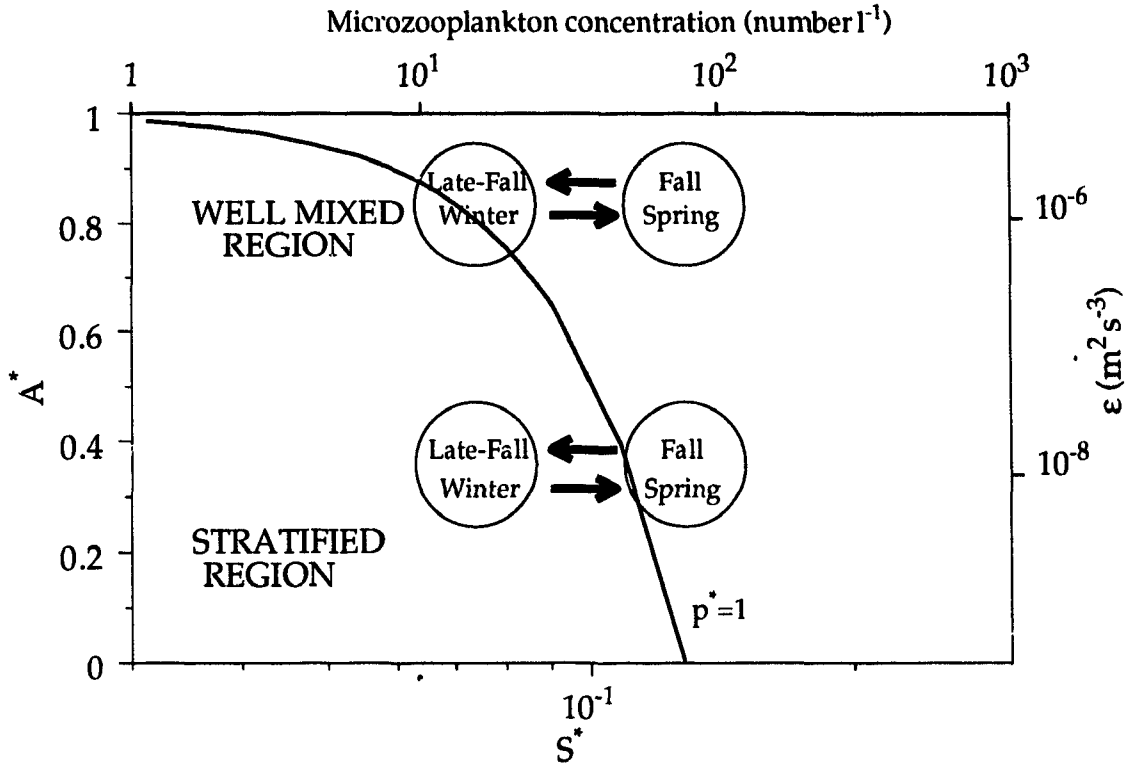

Figure 4.4: The growth cycle of herring larvae off SW Nova Scotia explained by the maintenance of minimum growth rates due to enhancement in encounter rates by turbulence. The non-dimensional parameter space is divided by the $p^*= 1$ curve for herring larvae requiring 80 nauplii d^{-1}. The arrows represent the displacement of the feeding environment for fall spawn herring larvae during their growth season prior to metamorphosis. The fate of larvae in the adjacent less turbulent stratified region is also shown.

60 cm from the bottom in the well mixed region off SW Nova Scotia [Stephenson and Sochasky, 1991]. Third, the shallow water columns have limited vertical range for dispersion of prey and predators because of the bottom. In deeper waters, mixing can disperse the food chain over a larger vertical extent and thus confound any advantage of increased turbulence. In these regions, intense winds ($> 10\ m\,s^{-1}$) that generate TKE dissipation rates that could enhance predator-prey encounter rates ($> 10^{-7}\ m^2\,s^{-3}$), seem to disrupt any food aggregation and result in detrimental conditions for fish larvae [Lasker, 1975; Peterman and Bradford, 1987; Wroblewski and Richman, 1987; Cury and Roy, 1989; Davis *et al.*, 1991; Maillet and Checkley, 1991].

The result of the scale analysis corroborates the alternative hypothesis that the tidally well mixed waters constitute a better feeding environment for herring larvae than do stratified waters. Larvae in the stratified region would not encounter the same favorable growth conditions and would be subjected to an enhancement in mortality during winter. In the winter, this differential mortality may account for the lack of larvae in the adjacent stratified waters, and contributes to the observation of an "apparent" retention in the well mixed regions. These results lend support to the Herring Stock hypothesis [Iles and Sinclair, 1982]. The relevant aspect of this hypothesis is not larval "retention", but is the coincidence of the spawning locations and of the larval distribution with the location of the physical features which would provide conditions for the maintenance of a reproductive unit [Sinclair and Iles, 1985]. This is the environmental factor, important in regulating population abundance, that allows for independence between larval fish and their food. The predictable and consistent nature of small-scale turbulence in tidally well mixed areas seems to be a determinant factor in assuring viability of this unit, and allowing for life cycle closure as hypothesized by Sinclair [1988].

Chapter 5

The condition of herring larvae

5.1 Introduction

The early life stages of marine fish are characterized by high and variable mortality rates, which are believed to influence the magnitude and variability of recruitment [Hjort, 1914; Hunter, 1976; Houde, 1987]. Starvation, predation and physical-biological interactions are the main factors that contribute to larval mortality [May, 1974; Cushing, 1975; Rothschild *et al.*, 1989]. Starvation itself is not always a direct source of mortality. Periods of food deprivation may induce slower growth rates [Buckley, 1982; Buckley, 1984], and lengthen the larval life time. This could increase the vulnerability to predation [Rice *et al.*, 1987; Gadomski and Petersen, 1988], and could favor transport of larvae into unsuitable environments [Houde, 1987], contributing as an indirect source of mortality.

In order to assess the influence of starvation, a variety of techniques have been developed to study larval condition. External appearance [Shelbourne, 1957] and morphometric measurements [Hempel and Blaxter, 1963; Blaxter and Staines, 1971; Koslow *et al.*, 1985; Neilson *et al.*, 1986; Frank and McRuer, 1989] were the first methods employed to determine larval condition. These methods are sometimes used in association with histological techniques [Theilacker, 1978; Ehrlich *et al.*, 1976; Theilacker, 1986; Uriarte and Balbontín, 1987]. Chemical or biochemical

methods have been used to study the chemical composition of herring [Ehrlich, 1974a] and plaice larvae [Ehrlich, 1974b]. They are generally based on determination of enzymatic activity [Ueberschär, 1988], lipid class analysis [Fraser *et al.*, 1987; Fraser, 1989; Klungsøyr *et al.*, 1989; Håkanson, 1989] and determination of the RNA/DNA ratio [Buckley, 1984; Buckley and Lough, 1987; Clemmesen, 1987; Clemmesen, 1988; Raae *et al.*, 1988; Robinson and Ware, 1988; Westerman and Holt, 1988; Hovenkamp and Witte, 1991; Richard *et al.*, 1991; Bergeron *et al.*, 1991; McGurk and Kusser, 1992; Clemmesen, 1993].

The ratio between ribonucleic acid (RNA) to deoxyribonucleic acid (DNA) has been shown to be a useful indicator of nutritional condition. This technique is based on the assumptions that total DNA per cell is constant in normal somatic tissues within a species, while the amount of RNA is variable, reflecting protein synthesis [Bulow, 1987]. Therefore, the RNA/DNA ratio is considered to be indicative of the recent growth of fish larvae. A series of laboratories studies have demonstrated relations between food availability and larval RNA/DNA ratios [Buckley, 1979; Buckley, 1980; Buckley, 1981; Clemmesen, 1987; Richard *et al.*, 1991]. The RNA/DNA ratio has a series of advantages: quantitative nucleic acid extraction is relatively simple and precise; the ratio has been related to larval growth [Buckley, 1984] and to the length of the starvation interval [Clemmesen, 1987]; and variations in the ratio can be interpreted physiologically. However, the use of different methods of extraction over the last 12 years [McGurk and Kusser, 1992], and the individual variability the ratio exhibits during ontogenetic development [Bergeron *et al.*, 1991], suggest that interpretation and direct inter-comparison of results must be done with caution.

In this chapter, the physiological condition of herring larvae in the well mixed and stratified waters is investigated using the RNA/DNA ratio. It was shown in Chapter 3 that the food available for the larvae is similar in both regions. If the condition of the larvae is only dependent on food abundance, it is hypothesized that larvae in both regions should have similar RNA/DNA levels. In Chapter 4, it was demonstrated that small scale turbulence would enhance the feeding of the larvae

by increasing the predator-prey encounter rate. If the influence of the physical environment is important, *i.e.* offers a feeding advantage, it is hypothesized that the RNA/DNA ratio in the well mixed region will be higher than on the stratified waters. Since it was shown on Chapter 4 that the amount of food available for the larvae was sufficient for growth, it is expected that few larvae will be in poor condition.

The distribution of the larval condition with respect to depth and period of the day is also investigated. Recent studies have shown that larvae in poor condition are more concentrated at the surface due to a decrease in their buoyancy [Neilson *et al.*, 1986, Frank and McRuer, 1989, Sclafani *et al.*, 1993]. Sclafani *et al.* [1993], modelling vertical migration through a vertical sheared water column, have proposed that buoyant, poor-condition, larvae are advected and dispersed in the surface layer. If a similar processes occurs off SW Nova Scotia, it is expected that larvae being transported to the stratified waters will be in poor condition. This mechanism may also contribute to account for the lack of larvae in the stratified region. However, as shown in Chapter 3, the tidally well mixed waters off SW Nova Scotia have uniform vertical food distribution, and should yield uniform vertical distribution of the condition index.

5.2 Material and methods

5.2.1 Collection and Preparation of the Larvae

Horizontal Condition Study

Herring larvae for the horizontal condition study were collected from the stations at Transect I in October 1989 (Figure 2.1). The contents of the starboard samples of the bongo net were transferred to a glass tray, and sorted for herring larvae. Between 10 and 20 larvae were removed at each station. Larvae were captured with forceps modified by adding brush ends, and transferred to a holding container with

cold seawater. Individual larvae were washed with filtered seawater, measured for standard length to the nearest 0.1 mm using an ocular micrometer, packed in a foil envelope and stored in liquid nitrogen.

In the laboratory, larvae were initially kept in liquid nitrogen and later transferred to a $-60\,^{\circ}C$ freezer. Prior to the nucleic acid extraction, larvae were lyophilized. Larvae were placed for 24 h in a Thermovac freeze drier coupled with a high pressure pump. Larvae were then placed in a vaccum desiccator at $4\,^{\circ}C$ for 24 h before dry weight determination on a Cahn gram electrobalance ($\pm 0.1\ \mu g$). Drierite was kept in the weighing chamber to control for humidity and increase the precision of the dry weight determinations.

Vertical Condition Study

During the 1990 vertical study up to 20 larvae were removed from each depth at each set for the condition analysis. Larval sampling and location of station are described in Chapter 2 (Figure 2.3). Each net from the Mininess was washed into a bucket, and the plankton were sorted for herring larvae in a plastic tray. Larvae were retrieved using brush-end forceps, and individually wrapped in foil. The group of larvae from each sample was placed in labeled 2 $m\ell$ cryovial tubes and stored in liquid nitrogen. In the laboratory, larvae were stored in a $-60\,^{\circ}C$ freezer. Prior to analysis, each larva was measured for standard length to the nearest 0.1 mm using an ocular micrometer.

5.2.2 Reagents and Solutions

The primary medium used was phosphate buffer saline (PBS), prepared according to Karsten and Wollenberger [1972]. One liter of PBS was prepared weekly or whenever necessary and contained 0.1 g of $CaC\ell_2$, 0.2 g of $KC\ell$, 0.2 g of KH_2PO_4, 0.1 g of $MgC\ell_2 \cdot 6H_2O$, 8.0 g of $NaC\ell$, and 1.15 g of Na_2HPO_4. The pH was adjusted to 7.5 with NaOH before making up to volume.

The deoxyribonucleic acid (DNA) standard used was purified herring sperm

DNA. A stock solution of 1 $\mu g\,\mu\ell^{-1}$ was used. From this solution, 120 $\mu\ell$ were diluted in 11,880 $\mu\ell$ of PBS to make 12,000 $\mu\ell$ of a working solution of 0.01 $\mu g\,\mu\ell^{-1}$. Purified yeast *t*-ribonucleic acid (*t*-RNA) was obtained from Boehringer-Mannheim. The stock solution was diluted in 11,988 $\mu\ell$ of PBS to make a working solution of 0.01 $\mu g\,\mu\ell^{-1}$ of RNA. Protease-free ribonuclease (Bovine pancreas) (RNAse) was obtained from Calbiochem. The stock solution (10,000 $\mu g\,m\ell^{-1}$) was diluted in PBS to make a working solution of 100 $\mu g\,m\ell^{-1}$.

The other reagents used were heparin (Hep) and ethidium bromide (EtBr). Heparin (*Porcine mucosa*) was used throughout the analysis. For the extraction procedures the stock solution (10,000 $\mu g\,m\ell^{-1}$) was diluted in PBS to make a working solution of 60 $\mu g\,m\ell^{-1}$. For the determination of the standard curve, a working solution of 170 $\mu g\,m\ell^{-1}$ was used. EtBr was used as the fluorescence dye, with a stock solution of 10,000 $\mu g\,m\ell^{-1}$. A working solution of 25 $\mu g\,m\ell^{-1}$ was prepared from the stock and PBS.

5.2.3 Determination of Standards

In order to convert the fluorescence measurements (volts) to concentration ($\mu g\,m\ell^{-1}$), a standard curve was determined for each nucleic acid. DNA and RNA were added to Hep, EtBr and PBS to achieve the following final concentrations of nucleic acids: 0, 0.2, 0.4, 0.6, 0.8, 1.0, 1.5 and 3.0 $\mu g\,m\ell^{-1}$ (Table 5.1). The volumes of the working solutions of the other added reagents are also expressed on Table 5.1.

The concentrations were prepared in culture test tubes and maintained in a water bath ($20 \pm 1\,^{\circ}C$) . Each tube was then randomly selected, transferred to a cuvette, and its fluorescence determined. Each concentration was read in triplicate. A standard curve was then calculated using linear regression (Figure 5.1). For a given fluorescence (volts), the DNA concentration ($\mu g\,m\ell^{-1}$) can be calculated using the equation:

$$DNA = \frac{F\ell_{DNA}}{0.759} \tag{5.1}$$

DNA or RNA ($\mu\ell$)	Heparin ($\mu\ell$)	EtBr ($\mu\ell$)	PBS ($\mu\ell$)	Final Conc. of Nucleic Ac. ($\mu g\, m\ell^{-1}$)
0	150	850	3,250	0
85	150	850	3,165	0.2
170	150	850	3,080	0.4
255	150	850	2,995	0.6
340	150	850	2,910	0.8
425	150	850	2,825	1.0
638	150	850	2,612	1.5
1,275	150	850	1,975	3.0

Table 5.1: Volumes of DNA, RNA and other reagents used for preparation of the nucleic acid standards.

The RNA concentration ($\mu g\, m\ell^{-1}$) can be calculated with the following equation:

$$RNA = \frac{F\ell_{RNA}}{0.104} \tag{5.2}$$

5.2.4 Nucleic Acid Extraction

Nucleic acids were extracted using the fluorimetric method of LePecq and Paoletti [1966] as modified by Karsten and Wollenberger [1972; 1977], and Robinson and Ware [1988]. This technique is based on the enhanced surface fluorescence of RNA and DNA after binding to the dye ethidium bromide. Nucleic acids are determined from tissue homogenates, and concentrations as low as 0.05 $\mu g\, m\ell^{-1}$ of DNA and 0.1 $\mu g\, m\ell^{-1}$ of RNA can be measured. The method is based on the measure of total nucleic acids and the measure of DNA. The tissue homogenate is digested with RNAse and the remaining fluorescence is assumed to be due entirely to DNA. This method has been used for fish larvae before [Raae *et al.*, 1988], including herring [Robinson and Ware, 1988; McGurk and Kusser, 19[illegible]].

A Turner Designs Fluorometer was used to measure the nucleic acid fluorescence. The fluorometer was adapted with the appropriate filters and light source for the determination of RNA and DNA. RNA and DNA are excited at 365 nm, and fluoresce at 590 nm. For excitation, a CS number 7-60 filter (Turner # 10-064) with 68 % transmittance at 365 nm was used. A Wratten number 16 filter (Turner # 10-053) with 88 % transmittance at 590 nm was used for emission. As reference filter, a CS number 3-66 (Turner # 10-052) was used. The light source was also changed to a quartz lamp (Turner # 10-052). One borosilicate cuvette with transmissibility of 95 % at 361 nm and 99 % transmissibility at 590 nm, always set at the same position, was used for all determinations. The fluorometer scale was set at 10 times amplification, and fluorescence, in volts, was recorded directly on a personal computer using a data acquisition board.

A flowchart of the extraction protocol is shown on Figure 5.2. Larvae from the

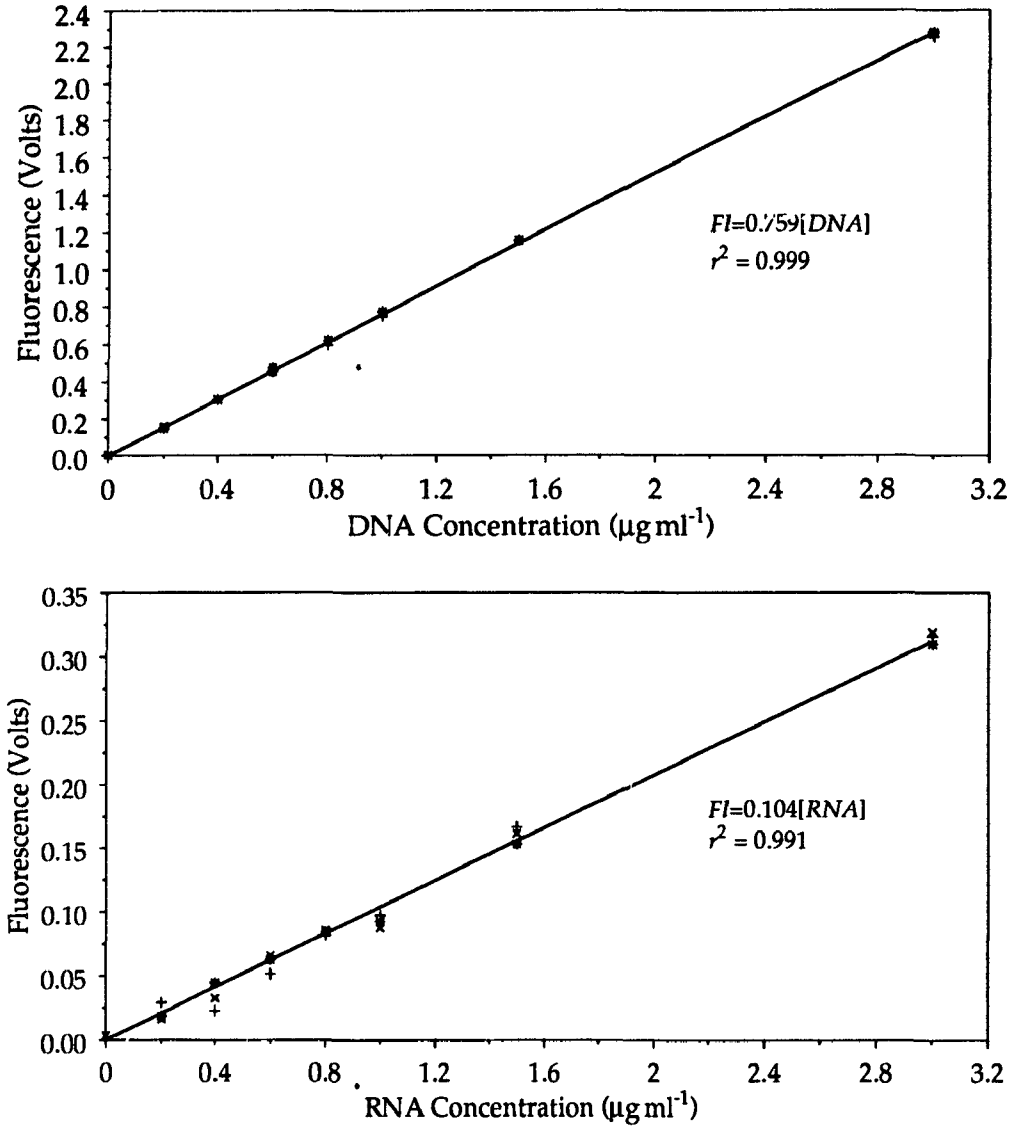

Figure 5.1: Standard curves for DNA (top panel) and RNA (bottom panel). Fluorescence values in volts, nucleic acid concentrations in $\mu g\, m\ell^{-1}$. Symbols represent individual readings for each concentration.

1989 samples were lyophilized and their dry weight determined prior to homogenization. Larvae from the 1990 study and the lyophilized material from 1989 were homogenized in a ice-bath with a Teflon tissue homogenizer in 4.25 mℓ of ice-cold PBS. The tissue was ground for 2 to 5 min, depending on the size of the larvae. The homogenate was then sonicated with four 5 s pulses at 400 W, using a Branson Instruments Sonifier LS-75. The sample was divided in 5 aliquots of 800 $\mu\ell$ each in culture test tubes.

Two of these aliquots were used for the determination of total nucleic acid, two for the determination of DNA, and 1 for background blank. An appropriate amount of PBS and 400 $\mu\ell$ of 60 $\mu g\, m\ell^{-1}$ heparin were added to all the aliquots. Heparin displaces DNA from nucleoproteins, and forms stable complexes with the nuclear proteins. It was introduced to the extraction procedure by Karsten and Wollenberger [1977]. They recommended the use of an amount more than twice that of DNA. Since DNA concentrations higher than 3 $\mu g\, m\ell^{-1}$ were not expected, a final concentration of heparin of 6 $\mu g\, m\ell^{-1}$ was used. The DNA determination aliquot also received 400 $\mu\ell$ of 100 $\mu g\, m\ell^{-1}$ RNAse.

The background aliquot, which accounted for the self-fluorescence of the homogenate, received only PBS and Hep. For each determination 4 additional blanks were made: 2 containing PBS and Hep; and 2 containing PBS, Hep and RNAse. These blanks are necessary because it is important to control for the effect of each component in the total fluorescence signal of the sample. All test tubes were gently agitated with a vortex mixer and placed in a 37 °C water bath for 30 minutes.

After incubation, EtBr was added to the aliquot for total nucleic acid determination, to the aliquot for DNA determination, and to two of the blanks. All test tubes were gently agitated and placed in a dark temperature controlled water bath (20 ± 1 °C). This prevented the samples from being exposed to light and temperature fluctuations in the laboratory. Samples were selected and transferred to the cuvette for fluorescence determination in a random order, within 30 minutes of addition of EtBr.

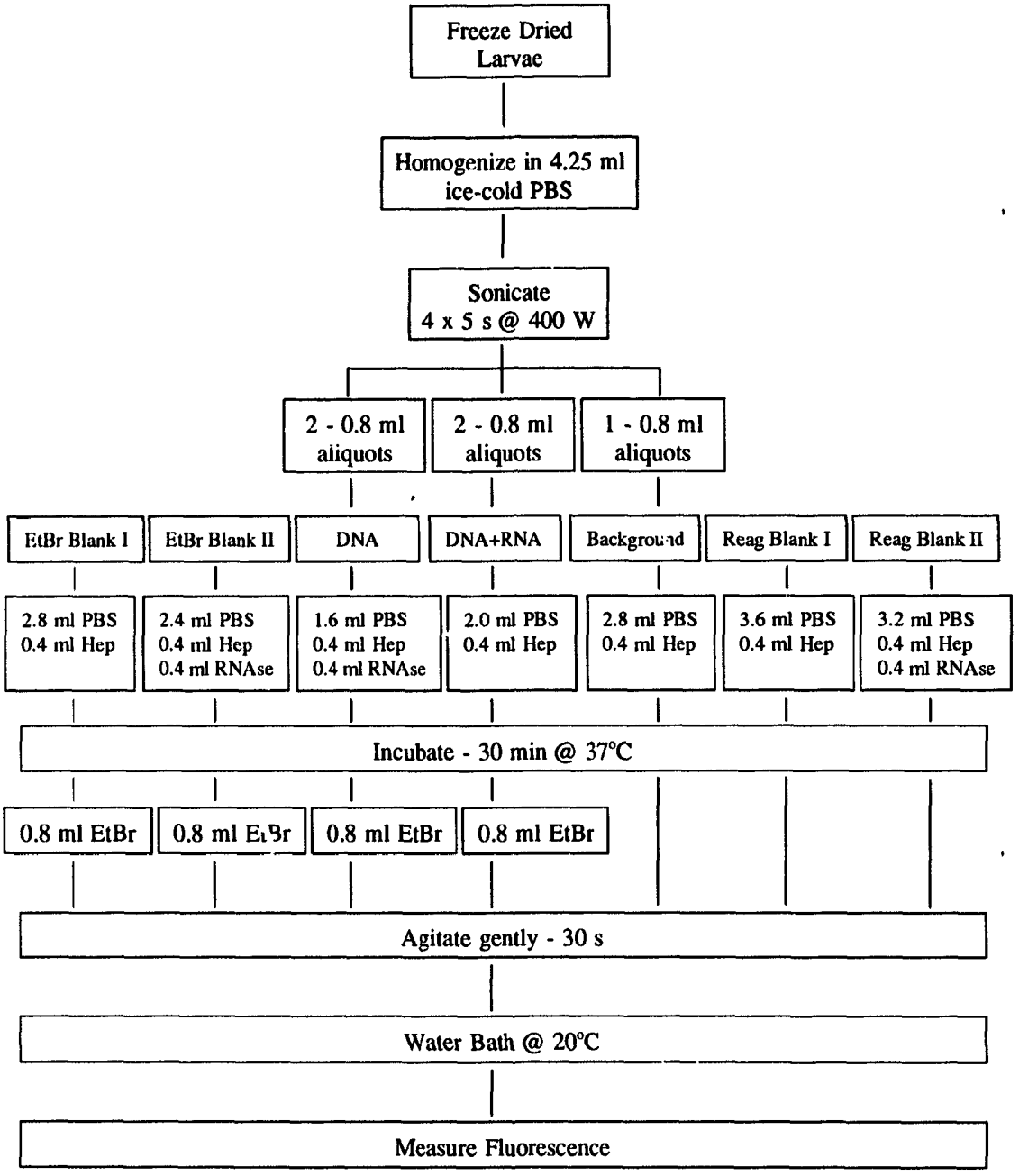

Figure 5.2: Flowchart of the protocol used for the extraction of RNA and DNA from herring larvae.

5.2.5 Calculation of Nucleic Acid Concentration

In order to use equations 5.1 and 5.2 to calculate the concentration of each nucleic acid in a herring larva, the fluorescence due exclusively to DNA and RNA has to be determined. The fluorescence due to the total nucleic acids ($F\ell_{TOT}$) is:

$$F\ell_{TOT} = F\ell_{utot} - F\ell_{EtBrI} - F\ell_{back} + F\ell_{ReagI} \tag{5.3}$$

where $F\ell_{utot}$ is the uncorrected fluorescence measured for the total nucleic acids, $F\ell_{EtBrI}$ is the blank fluorescence of the solution containing the reagents used in the determination of $F\ell_{utot}$, $F\ell_{back}$ is the background fluorescence, and $F\ell_{ReagI}$ is the self-fluorescence of the reagents used.

The fluorescence due to DNA ($F\ell_{DNA}$) can be expressed as:

$$F\ell_{DNA} = F\ell_{udna} - F\ell_{EtBrII} - F\ell_{back} + F\ell_{ReagII} \tag{5.4}$$

where $F\ell_{udna}$ is the uncorrected fluorescence measured for DNA, $F\ell_{EtBrII}$ is the blank fluorescence of the solution containing the reagents used in the determination of $F\ell_{udna}$, $F\ell_{back}$ is the background fluorescence, and $F\ell_{ReagII}$ is the self-fluorescence of the reagents used.

The fluorescence due to RNA ($F\ell_{RNA}$), is the difference between the total fluorescence ($F\ell_{TOT}$) and the fluorescence due to DNA ($F\ell_{DNA}$),

$$F\ell_{RNA} = F\ell_{TOT} - F\ell_{DNA} \tag{5.5}$$

Once $F\ell_{DNA}$ and $F\ell_{RNA}$ were determined, equations 5.1 and 5.2 were used to calculate the nucleic acid concentration. These values were then standardized to express the amount of nucleic acid per larva ($\mu g\,larva^{-1}$). The RNA/DNA ratio per larva was calculated by dividing the standardized amount of RNA by that of the DNA.

5.2.6 Correction for lyophilized weight

The nucleic acid contents for the horizontal condition of the study are expressed as the percentage of DNA or RNA in the dry weight of the analyzed material. In

this study I found that lyophilization caused the larvae to be very fragile. During the weighing of the lyophilized larvae, some parts were lost and thus the dry weight results do not correspond to that of a whole larvae. Figure 5.3 shows the dry weight versus length relationship for herring larvae. It can be seen that the dry weights obtained in this study are lower than those obtained in other studies [Werner and Blaxter, 1980; Gamble *et al.*, 1985; McGurk *et al.*, 1990]. The underestimation of the dry weight is more pronounced in the smaller larvae than in the larger ones.

Figure 5.4 shows the relationship for DNA, RNA and RNA/DNA versus length for the horizontal and vertical studies. Analysis of covariance indicated that the slopes of these relationships for larvae that were lyophilized and those that were not is the same ($p > 0.05$). This indicates that the handling of the larvae during lyophilization did not result in a preferential lost of nucleic acid between smaller and larger larvae. The loss of larval material results in lower nucleic acid values if they are reported as amount per larvae. The expression of the results as percentage of nucleic acid in the dry weight is a more appropriate choice. However, the values obtained are lower than those reported for herring larvae [Clemmesen, 1987]. Another advantage of this standardization is the removal of the effect of the larval size from the analysis (Figure 5.5). This is important since it was shown in Chapter 2 that larger larvae are more abundant in the offshore stratified waters (Figure 2.8).

5.2.7 Tests

Tests were conducted to verify the activity of the enzyme ribonuclease (RNAse), the purity of the herring sperm DNA, and to assess the presence of any systematic error during the process of nucleic acid extraction. RNAse is responsible for the catalysis of RNA. It is used in this extraction to allow a precise determination of DNA, after removal of the RNA by the enzyme. It has been shown that an excess of RNAse may affect the DNA concentration, while that if not used in sufficient concentrations not all RNA is removed from solution [Clemmesen, 1993]. She reported that final concentrations between 5 and 25 $\mu g\, m\ell^{-1}$ did not affect DNA and efficiently removed

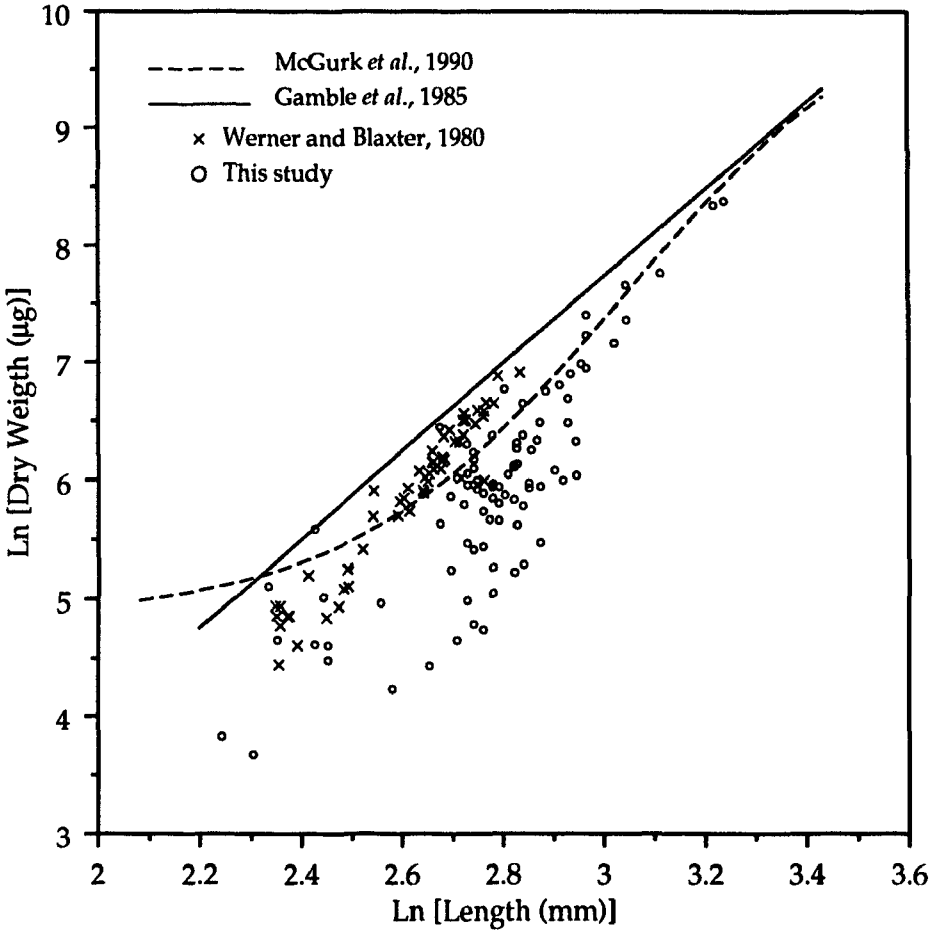

Figure 5.3: The relationship between the natural logarithm of dry weight (μg) and the natural logarithm of length (mm) for herring larvae. Dashed line from McGurk *et al.*, 1990; solid line from Gamble *et al.*, 1985; (×) data from Werner and Blaxter, 1980; (o) results form this study.

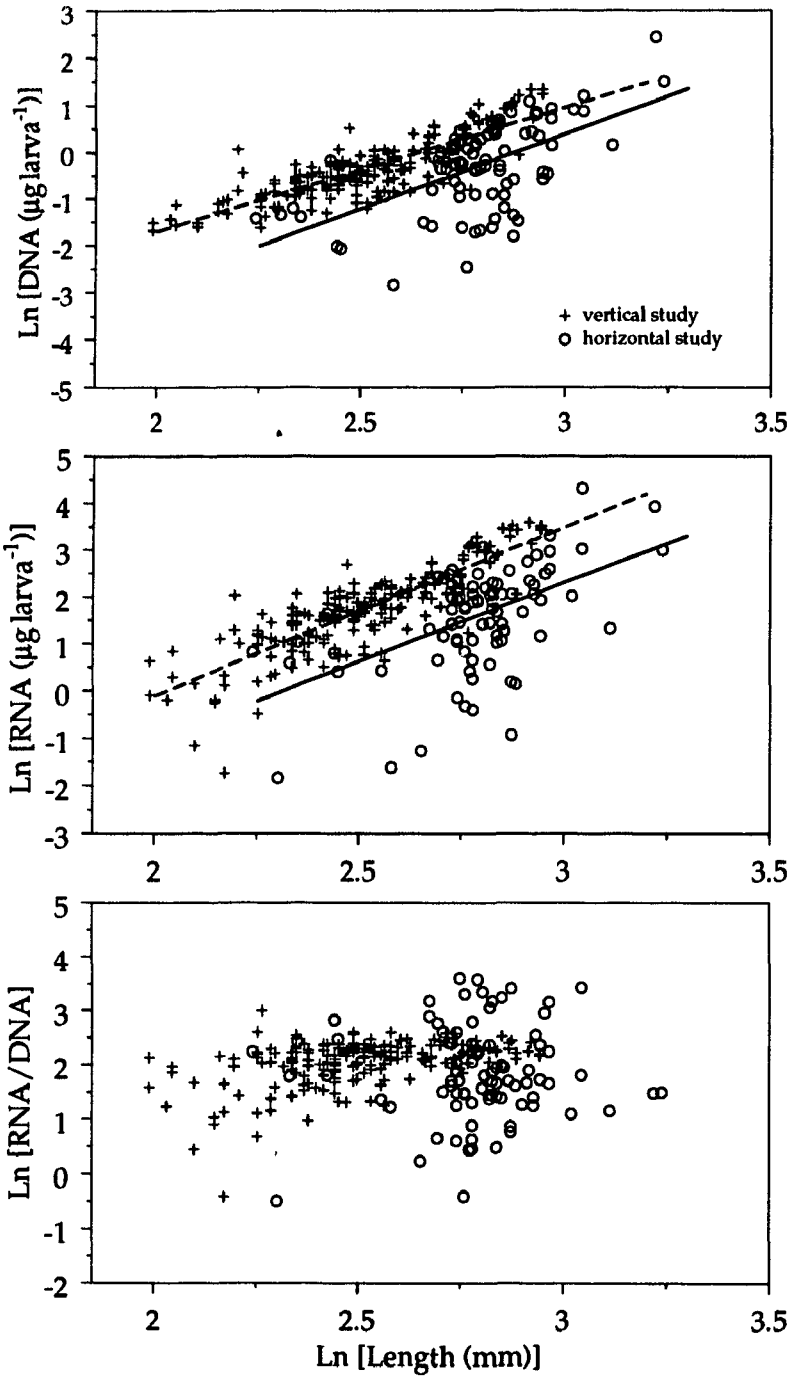

Figure 5.4: The relationship between the natural logarithm of nucleic acid concentration (μg larva^{-1}) and RNA/DNA versus the natural logarithm of length (mm). (o) results from the horizontal condition study; (+) results from the vertical study.

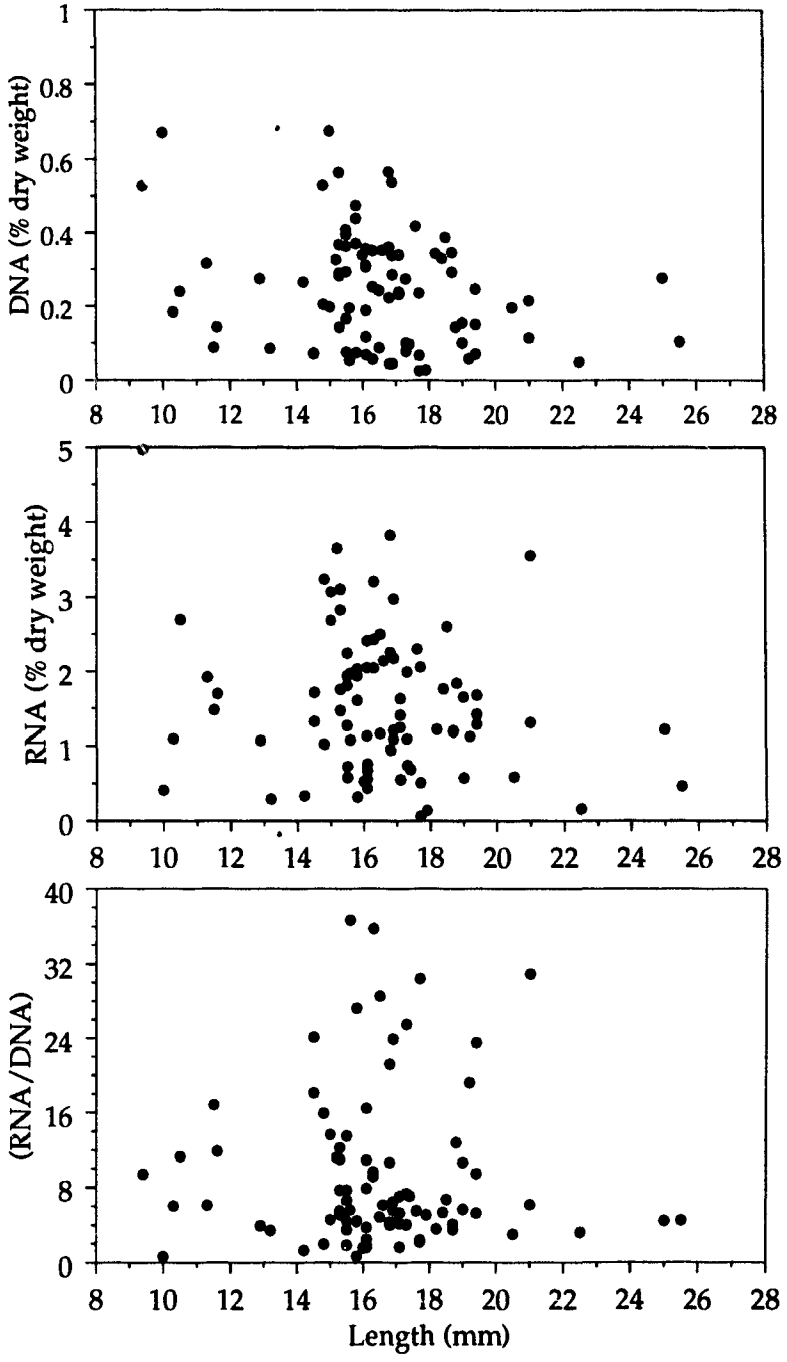

Figure 5.5: The relationship between the nucleic (% of dry weight) and RNA/DNA versus length (mm) for the larvae from the horizontal condition study.

the RNA at relevant DNA and RNA levels. Karsten and Wollenberger [1972, 1977] used a final concentration of 10 $\mu g\, m\ell^{-1}$ in their original study. Robinson and Ware [1988] and McGurk and Kusser [1992] each used a RNAse concentration of 100 $\mu g\, m\ell^{-1}$. It is not clear, however, if they are referring to the final concentration used or to the concentration of the working solution.

In this study, a final concentration of 10 $\mu g\, m\ell^{-1}$ is used. The effect of this concentration was tested by exposing solutions of 0.4 $\mu g\, m\ell^{-1}$ purified herring sperm DNA, 0.4 $\mu g\, m\ell^{-1}$ purified t-RNA, and a mixture of 0.4 $\mu g\, m\ell^{-1}$ DNA and 0.4 $\mu g\, m\ell^{-1}$ t-RNA to the enzyme. These levels were chosen as the samples were estimated to have similar amounts of DNA and RNA. These solutions were incubated for 30 minutes at 37 °C. Figure 5.6 summarizes the results of these tests. The results of triplicate readings were compared using a paired t-test ($p = 0.05$). The DNA solution was not affected by the addition of the enzyme, indicating that the herring sperm DNA used was free of RNA contamination. The fluorescence of the RNA solution exposed to the enzyme was reduced to insignificant levels. When the RNA and the DNA were together, the enzyme removed the fluorescence signal equivalent to that of the RNA and did not affect the DNA signal, indicating that the enzyme efficiently removed the RNA without affecting the DNA.

A third test, to determine if there were any systematic changes in the results due to the extraction procedure, was conducted by going through all the steps of the protocol without the larva. Each set of the protocol received the same volumes of reagents it would receive during an extraction, but instead of having 0.8 mℓ of homogenate, it received 0.8 mℓ of PBS. The test was conducted in triplicate, and the sets were randomly selected for the fluorescence reading. The results were treated by analysis of variance, followed by a Scheffé multiple comparison test. There were no statistically significant differences ($p > 0.05$) among the mean fluorescence values of the sets that received EtBr. There were also no significant differences among the sets that did not receive EtBr. This indicates that the process of grinding the larvae and handling the sets did not introduce any systematic error to the analysis.

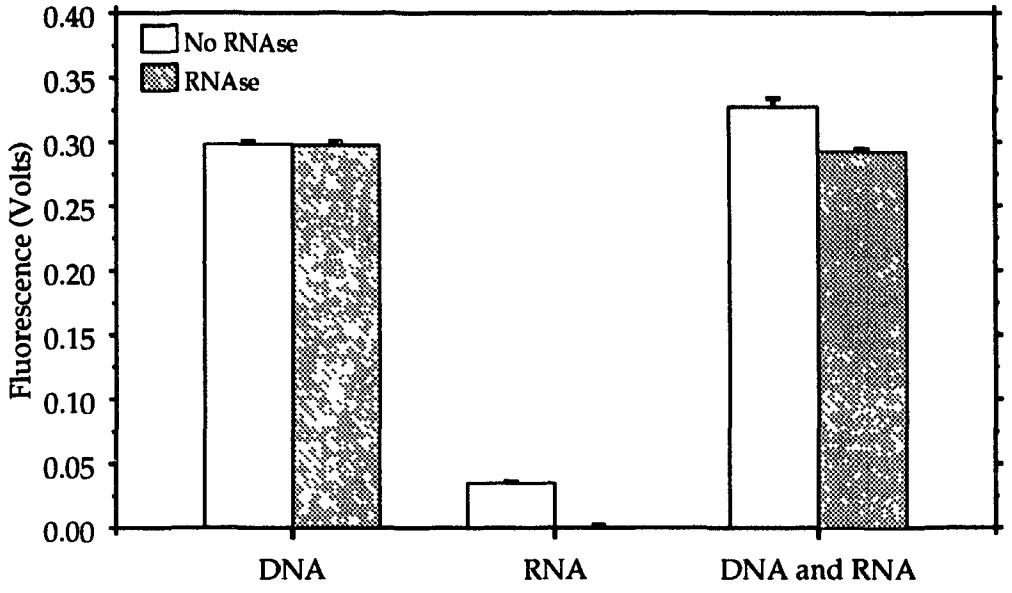

Figure 5.6: Results from the tests conducted to verify the activity of the RNAse. Height of the bars are mean fluorescence (volts). Open bars did not have RNAse added; shaded bars are results were RNAse was added. Error bars are one standard error.

5.2.8 Data Presentation and Statistical Analysis

A total of 298 larvae were analyzed for the condition study. Table 5.2 shows the number of larvae, their average size (mm), the $\Delta\sigma_t$ ($kg\,m^{-3}$), and the food available (integrated ash free biomass, $g\,m^{-2}$) for each station analyzed for the horizontal study of condition. For the vertical study, 209 larvae were analyzed, and the number of larvae and their mean size (mm) at each depth and set are represented in Table 5.3. Box-whisker plots are used to present the results of the nucleic acids with respect to the stratification of the water column, food abundance and the vertical position in the water column. The centre of the box is the median, while the edges of the box are the 25 and 75 % quartile of the distribution. The distance between the 25 and the 75 % quartile is called the inter-quartile range. The whiskers (lines with crosses at the end) extend to the furthest points still within 1.5 inter-quartile ranges of 25 and 75 %. Outliers up to a distance of 3 inter-quartile ranges beyond 25 and 75 % are shown as open circles, and as closed circles beyond that. This representation is appropriate since results of RNA/DNA ratios show high variability [Bergeron *et al.*, 1991; Richard *et al.*, 1991; McGurk and Kusser, 1992].

Analysis of covariance was used to test if there were any significant effects of depth and time of sampling on the data collected for the vertical condition study. In order to test for homogeneity of variance, the effect of larval size (expressed as length) was removed. This was achieved by subtracting from the observed nucleic acid concentration, the expected nucleic acid concentration obtained for a certain length using regression analysis. Homogeneity of variance was achieved only for sets 2 and 3. Analysis of covariance was then used for these sets with length as the covariate. When significant differences were found ($p < 0.05$), Duncan's multiple range test was used to identify these differences. All computations were performed using SPSS and SAS on a VAX 4500 computer.

Station number	Number of larvae	Length (mm)	$\Delta\sigma_t$ ($kg\,m^{-3}$)	Food ($g\,m^{-2}$)
107	11	17.6	0.003	0.511
105	8	17.9	0.011	1.391
70	4	16.5	0.140	1.485
71	15	14.4	0.241	4.448
51	2	13.8	0.413	2.666
11	6	16.4	0.448	2.190
75	15	15.0	0.818	1.940
76	2	15.6	1.270	4.624
77	9	17.6	0.797	2.733
78	14	17.5	0.915	3.142
79	3	17.8	1.250	9.396

Table 5.2: Number of larvae, their average size (mm), the $\Delta\sigma_t$ ($kg\,m^{-3}$), and the food available (as integrated ash free biomass, $g\,m^{-2}$) for each station analyzed for the horizontal study of condition.

Set number	Depth (m)	Number of larvae	Length (mm)
1	5	1	16.9
	10	6	–
	20	15	11.2
	30	8	12.7
	40	1	13.5
	50	3	10.1
2	5	19	10.4
	10	18	11.7
	20	20	11.1
	30	17	9.8
	40	20	11.3
	50	17	12.3
3	5	4	13.1
	10	7	12.7
	20	–	–
	30	19	11.9
	40	17	12.3
	50	17	11.9

Table 5.3: Number of larvae and their average size (mm) for each set and depth analyzed for the vertical study of condition. (–) data not available.

5.3 Results and Discussion

5.3.1 Horizontal Condition Study

The results of the horizontal condition study of herring larvae are summarized on Figure 5.7. DNA and RNA, as percentage of dry weight, and the RNA/DNA ratio are expressed with respect to the stratification of the water column ($\Delta\sigma_t$). The total quantity of DNA per cell is constant in normal somatic tissue within a given species, and this amount is apparently not altered by starvation or other stresses [Bulow, 1987]. In this study, DNA values vary between 0.05 and 0.7 % of dry weight, and are lower than previous values reported for herring larvae [Clemmesen, 1987]. Overall, larvae in the well mixed waters have lower values of DNA than larvae in the stratified region (Figure 5.7). Larvae in highly well mixed waters ($\Delta\sigma_t \approx 0$) present values similar to those of stratified waters. Richard *et al.* [1991] have shown a gradual decrease in DNA as percentage of dry weight in laboratory fed sole larvae. They have shown that before metamorphosis (13 to 15 days) starving sole had 3 % or more DNA per dry weight. After metamorphosis this limit was around 1.5 %. It has been suggested by Richard *et al.* [1991] and by Bergeron *et al.* [1991] that the percentage of DNA relative to dry weight is a better and simpler index of larval nutritional status than the RNA/DNA ratio, since it is more stable in fed larvae and since measurement of DNA alone is easier and more sensitive. A higher percentage of DNA in the dry weight would indicate that larvae are starving and are getting thiner. Larvae inhabiting highly well mixed and stratified waters have higher DNA percentage, suggesting that they are not feeding as well as larvae in the less well mixed region.

The quantity of RNA varies directly with the activity of protein synthesis, and it is expected to be higher in tissues undergoing faster growth or protein synthesis [Bulow, 1987]. In this study, RNA varies from approximately 0.1 to 5 % of dry weight, and it corresponds well to those previously reported in the literature for herring [Clemmesen, 1987] and for sole [Bergeron *et al.*, 1991; Richard *et al.*, 1991].

The percentage of RNA is higher at stratification values between 0.2 and 0.9 $kg\,m^{-3}$ (Figure 5.7). This indicates that larvae in this region are undergoing faster growth.

Since the amount of DNA per cell is assumed to be constant within a species, the ratio of RNA to DNA is indicative of the amount of RNA per cell. This ratio is usually considered a more accurate index of protein synthetic activity than RNA concentration alone, because the ratio is not affected by differences in cell numbers [Bulow, 1987]. The RNA/DNA values found in this study are extremely variable, changing from approximately 1 to 36. These values are higher and more variable in the well mixed region, although some outliers are also found in stratified waters (Figure 5.7). On average they indicate that larvae in the well mixed region are in better physiological condition than larvae in the stratified areas. The exception being the larvae in highly well mixed waters, which have an RNA/DNA ratio similar to those in the stratified regions.

The high variability of the RNA/DNA ratio in fish larvae has been reported in the literature for herring [Clemmesen, 1987; Robinson and Ware, 1988; McGurk and Kusser, 1992], for turbot [Clemmesen, 1987], for mackerel [Clemmesen, 1988], for cod [Raae *et al.*, 1988], for sole [Bergeron *et al.*, 1991; Richard *et al.*, 1991], and for red drum [Westerman and Holt, 1988]. Values in sea-caught larvae are generally higher and more variable than in reared larvae, oscillating between 1 and 20 [Buckley, 1984; Robinson and Ware, 1988; Clemmesen, 1989; McGurk and Kusser, 1992]. This high variability of the RNA/DNA ratio can be due to variability in the biochemical components of individual fish, either because of changes in its immediate feeding environment [Bulow, 1970; Buckley, 1981; Clemmesen, 1988], or because of changes during its ontogenetic development [Westerman and Holt, 1988; Robinson and Ware, 1988; Bergeron *et al.*, 1991; Richard *et al.*, 1991].

The high variability can also be the result of methodological differences. McGurk and Kusser [1992] have compared 3 different methods of extracting RNA and DNA. They have shown that the variability is greatest when the Karsten-Wollenberger

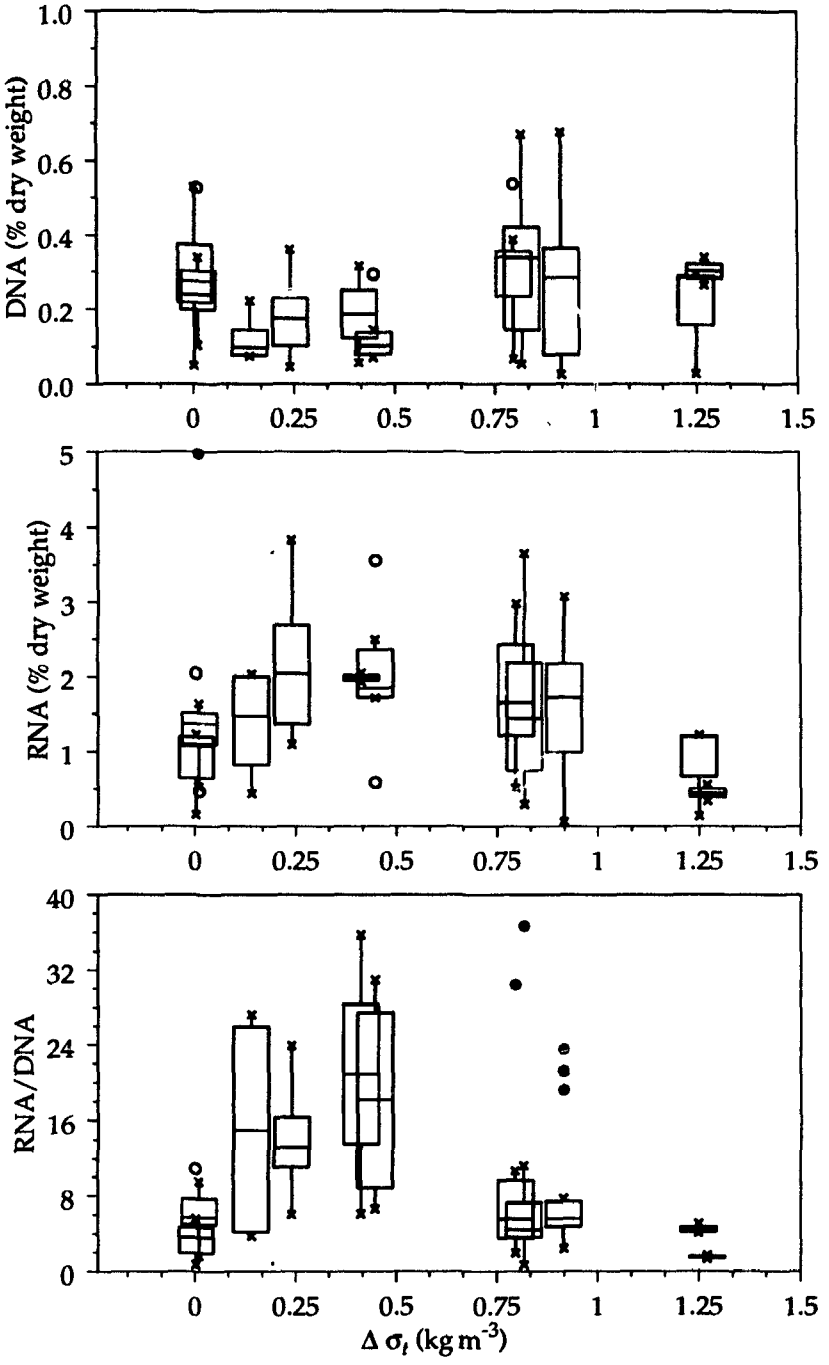

Figure 5.7: Box-whisker plots of DNA and RNA (% of dry weight) and RNA/DNA as a function of the stratification of the water column ($\Delta\sigma_t$ in kg m^{-3}). The centre of the box is the median, while the edges of the box are the 25 and 75 % quartile of the distribution. The whiskers (lines with crosses (×) at the end) extend to the furthest points still within 1.5 inter-quartile ranges of 25 and 75 %. Outliers up to a distance of 3 inter-quartile ranges beyond 25 and 75 % are shown as open circles (○), and as closed circles (●) beyond that.

method is used. Recently, Clemmesen [1993] has shown that despite all the purification steps used in her previous method [Clemmesen, 1988], the fluorescence dye bisbenzimidazole introduced problems arising from high self-fluorescence of the samples and from the influence of "quenching" substances disturbing the DNA-bisbenzimidazole determinations. It is generally agreed now that purification steps, and the use of RNAse contribute significantly to reduce the variability introduced by the extraction of nucleic acids [McGurk and Kusser, 1992; Clemmesen, 1993]. In this study, the lack of purification steps may have been responsible for the high variability in the RNA/DNA ratio.

Figure 5.8 shows the results for RNA, DNA and RNA/DNA plotted with respect to the integrated ash free biomass ($g\,m^{-2}$) of microzooplankton calculated on Chapter 3. As it was noticed in that chapter, larvae in the different regions had similar levels of food availability. However, figure 5.8 shows that larvae in the well mixed waters have higher median and more variable RNA/DNA ratios than larvae in the adjacent stratified waters.

Buckley [1984] suggested a model based on temperature and on the RNA/DNA ratio to estimate mean daily protein growth rate (G_{pi}). This model was based on temperature ranges from 2 to 20 °C, and eight species of marine fish larvae including Atlantic herring. Robinson and Ware [1988] set the daily protein growth rate to 0, and defined the theoretical RNA/DNA ratio at which there is no net protein growth in the larval fish to be:

$$R_{crit} = \frac{18.18 - 0.93T}{4.65} \tag{5.6}$$

They called this ratio the critical ratio (R_{crit}), which is only dependent on the larvae's ambient temperature (T).

Using equation 5.6 and temperature values of 9 °C for the well mixed waters and 11 °C for the stratified region, R_{crit} can be estimated to be 2.1 for the well mixed and 1.7 for the stratified waters. It can be seen from figures 5.7 and 5.8 that the ratios found in this study are much higher that these critical values, indicating that overall all larvae are healthy. This supports initial results from this thesis.

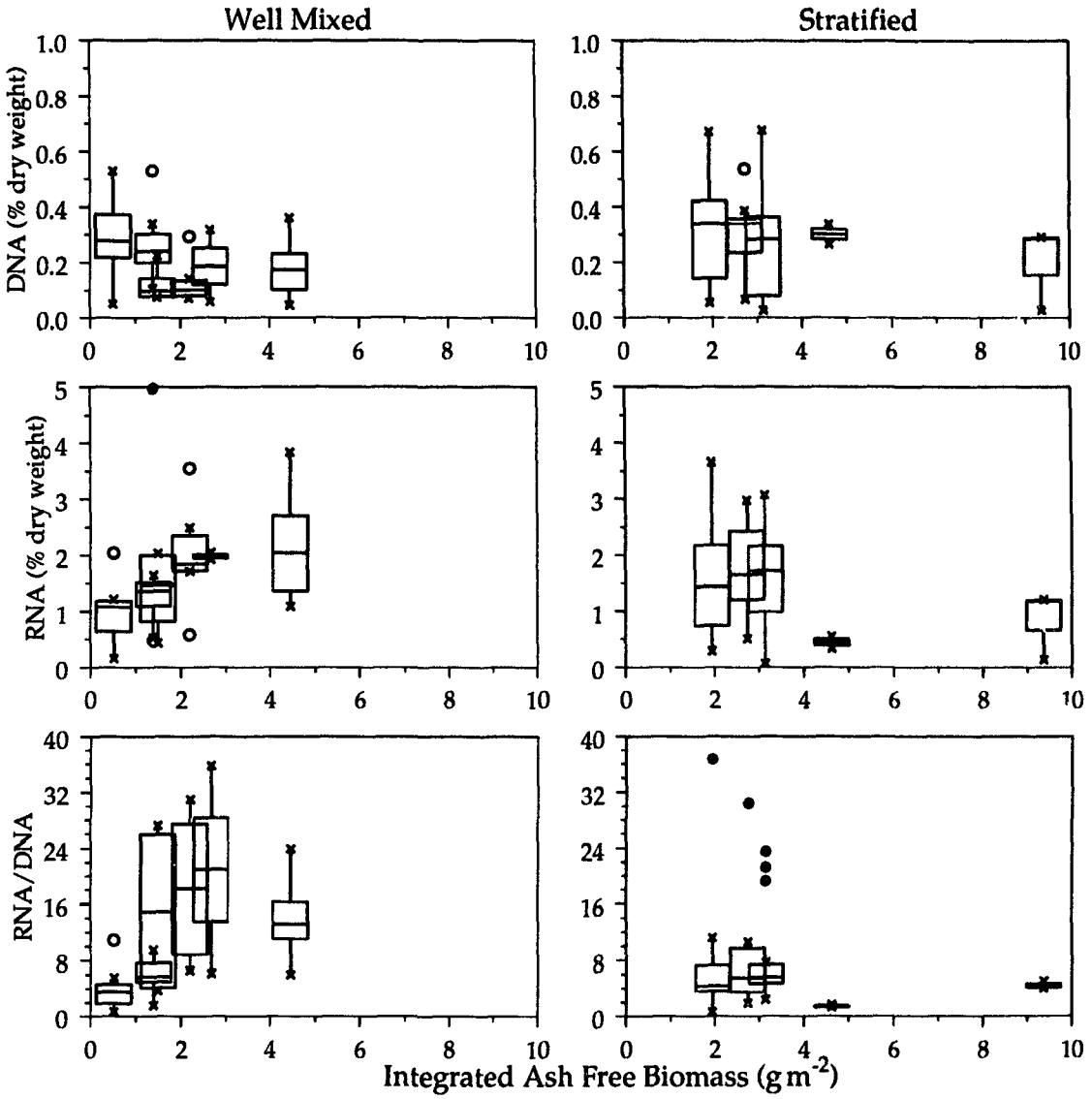

Figure 5.8: Box-whisker plots of DNA and RNA (% of dry weight) and RNA/DNA as a function of the food abundance expressed as integrated ash-free biomass ($g\,m^{-2}$) for tidally well mixed and stratified waters off SW Nova Scotia. Please refer to the caption of figure 5.7 for explanation on the box-whisker plots.

In Chapter 3 it was shown that the amount of food available for the larvae was relatively the same in the stratified and well mixed waters (Figure 3.13), and in Chapter 4 it was shown that this abundance of food was appropriate for herring larval growth (Figure 4.4). Thus, larvae in the different regions during the study period are in good condition.

It is also interesting that the scale analysis in Chapter 4 predicted that given similar levels of food, larvae subjected to small scale turbulence would perform better (Figure 4.3). As it was shown in that chapter, small scale turbulence increases predator-prey encounter rates, favoring growth of herring larvae in tidally well mixed regions (Figure 4.4). The results of the condition study supports this hypothesis. Despite similar food abundance, herring larvae in regions subjected to higher levels of small scale turbulence are in better physiological condition than larvae in the adjacent stratified waters (Figure 5.8.

Buckley and Lough [1987] have used the RNA/DNA ratio to compare the condition of haddock and cod larvae between tidally well mixed and stratified waters off Georges Bank. They showed that haddock larvae were in better condition in the stratified waters. Frank and McRuer [1989] using a morphometric condition index (Fulton's K) also reported that haddock larvae were in better condition in the stratified regions off SW Nova Scotia. However, cod larvae were healthier in the well mixed region [Buckley and Lough, 1987]. According to Buckley and Lough [1987] their result, combined with results from Laurence [1985] stochastic models of food-limited growth that indicate that haddock are considerably more food limited than cod during the larval stage, support the hypotheses that (1) stratified conditions in the spring favor good growth and survival of haddock larvae and (2) cod larvae are better adapted to grow and survive in well mixed waters at lower levels of available food than haddock. Although during the fall the food abundance was the same at both regions off SW Nova Scotia, herring larvae seems to follow the same strategy as cod, once they overwinter in regions with lower food levels. The results of this thesis indicate that what allows these two species to perform well in these

distinct oceanographic conditions is their ability to take advantage of the effects of small-scale turbulence in their feeding.

An interesting outcome of this hypothesis is the separation of the early life history of marine fish larvae in two distinct strategies. The most important hypotheses in larval fish ecology lack universality, and the recognition and acceptance of these strategies could improve our understanding of the subject and reconcile these hypotheses. One strategy requires stabilization of the water column and production of sufficient food abundance to warrant successful growth conditions. This strategy would include small, fast growing pelagic larvae such as haddock, anchovy and menhaden. These species require the stabilization of the surface of the ocean as proposed by Lasker [1975], and a match-mismatch [Cushing, 1975] of the production cycle to enhance their feeding and be successful. It has been shown that these species are susceptible to the destruction of stratification of the water column [Lasker, 1975; Buckley and Lough, 1987; Peterman and Bradford, 1987; Maillet and Checkley, 1991].

The other strategy would include relatively larger, slow growing species such as cod and herring. These species do not rely for their success on either a tight match with the production cycle or the concentration of prey caused by the stabilization of the surface of the ocean. These species would conform better to the herring stock hypothesis of Iles and Sinclair [1982]. According to this hypothesis, these larvae are maintained in a favorable environment, where a series of factors would interact to provide adequate conditions that allow for the maintenance of a reproductive unit. This would permit closure of the life cycle and regulate population abundance.

Houde [1987], based on early life history dynamics of 5 species, has also suggested the existence of these 2 types of strategies. According to him, there are "anchovy-like" species and "cod-like" or "herring-like" species. Heath [1992] indicated that basic physiological differences may render some species more vulnerable to food chain processes than others. He noted, *e.g.* that because of fundamental differences in the searching abilities of first-feeding anchovy and herring, Lasker's

"stable ocean" hypothesis cannot be applied to herring. Houde [1987] examined the influence of these different strategies on the recruitment variability, and suggested that "anchovy-like" species are probably regulated at the larval stage, while "cod-herring-like" species could have their recruitment regulated during the juvenile stage, although control in the larval stage seems more likely. Buckley and Lough [1987], pointed out that the recruitment pattern of the Georges Bank gadid stocks may reflect these two strategies. Cod larvae have a relatively low but stable recruitment pattern [Hennemuth *et al.*, 1980], while haddock have an extremely variable recruitment. Interesting enough, herring off SW Nova Scotia have a relatively stable recruitment.

5.3.2 Vertical Condition Study

The results from the study of the vertical distribution of the physiological condition of herring larvae are presented in Figure 5.9. DNA concentration varied from approximately 0.1 to 4 μg larva^{-1} with an overall mean value of 0.8 μg larva^{-1}. RNA concentration ranged from approximately 0.3 to 37 μg larva^{-1}, with an overall average of 7.4 μg larva^{-1}. RNA/DNA results were less variable than the results for the horizontal study, ranging from 0.7 to 21, with an overall average of 8.3. The R_{crit} for these profiles is 1.8 ($T = 10.5\,^{\circ}$C, see Figure 2.10), indicating that the majority of the larvae are in very good condition. This result supports the previous findings that larvae in the well mixed regions have adequate amount of food available, and that small scale turbulence enhances feeding of herring larvae in this region.

Analysis of covariance revealed that the nucleic acid concentration and the RNA/DNA ratio were not significantly affected by the location of the larvae in the water column. It has been suggested that a combination of stratification of the water column and the effect of condition on larval buoyancy could account for vertical distribution patterns [Neilson *et al.*, 1986; Frank and McRuer, 1989; Sclafani *et al.*, 1993]. Larvae in poor condition would have higher buoyancy and would be distributed towards the surface of the water column. Larvae in better condition

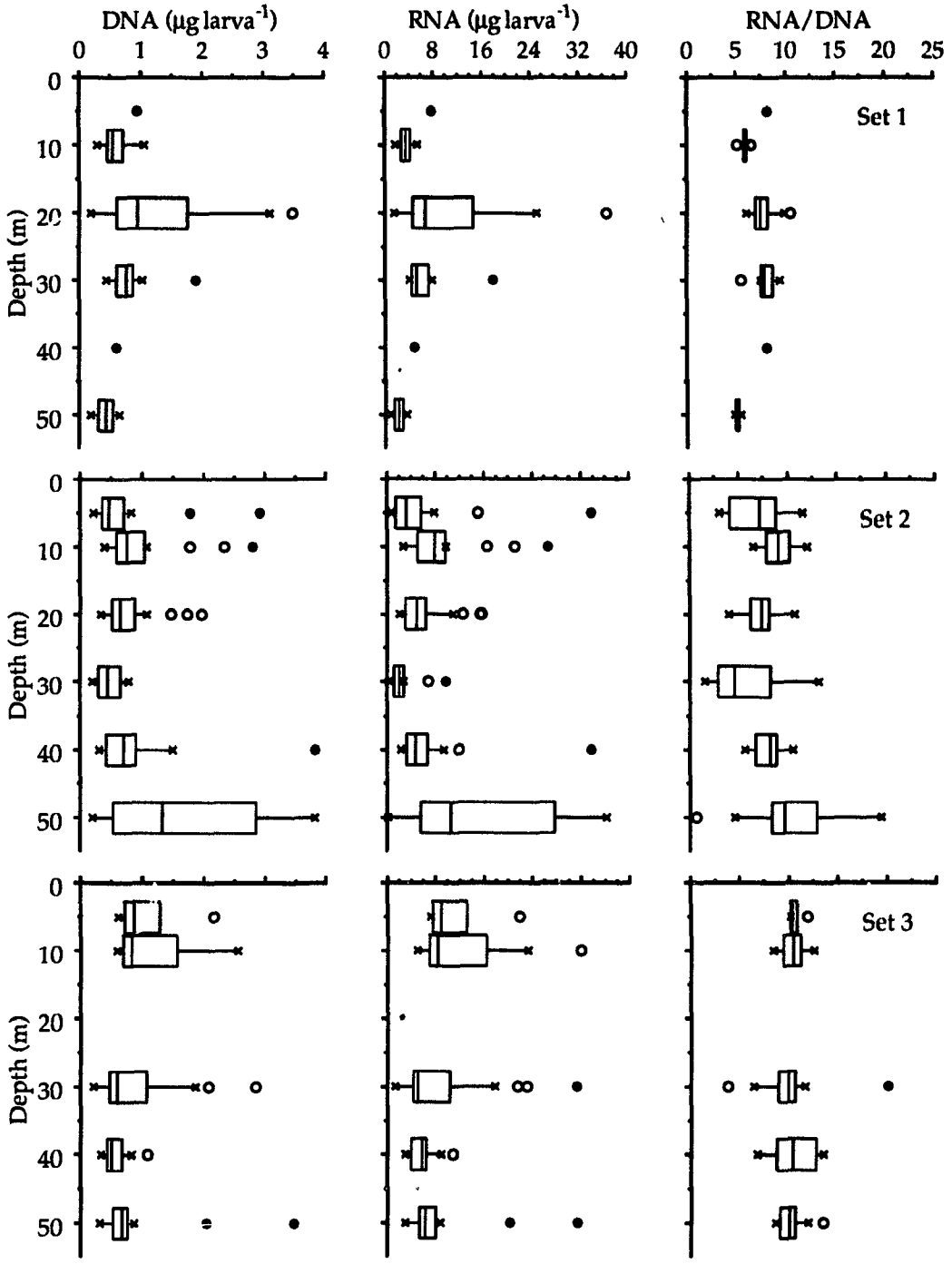

Figure 5.9: Box-whisker plots of DNA and RNA (μg larva^{-1}) and RNA/DNA at different depths for 3 sets of the vertical study. Top panel, set 1; middle panel, set 2; and bottom panel, set 3. Please refer to the caption of figure 5.7 for explanation on the box-whisker plots.

would concentrate around the pycnocline where food is more available.

In this study, however, the water column is completely well mixed (Figure 2.10), and so is the food (Figure 3.11). Thus, a differential vertical distribution of the condition of the larvae is not expected. Furthermore, Stephenson and Power [1991] have shown that larvae from all depths had food in their guts. Since the few larvae in poor condition are found at 30 and 50 m (Figure 5.9, set 2), it is suggested that the strong tidal mixing is distributing the larvae in poor condition throughout the water column, preventing their aggregation anywhere.

The analysis of covariance showed however, a significant effect of the time of the day on the mean RNA/DNA ratio. There was a significant increase of the mean RNA/DNA value from 7.4 at set 2 to 10 at set 3. Set 2 was collected at the end of the daytime, while set 3 was collected in the middle of the night. There are 2 possibilities to explain this difference. It can reflect a feeding pattern of the larvae, or it can be the result of net avoidance by the healthier larvae. One of the implications of the upward movement of the herring larvae during daytime is that they would be feeding (Chapter 2). This has also been the suggested as one of the factors affecting the diel migration [Stephenson and Power, 1989b] of these larvae, although these authors found in a later study that larvae had food in their guts during all times.

There are no studies that have investigated the short time response of the RNA/DNA ratio for herring larvae under different feeding conditions. Richard *et al.* [1991] have noted that for sole larvae, RNA content begins to decrease 1 day after beginning of starvation. Changes in the RNA/DNA ratio, however, could only be distinguished after 2 or 3 days for larvae that never fed. Longer periods were needed to distinguish changes if larvae fed for 5 or 10 days before being starved. Herring larvae are much bigger and robust than sole larvae, and probably more resistant to changes in their RNA/DNA than sole larvae. Clemmesen [1987] observed significant differences between fed and starved larvae only after 4 to 5 days of food deprivation.

The presence of temporal fluctuation in microzooplankton abundance (Chapter 3, Figure 3.11; Stephenson and Power [1991]) cannot be neglected. The RNA/DNA ratio of larvae from set 3 can be the result of feeding 2 to 3 days ago. For example, larvae that were collected in set 10, with relatively low food concentration, can have a high RNA/DNA ratio which resulted from feeding while under better conditions that existed in set 8.

Another possibility is that of net avoidance of the stronger herring during the day. In Chapter 2, net avoidance was shown not to be a problem with the sampling gear used. This was mainly the result of very small larvae being sampled, and was in agreement with the observations of Stephenson and Power [1988]. However, the larvae sampled for the condition analysis have a larger mean size (approximately 12 mm, Table 5.3). Brander and Thompson [1989] have shown that at 12 mm, there were almost 2 times more larvae capture at night than during the day with a Mocness (a larger version of the gear I used). This suggests that net avoidance of the stronger herring could also have influenced the changes observed between sets 2 and 3.

Chapter 6

Conclusions

This thesis addressed the relevance of food availability and of the feeding environment to the existence of large, persistent aggregations of Atlantic herring, *Clupea harengus*, larvae in tidally mixed waters off southwest Nova Scotia. The larval distribution and their food supply were characterized in relation to the well mixed and to the stratified environments, and discussed in light of current hypotheses that account for larval fish dynamics. Larvae in both regions are exposed to the same levels of food abundance. This information was coupled with dimensional analysis to investigate the influence of small scale turbulence on the feeding of herring larvae living in tidally mixed waters. The analysis reveals that turbulence enhances the feeding of herring larvae, and can contribute to the maintenance of the larval aggregations during winter months. Analysis of the physiological condition of the larvae was used to evaluate the influence of food supply and of the feeding environment on the condition of the larvae. Few larvae throughout the area were in poor condition, and the fact that larvae in well mixed waters were healthier than those in the stratified regions confirms the positive effect of turbulence in the feeding of herring larvae.

The results from Chapter 2 confirm that:

- Herring larvae are concentrated in the tidally well mixed waters off southwest Nova Scotia during the fall. The majority of the larvae are newly hatched,

indicating spawning activity.

- The vertical distribution of the larvae follows a diel pattern, with high concentration in the surface waters during the day and bottom waters at night.

It is proposed that the interaction of diel vertical migration with the complex circulation of the region minimizes transport due to the northerly residual flow. It is also proposed that an offshore displacement of the larvae occurs.

In Chapter 3, it was shown that:

- The amount of food available for the larvae is on average the same in the well mixed and in the stratified waters.

- The vertical distribution of the microzooplankton is uniform in the well mixed water column, confirming the results of previous studies.

It was also shown how methodological problems and data representation can influence the results of plankton studies targeted at larval fish food. In particular,

- Vertical and oblique sampling gear should be avoided. When this is not possible, results of food abundance should be presented as concentration and as integrated density;

- Fine mesh nets should be used to sample the appropriate food size for the larvae being studied. However, caution should be exercised, because due to intense mixing, fine sand remains in suspension and contaminates samples taken in the well mixed regions with fine mesh nets. This is most noticeable when expressing the results as dry weight.

The most important conclusions from this thesis are in Chapter 4. It was found that:

- Small scale turbulence significantly increases predator-prey contact rates and enhances the feeding of herring larvae in tidally well mixed waters off SW Nova Scotia.

- The results of the scale analysis indicate that the feeding environment on the adjacent stratified waters off southwest Nova Scotia in the winter is detrimental to herring, and high mortality is expected if larvae overwinter in this region.

The implication of this result is clear: in the ocean, food availability alone is not sufficient to characterize feeding conditions for planktonic organisms. The physical forcing that is an integral part of the feeding environment has to be taken into account.

In Chapter 5, the physiological condition of the larvae was studied. The most important conclusions were:

- The RNA/DNA ratio indicated that larvae are healthy in both regions during the study period. This corroborates the findings of Chapter 3, and confirms that in the fall food is sufficient for herring growth and development in both regions off SW Nova Scotia.

- Larvae collected in the well mixed regions were in better condition than larvae in the stratified area. This supports the results of the analysis in Chapter 4, that showed that small-scale turbulence increases predator-prey contact rates and enhances growth condition for herring larvae off SW Nova Scotia.

- Larval condition was the same for the whole water column.

- There was an increase in condition of the larvae collected at night. This could be the result of the interaction of temporal changes in food availability and avoidance by healthier larvae during day time.

The overall results of this thesis indicate that tidally well mixed waters off southwest Nova Scotia are a favourable feeding environment for herring larvae. This is not because of larger food concentrations in this region, but because of the influence of small-scale turbulence increasing the contact of prey and enhancing larval feeding. Although food concentrations for herring larvae feeding are sufficient in both

regions during fall, the benefits of turbulence may be essential for survival during the overwintering periods. These results suggest that differential mortality act in the larvae distributed in the different regions during the winter. This view is consistent with the "member/vagrant" hypothesis which emphasizes that membership in a population in the oceans requires being in the right place at the right time in the life cycle. The vagrants are lost from the population, and differential mortality contributes to enhance the observed retention of herring larvae off SW Nova Scotia.

The conclusions of this thesis provide an interesting insight into the influence of environmental factors in the variability of fish populations. Herring recruitment appears to be determined in the first year of life, and may be set by the time the larvae metamorphose [Anthony and Waring, 1980; Lough *et al.*, 1985]. Rothschild and Rooth [1982] pointed out that the survival of larval fish is dependent on events that operate in the micro- and fine-scale, and because trillions of these events must occur in any single recruitment year, a mechanism must exist which represents an integration or an averaging of them. The large aggregations of herring larvae observed in tidally well mixed regions of the Gulf of Maine may be the result of such an integration. Townsend [1992] reported that in the winter of 1990 about 75 % of the larvae hatched earlier in the fall are still retained within the tidally well mixed areas off SW Nova Scotia, while the rest has been advected to the offshore Gulf of Maine. The degree to which retention changes every year, will cause the micro- and fine-scale events to be integrated in different ways, leading to inter-annual variability in recruitment.

Further work remains to be done to improve our knowledge of the role played by early life history in fish recruitment. Long term surveys, such as the one currently being conducted in the fall off SW Nova Scotia, should be carried in the winter and spring. These studies, combined with the monitoring of mesoscale physical processes using remote sensing, *e.g.*, the spatial distribution of the cooler well mixed water, may be a powerful tool to understand recruitment variability in herring larvae. Simultaneous observations of the changes in the spatial distribution of the cooler

water and of the larval aggregations could give an indication of the proportion between "vagrants" and "members" in different years. Future field studies should incorporate physical measurements. The importance of the physical environment cannot be neglected. Specifically, in the case of herring larvae inhabiting tidally well mixed regions, it would be desirable that measurement of turbulent kinetic energy be made during studies of food availability. As demonstrated in this thesis, large scale and small scale physical processes should be taken into account if one wishes to understand the dynamics of larval marine fish.

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