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Growth patterns of fish larvae in relation to environmental conditions

- Diplomarbeit -

vorgelegt von
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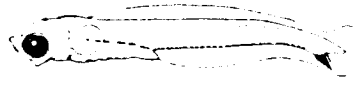

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Summary

Otolith microstructure analysis was used to reconstruct the growth histories of larval Radiated Shanny, *Ulvaria subbifurcata*, in Trinity Bay, Newfoundland. Larval fish and environmental conditions were studied during three surveys over a two week period in July 2000. Abundance of juvenile and adult capelin, *Mallotus villosus*, the dominant planktivorous fish in this area, was monitored using hydroacoustic integration. A dynamic three dimensional eddy-resolving circulation model of the region provided the advective history of the larvae. The goal was to determine whether spatial and temporal differences in environmental conditions could lead to detectable differences in the growth patterns of larval fish. Strong indications were found that ambient temperature had an overriding effect on larval growth. During the first part of the study, coastal upwelling caused considerable horizontal gradients in temperature, and the growth rates of larvae associated with cold water masses were significantly ($P<0.05$) lower than those of larvae in warm waters. During the second half of the study period, upwelling features disappeared, which resulted in an overall increase in surface temperature. Larval growth rates were significantly ($P<0.05$) increased after this period. Overall growth patterns indicated a selective loss of slower growing individuals throughout the study period; this result remains uncertain, however, as the ability to compare surveys was limited due partly to different origins and drift patterns of the larvae. Aggregated capelin schools occurred predominantly along the western coastline between 100-200m depth, and were considerably less frequent in the deep central areas of Trinity Bay. In western areas, low larval growth rates co-occurred with high predator densities, which may indicate that there was a selective loss of faster growing individuals in this area due to predation by capelin. The present findings suggest that larval microstructure analysis in combination with environmental observations and a reconstructed larval drift may prove a promising way to further understand the processes influencing growth and mortality on the larval fish.

A. Introduction

The role of starvation and predation in the early life history of fish

Most marine fish in temperate seas lay millions of eggs resulting in a tremendous, initial number of offspring. Unlike all other vertebrates, this unique reproductive strategy consequently entails that larval fish must be small in size (Houde 1997) and ontogenetically almost undeveloped at the time of hatch. As the word "larva" emphasizes, they thus differ fundamentally from the adults in terms of general appearance, the living environment, the food they rely on, behavior, and others traits. Scientific effort has elucidated various of these aspects but clearly remained focussed on two of the most important elements in the early life history: the high mortality and the outstanding growth of fish larvae.

When faced with the fact that normally more than 99% of all hatched fish in the open sea die before metamorphosis (Øiestad 1985) one automatically might get the impression that "a surviving larva has been just unusually lucky, with its survival being the result of a series of unrelated events, like winning coin tosses" (Pepin *et al.* 1999). However, it might not. This pivotal rationale comprises the most common basis of all investigations on larval fish; it assumes that there are detectable processes enhancing or decreasing a larva's probability of survival and subsequent recruitment into the adult population. The zeal to find variables describing these processes and detect traits that will characterize predominantly the "successful" larvae (Miller 1997, Conover and Schultz 1997) has not ceased in more than 100 years of fishery science.

Research on fish larvae has primarily been in the context of recruitment. This was and is the central problem of fishery science, as it represents the major source of uncertainty in management of exploited fish stocks (Sissenwine 1984). From the beginning, early life history was recognized to play a crucial role for the variability of recruitment. Relatively small changes in survival and growth on the larval level may lead to significant fluctuations in abundance and biomass of the

adult stock (Cushing 1975, Houde 1987, Bailey and Houde 1989).

With the formulation of his "Critical Period Hypothesis", the Norwegian fishery biologist, Johan Hjort (1914) was the first who explicitly advocated the importance of the very earliest stages of larval fish to the strength of recruitment. He suggested that large year classes of Atlanto-Scandian herring, *Clupea harengus*, result from high food levels available to the herring larvae, and that low food abundance may cause mass starvation of larvae and subsequent small year classes. Although he considered only food to be important and did not have measurements corroborating his concept, the hypothesis received much attention and inspired many of the work done in the past 30 years (an eminent review on the historical context is given by Sinclair [1997]).

In the late seventies, evidence from field studies and laboratory experiments was accumulated to elaborate upon Hjorts idea. Lasker (1975) found that the patchy aggregation of phytoplankton depends on stable wind conditions and is essential to the success of first feeding northern anchovy larvae, *Engraulis mordax*. His resultant "Stable ocean hypothesis" (Lasker 1981) postulated that coincidence in the timing of physical oceanographic conditions favoring food production and the timing of first feeding in fish larvae is critical to larval survival. In support to his concept, Parrish and MacCall (1978) noticed that weak upwelling at the Californian coast enhanced the survival of larval pacific mackerel, *Scomber japonicus*, in contrast to strong upwelling events that transported larvae away from favorable food conditions. The observation of storm-related variations in growth rates of Atlantic menhaden larvae, *Brevoortia tyrannus* (Maillet and Checkley 1991) fits in Laskers conceptual framework, too. In addition to the quantity of food available, a stable qualitative composition of planktonic food was found to be a pre-requisite for larval survival (Lasker *et al.* 1970, Lasker 1975, Scura and Jerde 1977).

However, various authors have emphasized (e.g. Lasker 1981, Heath 1992) that the "Stable ocean hypothesis" was build upon data on small, first feeding larvae and may not be applicable to older larvae or different species without further research. In fact, Mullin *et al.* (1985) found evidence for beneficial effects of storms for older anchovy larvae due to a stimulation of primary and secondary production. Similar results were presented by Kiørboe *et al.* (1988) investigating the fate of a larval herring patch in the North Sea.

Cushing (1975, 1990) proposed the "Match/Mismatch" hypothesis, whereby sufficient food levels are a critical requirement for all planktivorous larval stages. He suggested that reproductive strategies of fish in one area should reflect the mean annual cycle of primary and secondary production, and that a delayed phytoplankton bloom can cause a mismatch between larvae and the food they must rely on. The dominant role of food chain related processes for larval survival was questioned later by Sinclair (1988), who proposed that the stability of the physical environment has a dominant influence on population biology. The alternative "member/vagrant" hypothesis assumed both the integrity of cohorts and their retention in favorable areas due to oceanographic features to be of pivotal importance for survival.

It seems noteworthy that these conceptual frameworks were not only meant to increase the knowledge about larval biology, but had the objective to enhance the predictability of recruitment. In his review, Lasker (1981) explicitly advocated larval studies to be superior to catch studies for this purpose, and expressed his hope that "biological information on fish larvae [...] can be used to erect useful predictive models of recruitment [...]"

However, despite invaluable information has been accumulated about a number of processes acting on larval fish, the predictive power out of this information did not improve according to the expectations (Frank 1997). In the case of larval northern anchovy, even an unequivocal long term relationship between calm periods and recruitment has yet to be demonstrated (Heath 1992).

Increasingly, predation on fish larvae and eggs has become an issue of renewed scientific interest (Bailey and Houde 1989). Cushing (1974) already suggested that predation might be the major source of mortality for all early life stages of marine fishes, which was recognized later by a number of international meetings and workshops (e.g. Sharp 1980, Bakun *et al.* 1982, Rothschild and Rooth 1982, May 1984). Hunter (1981) argued that the high mortality estimates of eggs and yolksac stages in the open sea, ranging from 10% to 95% per day, must be due to predation because starvation cannot occur when larvae still subsist on their yolk reserves. Øiestad (1985) found that larvae have a very high potential survival rate even at marginal feeding conditions, and reasoned, if starvation alone would account for the high mortality rates, much more larvae in the state of starvation should be seen in sea samples. He concluded that predation is likely to be responsible for this discrepancy.

In their eminent review on predation on eggs and larvae of marine fish, Bailey and Houde (1989) compiled information of the numerous, mostly laboratory studies on potential predators of fish larvae. The diversity of organisms observed to be capable of eating a larval fish is astonishing and includes many taxonomic levels from dinoflagellates (*Noctiluca scintillans*, Hattori 1962) to marine birds (e.g. Hunt and Butler 1980). However, in view of a substantial impact on the ichthyoplankton community, four major groups of predators are generally considered (Frank and Leggett 1982, Bailey and Houde 1989): 1) Cnidarians (e.g. *Aurelia aurita*, Möller 1984), 2) Ctenophores (e.g. *Pleurobrachia pileus*, Fraser 1970), 3) various crustaceans like amphipods, euphausiids and copepods (e.g. *Hyperoche medusarum* (Amphipoda), Westernhagen and Rosenthal 1976), and 4) planktivorous fish (e.g. *Clupea harengus, Sprattus sprattus*, Pommeranz 1981). Chaetognaths (e.g. *Sagitta elegans*), which were observed feeding on fish larvae but usually prefer copepods, are unlikely to cause

high larval mortalities (Kuhlmann 1977, Hunter 1981). A more functional division in vertebrate and invertebrate predators was used by Gerritsen and Strickler (1977), because both groups differ fundamentally in size, feeding behavior, abundance, prey detection, attack speed, and other traits.

Although field studies on invertebrate predation outnumber those considering vertebrates (e.g. Frank & Leggett 1985), it is now generally believed that only eggs and the very early life stages of fish larvae are sufficiently vulnerable to planktonic invertebrate predators (Paradis *et al.*1996). As larvae grow, they rapidly develop swimming and escaping abilities (Heath 1992) and thus quickly attain a state, where they can render attacks by slowly approaching invertebrates unsuccessful (Webb 1981, Bailey 1984). To cause substantial mortality rates at older larvae, larger and more agile predators are required (Hunter 1981).

Are fish more important predators?

The strongest contender for the role of such agile predators are schooling pelagic juvenile and adult fishes (Hunter 1981). In the laboratory, Folkvord and Hunter (1986) observed adult northern anchovies and juvenile chub mackerel, *Scomber japonicus*, to prey voraciously on anchovy larvae. Other experiments showed larval herring to be vulnerable to predation by adult clupeids and sand eel, *Ammodytes tobianus* (Fuiman and Gamble 1988). In mid-size mesocosms Pepin *et al.* (1992) found that for larval capelin, *Mallotus villosus*, the overall vulnerability to fish (*Gasterosteus aculeatus*) was much higher than to an invertebrate predator (*Aurelia aurita*), and Øiestad (1985), using large enclosures, noted that "young cod [...] rapidly eradicated three groups of fish larvae".

In the field, however, evidence of planktivorous fish preying upon larvae is still relatively scarce (e.g. Pommeranz 1981, Hopkins 1989, Tsukamoto *et al.* 1989), which may not reflect a low importance of predacious fish but only the serious difficulties besetting such studies in the open sea. Even during peak abundances fish larvae remain an extremely scarce element of the plankton, with densities that are several orders of magnitudes lower than dominant observed zooplankton groups (e.g. copepods). In addition, soft bodied fish larvae quickly pass through a predators digestive system; Hunter and Kimbrell (1980) found that the smallest northern anchovy larvae (3-5mm SL) were digested beyond recognition in less than half an hour. Thus, stomach analyses of pelagic schooling fish (e.g. Huse and Toresen 1996 on *Mallotus villosus*) are likely to underestimate the potential impact of these predators on the ichthyoplankton community (Pepin *et al.* 1987). Alternative approaches seem to corroborate this. By combining field data with an individual-based model, Paradis and Pepin (2001) concluded that the larval fish community of a bay in Newfoundland is generally not affected by predation by macrozooplankton, but appears to be more vulnerable to predation by adult capelin, which is the dominant planktivorous fish in this area (Pepin *et al.* 2000).

Unfortunately, and despite the ample recognition of both predation and starvation as major agents of larval mortality, it still seems difficult to relate the entirety of the results to recruitment variability (Heath 1992, Houde 1997). Various authors, thus, have emphasized that this ultimate goal will only be achieved if further research pursues a better and thorough understanding of the mechanisms acting on larval growth and mortality (Miller *et al.* 1988, Leggett and DeBlois 1994, Chambers and Trippel 1997). Yet apart from a mere demand for new studies, recent work also seems to encourage a different consideration of some of the key aspects in larval research. First, to comprehend the dynamics of populations it will be necessary to understand the ecology on the individual level (Miller *et al.* 1988, DeAngelis and Gross 1992). Second, the variability of a trait under study should no longer be perceived as "noise" but as a source of valuable information, as a "signal" itself (Sharp 1987, Parma and Deriso 1990, Shepherd and Cushing 1990). As Miller (1997) and Pepin (1989) have pointed out, many relevant processes may only be detectable in the changing patterns (e.g. magnitude, shape) of variability. This has also been recognized in other modeling approaches. For example, Rice *et al.* (1993) reported a four-fold increase in the survival rate of modeled bloater, *Coregonus hoyi*, larvae, when larval growth variability, but not the mean growth rate, was increased. A third recurrent directive emerging from recent studies, is the need to properly consider the spatial and temporal scale of the processes under study, and to adjust sampling programs according to these scales (Paradis *et al.* 1996, Houde 1997).

Larval growth rates: A trait sensible for environmental influences?

In search for a trait that may characterize predominantly the successful, i.e. surviving larvae, much attention is given to larval growth rates, because growth and mortality are closely linked (Houde 1997). Growth leads to an increase in body size, and mortality rates of a larval cohort generally decline with size due to better foraging abilities and a decreasing vulnerability to predation (Cowan *et al.* 1997). These basic tenets, tested mostly in laboratory experiments (Hutchings 1997), gave rise to the presumption that a bigger individual has always a higher probability of survival (the so called "bigger-is-better" hypothesis), and in order to attain the big size as fast as possible, a directional selection will favor the highest growth rates.

In laboratory (Litvak and Leggett 1992, Pepin *et al.* 1992) and field studies (Pepin *et al.* 2000, Conover and Present 1990) the generality of this concept was falsified. Because predation is a complex process consisting at least of the events encounter, attack, and capture, resulting vulnerability to predation was hypothesized to be

the product of the probabilities of each of these events (Bailey and Houde 1989, Gerritsen and Strickler 1977). Thus, faster growth leading to a bigger size at a given age is likely to be a trade-off between a decreased probability of capture and an increased probability of encounter, especially by visual predators like fish (Folkvord and Hunter 1986). Litvak and Leggett (1992) demonstrated that three-spine sticklebacks, *Gasterosteus aculeatus*, clearly selected for older and larger larvae. Beside the higher risk of predation, outstanding growth rates may also lead to rampant metabolic energy demands (Conover and Schultz 1997). Which set of initial growth rates eventually survives, depends on the actual environmental conditions and the varying influence they will have on growth rates throughout the entire larval period.

Growth rates of fish larvae, no matter how they were derived, are known to vary widely within any set of individuals sampled at the sea. There is a general consensus that this variability can be seen as a consequence of both intrinsic factors, determining the growth potential of an individual larva, and environmental effects determining the actual outcome of this potential (Parma and Deriso 1990, Heath 1992).

From laboratory experiments and field studies (reviewed for example by Lasker 1981, Houde 1989, and Heath 1992) it emerged that ambient temperature is probably the strongest abiotic factor influencing larval growth (Heath 1992). Within physiological limits, a higher temperature will have a direct effect on the metabolism, leading to approximately 10% increase in growth per Celsius degree given an adequate food supply (Heath 1992). In the field clear relationships between sea temperature and otolith growth rate were demonstrated by Thomas (1986) on larval fish in the south-east Atlantic, and Hovenkamp (1989) on plaice larvae in the North Sea. By contrasting environments of different latitudes, Houde (1989) was able to show that weight specific growth rates at temperatures in tropical seas (30°C) are six times higher than at temperatures in cold seas (5°C). And Pepin (1991), synthesizing available data of temperature, growth and mortality for a number of marine and estuarine fishes, reported that daily developmental rates of all early life stages (eggs, yolk-sac, postlarvae) are significantly influenced by temperature.

However, possible effects of temperature on growth rates strongly depend on the quality and quantity of the available planktonic food. The dual role of these environmental conditions in controlling growth rates (Heath 1992, Cowen and Sponaugle 1997) is intuitive. Higher growth rates induced by higher temperatures, for example, must be supported by increased food consumption or may otherwise lead to a higher risk of starvation (Houde 1989). Conversely, if fluctuating ambient food levels are considered to influence growth rates, temperature has to be controlled, either experimentally or statistically. In a laboratory experiment on three different subtropical species, Houde (1978) demonstrated that under constant temperatures growth rates increased with increasing prey densities. In the North Sea, Munk *et al.* (1991) found that, while seasonal fluctuations in sea temperature explained higher growth rates of herring larvae in autumn versus winter months, spatial differences in zooplankton production (Hay *et al.* 1991) were probably responsible for the consistently higher growth rates in southern versus northern areas.

In general, however, attempts to relate spatial variations in prey biomass or temperature to larval growth rate (e.g. Methot 1981, Hewitt *et al.* 1985) have met with rather limited success (Heath 1992). Heath argued that many of the past studies estimated lifetime mean growth rates using size-at-age relationships, derived from pooled individuals. While this approach may be acceptable to describe general species- or stock-specific growth characteristics, only back-calculated daily growth rate trajectories of individuals will truly allow the attempt to relate measurements of temperature and food abundance to growth rates (Heath 1992).

How does predation by fish act on larval growth?

In contrast to temperature or food density, predation cannot directly affect the growth of a single larva. But as predation is recognized to be a size-selective process (Pepin *et al.* 1987, van der Veer *et al.* 1997), and differences in larval growth rates lead to increasing differences in body size (Paradis and Pepin 2001), it is likely that predation will result in a selective removal of certain growth rates from the initial population. However, field studies are bound to focus on the survivors of predation. Nevertheless, to assess the patterns of surviving growth rates may comprise an alternative way of understanding the predation process. Especially over short time intervals, growth rates are thought to be more sensitive to the effects of predation than other traits, such as mean length (Paradis and Pepin 2001). In a simulation study, Pepin (1989) showed that for any given mean the variance of growth rates was negatively correlated to predator abundance.

In the field, however, detecting the impact of predation in a given distribution of growth rates may prove a quite complicated task (Paradis *et al.* 1999). Especially at the very early life stages, absolute differences in size due to different growth rates are minimal, hence decreasing the probability of a detectable size-selection. In addition, estimates of growth rates are generally poorest for the youngest larvae, and measurement error is likely to explain most of the variation. Pepin *et al.* (2001) investigated the role of measurement error to larval growth studies, concluding that size-selective processes seem to be detectable during a rather small age interval of larvae being five to 15 days old.

In order to be detectable in a cohorts growth rate distribution, size-selective predation further needs to lead to substantial mortality rates. Cowan *et al.* (1996) demonstrated that size-selective mortality was apparent only after 70% of the original cohort had died, and Paradis *et al.* (1999), using an individual-based model for

fish larvae, could only detect size-selection when losses exceeded 50% in 30 days.

Furthermore, the vulnerability to predation by pelagic fish continuously changes depending on the size distribution of larvae and predators (Paradis et al 1996, Rice *et al.* 1993). General concepts of vulnerability, as in Bailey and Houde (1989), hypothesize a dome-shaped curve for predacious fish, where fish larvae are most vulnerable at a size of 10% of the predator length (Paradis *et al.* 1996). This implies that a larval cohort will first grow into the vulnerability window of a certain predator field, before being maximal vulnerable, and subsequently outgrow the predators preferred prey size range. In both stages, the effects of a possible size-selection may in fact counteract and cancel itself out, leaving the impression that no size-selection occurred at all (Rice *et al.* 1997, van der Veer 1997). It will thus depend on the ability to sufficiently consider size distributions of both predator and ichthyoplankton, and the use of an appropriate temporal scale, if one aims to find patterns of size-selective predation in the distribution of larval growth rates.

Sufficient abundance estimates of both predators and prey are a further challenge to all field studies of larval growth patterns in conjunction with predacious fish. Unlike carnivore invertebrates, foraging fish schools are not a subject to advection (Pepin *et al.* 2000), they occur highly aggregated and are able to migrate fast in both vertical and horizontal dimensions. Especially in small scale systems, this may cause serious limitations to an adequate description of the predator environment encountered by the larvae (Pepin *et al.* 2000). Despite the difficulties, some studies could show that spatial differences in predator abundance can indeed evoke spatially different larval growth patterns (Paradis *et al.* 1999, Pepin *et al.* 2000).

Otolith microstructure analysis as a tool for larval growth studies

Little has been said so far about how to derive the growth characteristics of larval fish sampled in the open sea. This is in spite of the fact that the methodology used in growth studies greatly determines the scope of any potential conclusions.

Estimation of somatic growth rates, either expressed as a gain in length, weight, volume, or percentage per unit time, requires knowledge about the age of the larvae. While in experiments this could be achieved by considering only individuals of the same hatch day (given that larvae are reared from eggs), it is not possible in field samples, which usually consist of a broad variety of larval ages. Developmental features such as pigmentation, fin expression, fin rays, and swim bladder appearance, though generally related to larval age, are too variable to yield more than a coarse impression of the age structure in a given sample.

With the discovery of daily growth increments in fish otoliths (Pannella 1971), a much better tool for age determination became available (Campana and Neilson 1985). Otoliths are acellular, mineralized structures consisting of calcium carbonate crystals embedded in a proteinaceous matrix (Carlstrom 1963). The three pairs of otoliths are located in the inner ear, where they aid maintaining equilibrium and facilitate hearing (Helfman *et al.* 1997). Under endocrinological control (Simkiss 1974), a differential deposition of calcium carbonate and protein over a 24-h period leads to the formation of a translucent, incremental zone (crystals and protein), followed by an opaque, discontinuous zone (protein), which together comprise one daily increment. In past studies, the daily periodicity of increment formation has been verified and is now recognized as a widespread phenomenon of marine and freshwater fishes of all habitats (Campana 1989). Furthermore, otoliths are often the first calcified structures appearing during the early development of teleosts, making them especially appropriate for larval studies (Campana and Neilson 1985).

Counting increments of an otolith yields larval age in days (given the age at first increment deposition is known), and gross-estimates of a populations somatic growth rate can then be estimated by relating all sizes to age at capture for a random sample of individuals (e.g. Lough *et al.* 1982, Bolz and Lough 1983, May and Jenkins 1992). However, this practice carries an inherent assumption that a cohort of individuals sampled at age T + t represents a random sample of those present at age T. If there is size-dependent bias, due for instance to size-dependent mortality or gear selectivity (Campana 1990), then the mean growth trajectory will be inaccurate (Heath 1992). Therefore, the approach is used to describe only general species- or stock-specific growth characteristics.

The true potential of otoliths for growth studies is based on the fact that otolith growth reflects somatic growth very closely (Campana and Neilson 1985). Thus, microstructure of otoliths may comprise a tool to reconstruct the past state (e.g. growth rate) of an individual (Pepin 1989). The general correspondence of fish-otolith size has been used primarily to derive fish length – otolith length regressions of a population sample in order to back-calculate an individuals length at previous ages. Although this is considered to yield the true growth rates of an individual (Campana 1990) in contrast to the population growth rate (Ricker 1975), it was demonstrated that this approach may result in a systematic underestimation of previous fish lengths (Campana 1990). To reduce the potential error inherent to length back-calculations, a mean width of only peripheral (most recent) increments has been used to derive recent growth estimates (e.g. length increase per day), and relate them to the environmental conditions at capture (Suthers [1998] provides a summary of such field studies).

Studies dealing with the influence of environmental factors on growth, however, may not need to back-calculate larval lengths (Gallego *et al.* 1996). If the environment affects growth rates (Heath 1992), and these are generally linked to otolith increment widths (Moksness

and Wespestad 1989), then patterns of increment widths can be expected to reflect environmental processes as well. For example, mean increment widths of otoliths were shown to be proportional to ambient temperature (Neilson and Geen 1982) and prey ration (Volk *et al.* 1984) without affecting the circadian rhythm of increment formation (Moksness and Wespestad 1989). Gallego *et al.* (1996) used individual increment widths of larval herring otoliths to assess the impact of turbulence, food and illumination on growth rates. They emphasized that the short-term variability of increment widths may comprise an important source of information, depending on both intrinsic and environmental factors. Selective removal of growth rates (e.g. by predators) is another issue which can be addressed by contrasting the distributions of increment widths from temporally separated samples. Pepin *et al.* (2000) investigated patterns of increment widths for larvae, which had drifted from an area of low to higher predator abundance, and found that this was associated with a loss of faster growing individuals from the distribution.

All attempts to link environmental parameters to growth variability on the individual level need to be based on temporally and spatially intensive sampling programs (Rilling and Houde 1999), because large scale features may account for only a small part of the total variability in growth (Gallego *et al.* 1996). For logistical reasons, sampling of ichthyoplankton and the considered biotic or abiotic variables is often done simultaneously, leading to a relatively good description of the environment on the day of capture. However, several workers have pointed out that a larva's instantaneous growth rate does not reflect the actual but the past environment because of the autocorrelation within subsequent increment widths (Mosegaard *et al.* 1988, Secor *et al.* 1989, Pepin *et al.* 2000, 2001). Gallego *et al.* (1996) estimated that 65.7% of the observed variability in growth was explained by the past growth history of the larvae. And Pepin *et al.* (2001) concluded that due to serial correlation "an individual's growth increments did not show the effect of changes in local environmental conditions for at least three days." Therefore, it may be inappropriate (at least inaccurate) to infer the processes that have affected larvae based on the environmental conditions they were associated with on the sampling day. As a consequence of that, it was proposed to assess the advective history of a larval patch and infer then the environmental conditions, the individuals will likely have experienced along their way (Pepin 2000).

How to assess larval advection?

Two main approaches have been used to assess the drift patterns of fish larvae in the open sea. Once a patch of larvae is detected, a buoy or drogue may be released and tracked in the hope that the buoy drift reflects the main drift of the larval patch. Taggart *et al.* (1996) investigated the fate of a cohort of larval cod, *Gadus morhua*, by tracking a well-mixed, gyre-like water mass for a period of 20 days. To assess how small-scale variability in food abundance affected a large patch of walleye pollock larvae, *Theragra chalcogramma*, Incze *et al.* (1990) used a satellite-tracked drifter. In other cases, the utility of drifters has proven to be limited, because strong vertical current shears decoupled the buoy from the drift of the larval patch. Davis *et al.* (1991) intended to follow a drogue to study 7-8 day old larval southern blue fin tuna, *Thynnus maccoyii*, over a six days period. They reported that wind-induced surface currents dragged the buoy in a direction contrary to the main drift the of larval patch rendering the approach unsuccessful. Another stipulation for such Lagrangian drifters is that one needs to know the initial location of a dense larval patch, which in some cases may be a rather fortuitous matter (Davis *et al.* 1991).

An alternative approach is to couple survey observations with a dynamic circulation model that provides a reliable forecast of the variations in the physical environment encountered by the larvae (Pepin *et al.* 2000). Schemes of larval drift or dispersal may then be inferred by tracking computer-generated particles through the model domain (e.g. Heath and Gallego 1998, Voss *et al.* 1999). The reliability of this approach depends on the quality and resolution of the model, and on the degree to which larvae are treatable like passive drifters. For this reason Davidson and deYoung (1995), modeling advection of cod eggs and larvae on the Newfoundland Shelf, limited their analysis to a period of 50 days. Voss *et al.* (1999) and Hinrichsen *et al.* (2001) applied a 3D eddy resolving baroclinic model of the Bornholm Basin and the entire Baltic Sea respectively, to study drift and dispersal of cod eggs and larvae for a period of 60 days. They hypothesized that meteorological scenarios favoring the rapid advection of larvae into shallower areas may lead to enhanced growth and survival of the early life stages of Baltic cod. Davidson (1999) and Davidson *et al.* (2000) developed a dynamic 3D eddy resolving CANDIE model for three of the major embayments in eastern Newfoundland. They showed that the model was able to predict changes in both surface circulation and the rise and fall of isopycnals as a function of variable wind forcing. This model was used later by Pepin *et al.* (2000) in a larval study in Conception Bay, Newfoundland. The authors concluded that the general circulation features were adequately represented by the model's forecasts and it therefore provided appropriate means to assess the advective history of larval fish during the study period.

Objectives

Past research has emphasized the importance of larval growth studies to understand the dynamics of fish populations (Trippel and Chambers 1997). It was shown that a variety of environmental factors have the potential to influence an individuals or cohorts growth characteristics, and for the most instances a number of those factors will act together (Heath 1992). To credit the com-

and Wespestad 1989), then patterns of increment widths can be expected to reflect environmental processes as well. For example, mean increment widths of otoliths were shown to be proportional to ambient temperature (Neilson and Geen 1982) and prey ration (Volk *et al.* 1984) without affecting the circadian rhythm of increment formation (Moksness and Wespestad 1989). Gallego *et al.* (1996) used individual increment widths of larval herring otoliths to assess the impact of turbulence, food and illumination on growth rates. They emphasized that the short-term variability of increment widths may comprise an important source of information, depending on both intrinsic and environmental factors. Selective removal of growth rates (e.g. by predators) is another issue which can be addressed by contrasting the distributions of increment widths from temporally separated samples. Pepin *et al.* (2000) investigated patterns of increment widths for larvae, which had drifted from an area of low to higher predator abundance, and found that this was associated with a loss of faster growing individuals from the distribution.

All attempts to link environmental parameters to growth variability on the individual level need to be based on temporally and spatially intensive sampling programs (Rilling and Houde 1999), because large scale features may account for only a small part of the total variability in growth (Gallego *et al.* 1996). For logistical reasons, sampling of ichthyoplankton and the considered biotic or abiotic variables is often done simultaneously, leading to a relatively good description of the environment on the day of capture. However, several workers have pointed out that a larva´s instantaneous growth rate does not reflect the actual but the past environment because of the autocorrelation within subsequent increment widths (Mosegaard *et al.* 1988, Secor *et al.* 1989, Pepin *et al.* 2000, 2001). Gallego *et al.* (1996) estimated that 65.7% of the observed variability in growth was explained by the past growth history of the larvae. And Pepin *et al.* (2001) concluded that due to serial correlation "an individual´s growth increments did not show the effect of changes in local environmental conditions for at least three days." Therefore, it may be inappropriate (at least inaccurate) to infer the processes that have affected larvae based on the environmental conditions they were associated with on the sampling day. As a consequence of that, it was proposed to assess the advective history of a larval patch and infer then the environmental conditions, the individuals will likely have experienced along their way (Pepin 2000).

How to assess larval advection?

Two main approaches have been used to assess the drift patterns of fish larvae in the open sea. Once a patch of larvae is detected, a buoy or drogue may be released and tracked in the hope that the buoy drift reflects the main drift of the larval patch. Taggart *et al.* (1996) investigated the fate of a cohort of larval cod, *Gadus morhua*, by tracking a well-mixed, gyre-like water mass for a period of 20 days. To assess how small-scale variability in food abundance affected a large patch of walleye pollock larvae, *Theragra chalcogramma*, Incze *et al.* (1990) used a satellite-tracked drifter. In other cases, the utility of drifters has proven to be limited, because strong vertical current shears decoupled the buoy from the drift of the larval patch. Davis *et al.* (1991) intended to follow a drogue to study 7-8 day old larval southern blue fin tuna, *Thynnus maccoyii*, over a six days period. They reported that wind-induced surface currents dragged the buoy in a direction contrary to the main drift the of larval patch rendering the approach unsuccessful. Another stipulation for such Lagrangian drifters is that one needs to know the initial location of a dense larval patch, which in some cases may be a rather fortuitous matter (Davis *et al.* 1991).

An alternative approach is to couple survey observations with a dynamic circulation model that provides a reliable forecast of the variations in the physical environment encountered by the larvae (Pepin *et al.* 2000). Schemes of larval drift or dispersal may then be inferred by tracking computer-generated particles through the model domain (e.g. Heath and Gallego 1998, Voss *et al.* 1999). The reliability of this approach depends on the quality and resolution of the model, and on the degree to which larvae are treatable like passive drifters. For this reason Davidson and deYoung (1995), modeling advection of cod eggs and larvae on the Newfoundland Shelf, limited their analysis to a period of 50 days. Voss *et al.* (1999) and Hinrichsen *et al.* (2001) applied a 3D eddy resolving baroclinic model of the Bornholm Basin and the entire Baltic Sea respectively, to study drift and dispersal of cod eggs and larvae for a period of 60 days. They hypothesized that meteorological scenarios favoring the rapid advection of larvae into shallower areas may lead to enhanced growth and survival of the early life stages of Baltic cod. Davidson (1999) and Davidson *et al.* (2000) developed a dynamic 3D eddy resolving CANDIE model for three of the major embayments in eastern Newfoundland. They showed that the model was able to predict changes in both surface circulation and the rise and fall of isopycnals as a function of variable wind forcing. This model was used later by Pepin *et al.* (2000) in a larval study in Conception Bay, Newfoundland. The authors concluded that the general circulation features were adequately represented by the model´s forecasts and it therefore provided appropriate means to assess the advective history of larval fish during the study period.

Objectives

Past research has emphasized the importance of larval growth studies to understand the dynamics of fish populations (Trippel and Chambers 1997). It was shown that a variety of environmental factors have the potential to influence an individuals or cohorts growth characteristics, and for the most instances a number of those factors will act together (Heath 1992). To credit the com-

plexity of interaction between larval growth and the environmental influence, it will be necessary to study these processes on the individual level (Miller *et al.* 1988). This can be done by inferring larval growth histories from otolith microstructure analysis without the need to back-calculate previous lengths at age (Gallego *et al.* 1996). As most environmental factors affect the variability rather than the average of growth rates, it seems critical to study the changes of the whole distribution of increment widths (Pepin *et al.* 2000). In addition, only spatially and temporally intensive sampling programs are likely to provide an appropriate description of the environment encountered by the larvae (Rilling and Houde 1999). It is further necessary to assess the advective history of larval fish (e.g. by a circulation model), because the width of an increment reflects the influence of a past environment (Pepin *et al.* 2001). To date, few studies have made explicit use of these concepts.

Applying these approaches, the goal of the present study was to investigate the growth patterns of larval radiated shanny, *Ulvaria subbifurcata*, in relation to temperature, food concentration, and the abundance of planktivorous pelagic fish schools. Of particular interest was whether spatial differences in these environmental conditions could be seen to lead to spatial differences in growth rates and how changes in the environment during the study period are reflected by the shanny growth rate distributions. A second objective was to determine whether there was evidence for a selective removal of slower or faster growing individuals throughout the study period. If so, then larval growth rates may comprise a tool to describe predominantly the successful, i.e. surviving larvae. To meet these objectives, three surveys were conducted over a two week period in July 2000 in Trinity Bay, Newfoundland. They provided a comprehensive set of data of the spatial and temporal variability of the environmental conditions. Abundance of capelin, *Mallotus villosus*, the dominant planktivorous fish in the area, was monitored using hydroacoustic integration, whereas larval drift trajectories were simulated using a 3D eddy resolving circulation model.

Radiated Shanny, Ulvaria subbifurcata (Stichaeidae)

Previous studies of the ichthyoplankton community in Newfoundland (e.g. Frank and Leggett 1982, Laprise and Pepin 1995) frequently observed larvae of the Radiated Shanny (Fig.A1), *Ulvaria subbifurcata* (Storer, 1839) to be very abundant in their plankton samples between late spring and early summer. Especially in July, this member of the stichaeid family seems to be among the five most important larval species in coastal Newfoundland waters (Pepin *et al.* 1995). Explicit use of *U.subbifurcata* larvae in growth studies has been made by Pepin *et al.* (2000 and 2001), who reported the broad suitability of this species for otolith microstructure analyses.

The radiated shanny is a common, benthic fish in littoral and sublittoral waters along the east coast of North America (Scott and Scott 1988). Adults are territorial; they occupy sites of approximately 3m² year-round (Green et al. 1987) and leave them at night to feed on a large variety of benthic invertebrates (LeDrew and Green 1975). Radiated shannies attain a maximum size of 16.5 to 18 cm (Scott and Scott 1988), and are of no commercial value for the fishery. However, because there is evidence of juveniles in cod stomachs (Leim & Scott 1966), shannies may have some importance as a food source for species targeted by the fishery (Scott and Scott 1988).

In the Newfoundland area, radiated shannies spawn in spring and early summer months in relatively cold waters between 1.5 and 4°C (Green *et al.* 1987). The adherent, demersal eggs are guarded and fanned by a male (LeDrew and Green 1975) until larvae hatch after 35 to 40 days and start to ascend to the surface layer. The average length at hatch was estimated by LeDrew and Green (1975) with 6.58 mm TL. The same study reported that settlement normally occurs in august, when larvae average 18.4 mm TL.

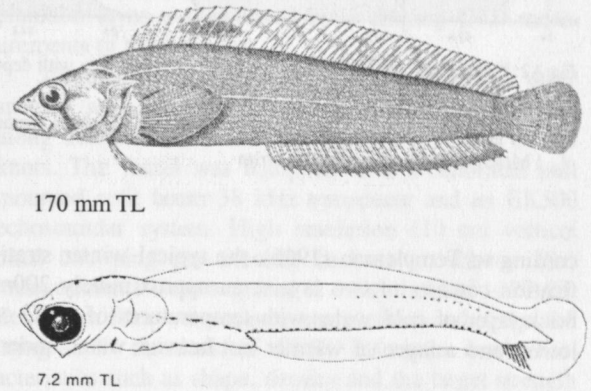

Fig.A1. Adult male and larva of the Radiated Shanny, *Ulvaria subbifurcata*, a member of the Stichaeid family

Description of Trinity Bay, the study area in eastern Newfoundland

Trinity Bay (Fig.A2) is one of several major bays along the Newfoundland Atlantic coast. With approximately 100 km length and 30 km width (Yao 1986), it is about three times bigger than the adjacent Conception Bay. In its central area, where a deep trench runs parallel to the coastline, maximum depth is 630 metres, whereas the sill outside the bays mouth has a maximum depth of 240 metres (Yao 1986). The bay is influenced by the inshore branch of the cold Labrador Current, which is strongest in spring (Davidson and deYoung 1995). Ac-

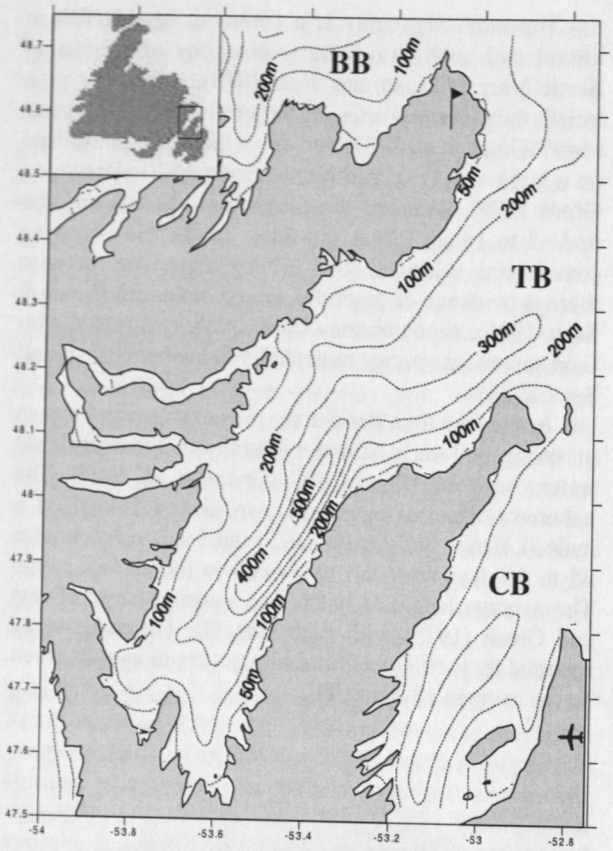

Fig.A2: Newfoundland and Trinity Bay (TB), the study area with depth contours. CB: Conception Bay, BB: Bonavista Bay.
Meteorological stations: +) Environment Canada at St.John´s airport, ⚑) Meteorological station in Bonavista

cording to Templeman (1966), the typical winter stratification consists of two layers: an approximately 200m thick layer of cold water with temperatures of –1°C or lower, and a layer of warmer but heavier water underneath, derived from the West Greenland Current. Warming in spring and summer leads to the formation of a third distinct layer at the surface, usually of a thickness of 10-30 m (Templeman and Fleming 1963), and especially in bays and shallow areas surface temperature can reach 15°C - 20°C (from satellite images of surface temperature in July/August, in Davidson [1999]).

Stratification and circulation in the bays of Newfoundland are highly responsive to wind forcing (Templeman 1966, Frank and Leggett 1982, Yao 1986). In summer, north-easterly, offshore winds prevail (long-term mean for July from 1960-1980: 26.8d, SD=3.0d [Frank and Leggett 1982]), inducing upwelling of colder, intermediate water masses on appropriate coastlines, such as the western shore of Trinity Bay. Conversely, periods of onshore winds are likely to suppress upwelling and intensify surface heating (Fig.A3). Frank and Leggett (1982) demonstrated that the wind-induced water mass replacement (Templeman 1966) may be of great biological importance for the ichthyoplankton community in the bays.

Similar to Conception Bay, as well Trinity Bay is part of the Labrador/north-east Newfoundland shelf ecosystem, and may therefore comprise a nursery area for larval fish of all species inhabiting the extensive shelf off the coast (Laprise and Pepin 1995). In general, embayments are known as favorable areas for early life stages of marine fish because of the higher temperatures (Laprise and Pepin 1995), a higher primary and secondary production, and fewer predators (Frank and Leggett 1982). Retention in those areas has been hypothesized to be crucial for larval survival (Sinclair 1988). De Young *et al.* (1994) estimated the retention time for Conception Bay with 30 days, a period sufficient for larvae of many species to complete their development inside the bay (Laprise and Pepin 1995). Given that Trinity Bay is twice as long as Conception bay, an even longer retention time appears possible.

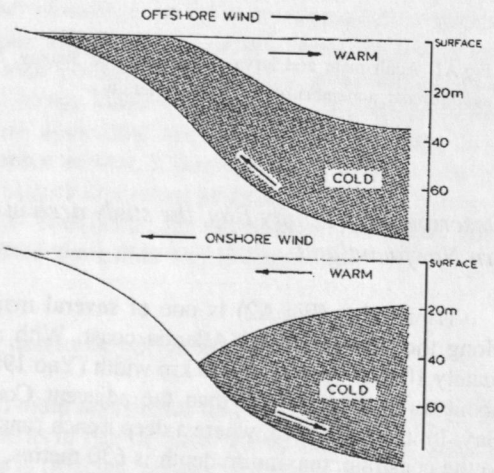

Fig.A3: Schematic representation of the effect of offshore and onshore winds on the summer water temperatures and water layers in the nearshore zone along Newfoundland´s east coast (redrawn from Templeman 1966, in Frank and Leggett 1982)

B. Material & Methods

Survey design and data collection

Between July 18 and July 30, 2000, three surveys were conducted on board the research vessel *CSS Wilfred Templeman* to study the ichthyoplankton community in Trinity Bay, Newfoundland (48°N, 53.5°E). Each survey was designed to cover the whole bay with a uniform sampling grid that consisted of 29 stations along nine transects of three to four sampling stations with an approximate distance between stations of eight km (Fig.B1) The 2nd survey was separated from the end of the 1st survey by five days, whereas the 3rd survey was conducted four days after the end of the 2nd survey. Each survey lasted between 35 and 44 hours.

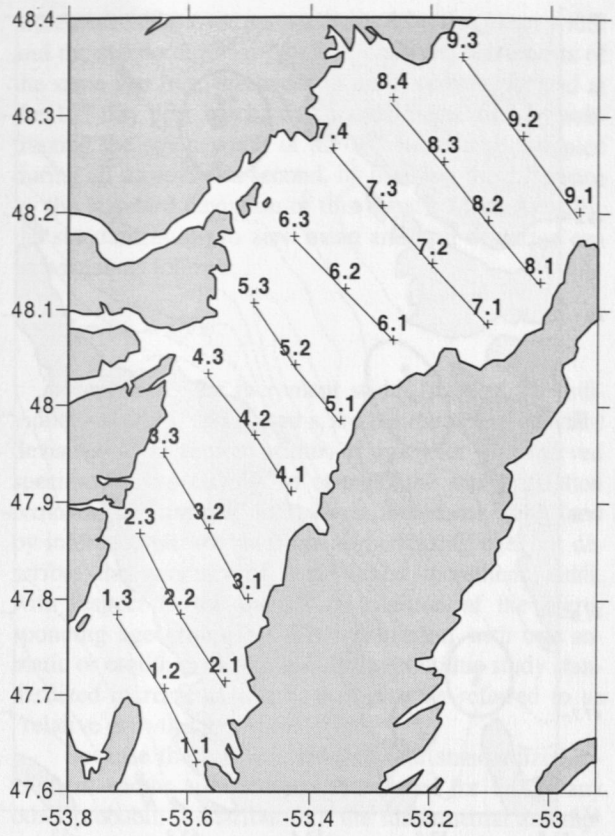

Fig.B1: Sampling grid for each of the three surveys conducted in Trinity Bay.

Sampling procedures were similar to an ichthyoplankton survey conducted in 1998 in Conception Bay (Pepin *et al.* 2000). Larval fish were collected by performing a single oblique tow with a 4m² Tucker trawl deployed from the surface to approximately 40m depth. As previously shown (Pepin *et al.* 1995, Frank & Leggett 1982, de Young *et al.* 1994), this sampling layer (0-40m) was likely to contain more than 95% of the occurring ichthyoplankton. The gear was equipped with sections of 1000, 570, and 333 µm mesh nitex (Pepin and Shears 1997) and towed for 10-15 minutes at 1 m/s. Two General Oceanics flow meters, mounted at the mouth of the net, were used to estimate the volume of water filtered during the tow. On deck, samples were immediately preserved in 95% ethanol but were drained again after one week to renew the preservative. All fish larvae were subsequently separated from other planktonic organisms and identified to species or to the lowest taxonomic level possible (Fahay 1983). Up to 200 specimens per taxa per station were measured for their standard length (nearest mm) using a dissecting microscope and a gridded background. Estimates of larval abundance (expressed as larvae/1000m³) were corrected for larvae apparently damaged during the sampling procedure, by applying the length frequencies from undamaged individuals.

At each station, a 0.5m diameter plankton net (70µm mesh) was deployed to 40m depth and hauled vertically at 1m/s to the surface, where zooplankton samples were preserved in 2% buffered formaldehyde. In the laboratory, abundance of microzooplankton was estimated using a Coulter Multisizer II® particle counter. The counting principle of this device is based on the relationship between particle size (Volume) and the proportional increase of electrical resistance, each time particles move through an electric field. The method required particles to be kept in suspension in a conductible medium being double-filtered seawater in this case. A Coulter Multisizer II® tube equipped with a 560 µm diameter orifice was used to record the size and number of particles flowing from a standardized sample jar (400 ml) through the electric field of the tube orifice. Prior to counting, samples were rinsed through 500-65µm sieves to separate the microzooplankton fraction, which then was split 6 to 8 times using a Metoda splitter and double-filtered seawater until dilution was appropriate for the particle counter. Particles were discriminated at size intervals of 1.57µm. Later, counts of all size-classes greater than 65 µm were summed to yield the overall abundance of microzooplankton per station [particles/m³].

At each station, a Seabird-25 CTD (sampling rate of 8 Hz) was lowered at 1 m/s to record temperature, salinity and fluorescence profiles of the water column down to 100m depth. A value representative for the ichthyoplankton layer was obtained by averaging CTD measurements of the top 30 m.

Abundance of juvenile and adult capelin (no other species were quantified) was estimated continuously along transects while the ship traveled at speeds of 5-8 knots. The vessel was equipped with a calibrated hull mounted split beam 38 kHz transducer and an EK500 echosounder system. High resolution (10 cm vertical bins, one ping per second) backscatter volume (Sv) measurements were acquired at a threshold of –100 dB. Echogram files were subsequently edited and integrated using an Sv threshold of -85dB. Echogram mark characteristics such as shape, density and the target strength distribution were used to differentiate between fish and crustaceans (Simard and Lavoie 1999). Capelin were distinguished from other fish backscatter using echogram characteristics combined with species composition and biological characteristics obtained during fishing sets. Biological data originated from 26 IYGPT[1] trawls at four different sites in Trinity Bay (Fig.B2) conducted during the course of the study. At each site, all trawls were finished within a 24-hour period. From the IYGPT samples, up to 200 capelin were selected at random and measured to the nearest mm using a measuring board.

Backscatter (Sv) values originating from capelin were integrated over the whole water column in 10m depth intervals and 100 m horizontal bins to produce estimates of the back-scatter area (Sa) in m²/m² (Mac Lennan and Simmonds 1992). Backscatter values originating from the top 10m were generally not included, because capelin above or near the transducer are not

[1] International Young Gadoids Pelagic Trawl. An IYGPT is a 10x10m pelagic mid-water trawl (Koeller *et al.* 1986)

detected by the acoustic method. Sa was then scaled to numbers of individuals per square meter by applying the length-frequency distribution of capelin, sampled during IYGPT trawls, and the target strength relationship 20*logL - 73.1, where L is length in cm (Rose 1998). Average vertical distribution of capelin was calculated from the mean depth of capelin backscatter between 20 – 300 m depths and for each of the 100 m horizontal integration bins (13,500).

Echo data about capelin distribution were complemented by two additional dedicated hydroacoustic surveys carried out between the 1st and 2nd, and 2nd and 3rd surveys along the same transects and at the same speeds. The two additional surveys were used to ascertain the stability of capelin distribution patterns and abundance during the study period.

Except for the microzooplankton counts, the material and results from above mentioned methods were made available for further analyses in the present study.

Otolith microstructure analysis

For otolith microstructure analysis up to 15 radiated shanny larvae were chosen at random from each sample. Each was measured for total and standard length (to the nearest 0.1mm) with the aid of an Optimas® image analysis system connected to a dissecting microscope. Prior to dissection a unique identification number was assigned to each specimen. Using two dissecting needles and a dissecting microscope, both sagittal otoliths of 359 larvae were extracted; each otolith was subsequently mounted on a drop of Crystal Bond® thermoplastic cement on a microscope slide. Choosing randomly the left or right sagitta, unless one side proved impossible to read, the otolith was then ground to near mid-plane using a 0.3µm lapping film. All otoliths were read under 500x magnification with a Olympus BH-2 compound microscope connected to an Optimas® image analysis system. To minimize measurement errors, the operator first determined the longest axis between the nucleus and the periphery of the otolith, and measured then every increment along this axis by marking its outer edge. For large otoliths, this required a refocusing of the image up to three times. Additional measurements included the length, width (µm) and total area of the otolith (µm²) as well as the diameter of the hatch-check (µm).

Because of a greater potential for measurement error for the earliest narrow increments (Pepin *et al.* 2001), all otoliths from individuals younger than 12 days were read twice. In older larvae the measurement of increment widths was repeated in every 10th individual. In both cases otoliths were rejected if the number of increments (age) differed more than 10% between counts, which led to 12 exclusions from the data set. Attention was paid that otolith readings were not ordered by station number, survey, or larval length. Throughout this study, every increment is considered to represent one day. Therefore, the last increment of each

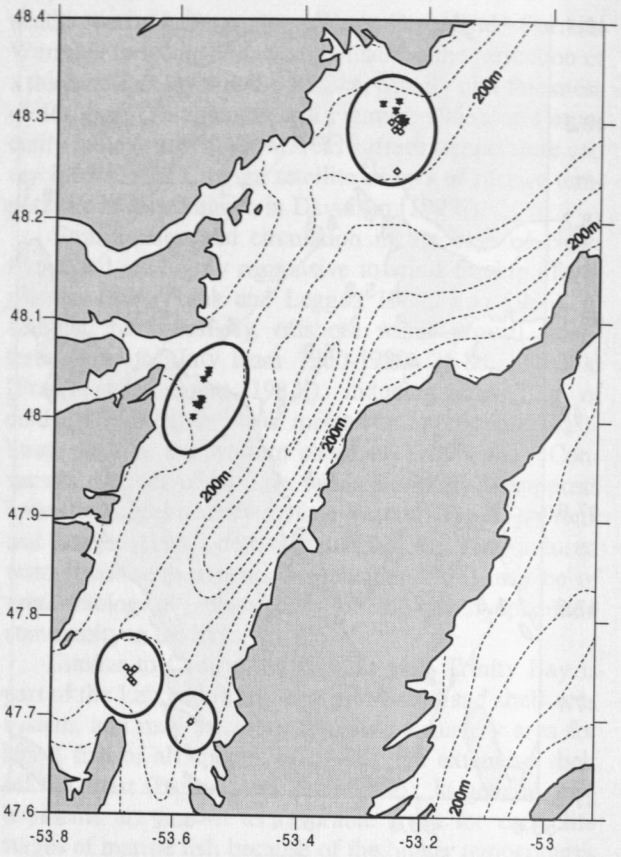

Fig.B2: Sites of the 26 IYGPT trawls and hydroacoustic monitoring of capelin vertical migration patterns.

otolith was generally excluded from analyses, since its formation probably had not been completed on the day the specimen was sampled.

A major objective of the present work was to determine whether selective mortality had notably altered the distribution of larval growth rates throughout the study period. To achieve this, distributions of growth increments were contrasted, which were formed on a given day by a "cohort" of larvae, sampled repeatedly during subsequent surveys. In this context, "cohort" refers to a group of larvae, hatched throughout a period of five days prior to the first survey. Larvae were grouped into four hatch intervals, including the days of hatch 190-194 (HI I), 185-189 (HI II), 180-184 (HI III), and 175-179 (HI IV). Based on the above assumption of daily incrementation, the day on which each increment was formed, was back-calculated as follows:

day of increment formation = sampling day – age at catch + increment number

However, because larvae hatch on different days, assigning increment widths to the day of their formation entails that a particular day will contain the widths of increments, which were formed at different larval ages. This poses a problem, because both the mean and the variance of increment widths are increasing with increasing age (Pepin *et al.* 2000, 2001, this study: Fig.C20). Therefore, to make different ages comparable,

increment widths were standardized by the mean width and the standard deviation of all observed increments of the same age (e.g. the width of an increment, formed at the 10^{th} day post hatch, was standardized, first by subtracting the mean width of all 10^{th} increments sampled during all surveys and second, by dividing the difference by the standard deviation of this mean). More formally, the standardization to zero mean and unit deviation can be written as follows:

$$z_{ij} = (x_{ij} - x_j)/s_j$$

where x_{ij} is the increment width (µm) of the individual i at age j, and x_j and s_j are the mean and standard deviation of increment widths at age j for all observed specimens, respectively. In essence, the standardization removes the "normal" increase in increment width (and by inference growth rate) due to increasing age, but describes the anomaly of a particular increment width, with respect to the overall distribution of the corresponding age group. To avoid confusion with true somatic or otolith growth rates, throughout this study standardized increments widths will also be referred to as "relative growth rates".

Because there is no evidence that standardized increment widths are normally distributed (or follow any other probability distribution), the fundamental assumptions for using parametric analytical methods are often not satisfied. Furthermore, it was not desirable to describe possible changes in the distribution of growth rates, for example, by linear regression, because there is no theory about the form of such a dependence. To characterize shape and changes of the entire distribution of growth rates, age-dependent cumulative probability distributions (CDF) were derived using local non-parametric density estimations (Davison and Hinkley 1997, Pepin *et al.* 1999, Evans 2000). The method did not estimate a single distribution but a separate, locally weighted CDF for each possible value of x (age), assuming that observations nearest to the target x (age) were most relevant for the distribution at x. The exact algorithms for building a cumulative probability distribution can be found in Davison and Hinkley (1997), and comprehensive descriptions of the weighting function and its components (bandwidths) are provided by Evans and Rice (1988), Pepin *et al.* (1999) or Evans (2000). The 10%, 50%, and 90% probabilities were used to describe the whole CDF of standardized increment widths as a function of days of increment formation. As a measure of variability, the difference in growth rates between the 90% and 10% cumulative probabilities was calculated (also referred to as the "scatter").

If certain growth rates disappeared selectively during the study period, the CDF's of standardized increment widths are expected to reflect this selective loss. If lower percentiles are seen to be shifted upwards from one survey to the next, one would interpret this as a loss of slower growing larvae. Conversely, decreased upper percentiles may indicate that faster growing specimens disappeared between surveys. Furthermore, a comparison of the scatter was used to address questions like: was the distribution of growth rates narrower for larvae sampled during later surveys? Or are there spatial differences in the variability of relative growth rates, when larvae from different areas of the bay are contrasted?

To decide whether median relative growth rates changed, or two medians differed significantly, 95% confidence intervals around the median were estimated from 500 randomizations of the data. If confidence intervals of two medians did not overlap, median increment widths were considered to be significantly different.

Drift projections

For comparison with the larvae data, results were made available for this study from a sophisticated 3-D eddy resolving CANDIE model of Davidson (1999) and Davidson *et al.* 2000), which simulates the wind-driven circulation that affected the larval distribution in Trinity Bay. The model solves 3-D non-linear Navier-Stockes equations (i.e. the equations of x, y, and z momentum as well as the density and continuity equations) on an f-plane using three standard oceanographic approximations: hydrostatic and rigid lid (Gill 1982), and the Boussinesq approximation (Spiegel and Veronis 1960). The equations are finite differenced on a 3-D, Arakawa C-grid with one km horizontal and 10 m vertical resolution. The model domain consisted of both a realistic coastline geometry and a bottom topography of Trinity Bay and the two adjacent bays (Bonavista Bay, Conception Bay). On the lateral land boundaries, a free-slip condition was applied to avoid a flux of momentum or density through the water-land interface, whereas for all three open boundaries a Neumann boundary condition (Greatbatch and Otterson 1991) was used. Because all applied boundary conditions were passive, meaning no explicit influence of external forces (e.g. Labrador Current), the modeled water circulation was driven entirely by the effects of local wind forcing.

Winds were assumed to be spatially homogeneous over Trinity Bay (de Young *et al.* 1993), and were measured hourly by Environment Canada at St.John's airport (10 km east of Conception Bay) and by the Meteorological station in Bonavista (western shore of Trinity Bay, Fig.A2). Because data were sufficiently similar between these two points of observation (Fig.C2), only the St.John's data were eventually used in the model. All circulation runs were initialized at rest (i.e. no motion) using a horizontally uniform stratification based on the long term mean (1957-1997) for the month of July at Station 27 (5 km east of St.John's). Wind stress derived from velocities by the quadratic formulation of Large and Pond (1981) was smoothly introduced over two days using a hyperbolic tangent ramping function. The time measurement began on day 190 after winds reached 50% strength, and ended after 35 days of simulation on day 125.

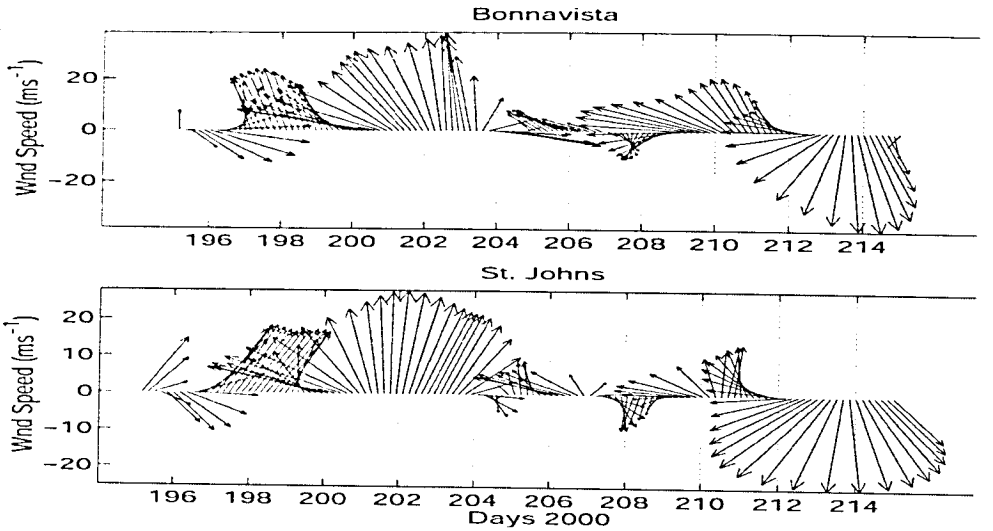

Fig.C2: Wind observations between d196 and d214 at meteorological stations Bonavista and St.John's airport. For layout reasons arrows are not drawn on cartesian (north-south) coordinates but are re-arranged for prevailing wind directions, i.e. out-of-the-bay and into-the-bay (y-axis points 30° east of north)

To simulate the drift of larvae in Trinity Bay, computer-generated particles were released into the model domain on day 201 at 12 am. The drifter mode implemented is described in Davidson and de Young (1995) and allows particles to be tracked smoothly through a finite resolution velocity field. Because the main interest laid on the horizontal dynamics of particle movement, no vertical component of transport was modeled. Particles, thus, were constrained to one of two layers (0-10m and 10-20m), and were anticipated to accumulate near coastlines if downwelling occurred there. The drifters were given a random walk component to their displacement at every time step equivalent to a diffusion coefficient of 10 m²/s. Otherwise, particles seeded at the same location would unrealistically cling together over the simulation period.

Two different backward projections of particle drift were conducted in both layers of the model to reveal larval drift tracks. In the first backward run over a simulation period of six days, particles were uniformly seeded on day 201 (500m apart) and assigned to sampling stations on day 207 (the end of the 2nd survey) only if they were located within 3km of the station location. Starting on day 201, the second backward simulation lasted 11 days, similarly collecting particles on day 212 (the end of the 3rd survey). In addition, an 12 days forward simulation was run by seeding 1000 particles within a radius of 1km around every sampling station on day 201, and recording particle positions at 24h intervals until day 212. A similar forward run was started on day 206 to model larval drift patterns between the 2nd and 3rd surveys.

Although all simulations of particle drift were done separately for both the surface layer (0-10m) and the second layer (10-20m), only the results of the latter were used to infer larval drift patterns. It was assumed that differences between both strata are only due to a higher responsiveness of the surface layer to wind forcing (Pepin *et al.* 2000), which may even obscure the more relevant general patterns.

C. Results

Environmental conditions

Between July 18 and July 30, environmental conditions conducive for larval growth changed considerably in the mixed surface layer (30m) of Trinity Bay (Fig.C1). During the 1st survey low temperatures (Fig.C1:a) along with higher salinities (Fig.C1:b) on the bays western shore revealed the occurrence of strong upwelling that coincided with south-westerly winds, which had blown steadily at 20ms^{-1} for three preceding days (Fig.C2). Average temperature at western shore stations ($T_{5\text{-}30m}$=2.97°C) was more than 2°C lower than at other stations ($T_{5\text{-}30m}$=5.24°C). Probably in response to sharply relaxing wind fields on day 204 (July 22), upwelling features had completely vanished by day 206 (July, 24) when the 2nd survey was conducted. On this day, the cold and high salinity water ($T_{5\text{-}30m}$=2.95°C) was seen to cover the entire inner half of Trinity Bay (to approx. 48.1°N), whereas warmer and fresher water masses ($T_{5\text{-}30m}$=5.16°C), apparently propagating south, covered the outer half of the study area. By the time the 3rd survey was conducted (July 29/30), an overall temperature increase along with a remarkable depression of isothermes (Fig.C3) indicated that the warmer and fresher water masses had fully displaced the cold water body from the surface.

Fluorescence, as a measure of chlorophyll and hence phytoplankton concentration (Fig.C1:c), almost

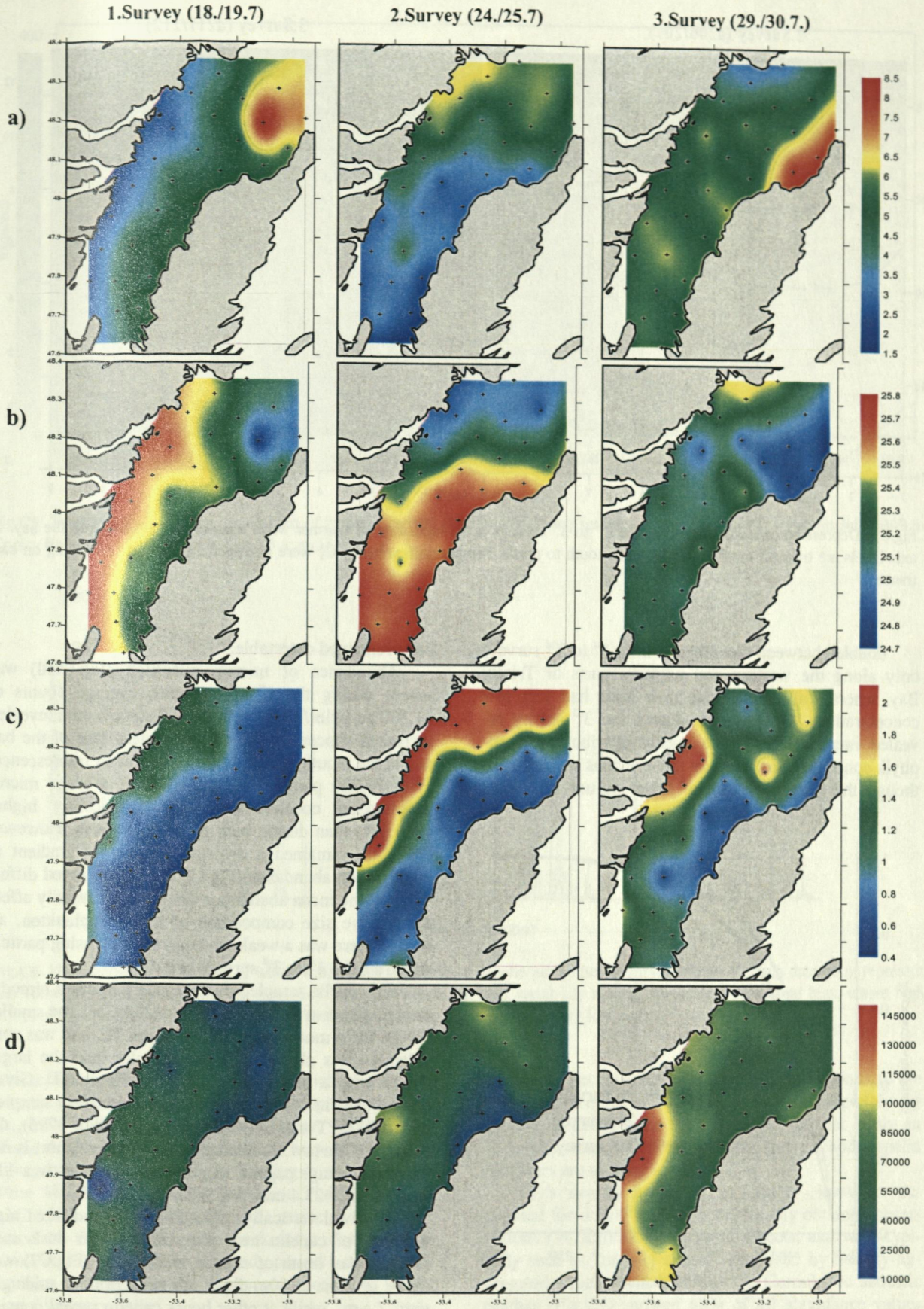

Fig.C1: Environmental conditions in Trinity Bay between July 18 and July 30, 2000. Contour plots of a) temperature [C°], b) salinity [psu], and c) fluorescence in the upper 30 metres, as well as d) concentration of microzooplankton (65-500µm) in the upper 40 metres [particles/m³] during three different surveys. Kridging was used for the interpolation between data points (crosses). Descriptions are given in the text.

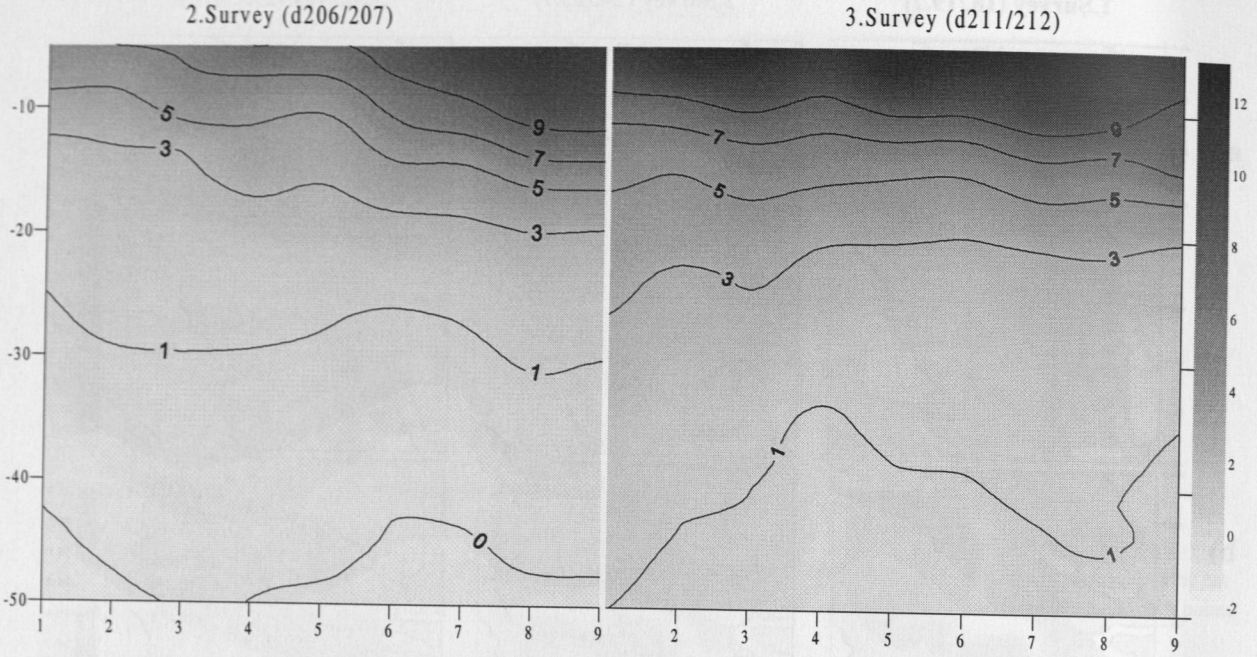

Fig.C3: Depression of isothermes from the 2nd to 3rd surveys as an indication of warmer water masses propagating into the bay. X-axis labels are transect numbers going from south to north. Temperature values [°C] were averaged for all stations laying on each transect.

doubled between day 200 and 206 (1st to 2nd survey) only along the western and northern parts of Trinity Bay, whereas all eastern and inner areas had very low concentrations. Observations during the 3rd survey revealed increased and more evenly distributed chlorophyll concentrations than in the previous surveys, although the general feature of lower values in eastern parts remained detectable.

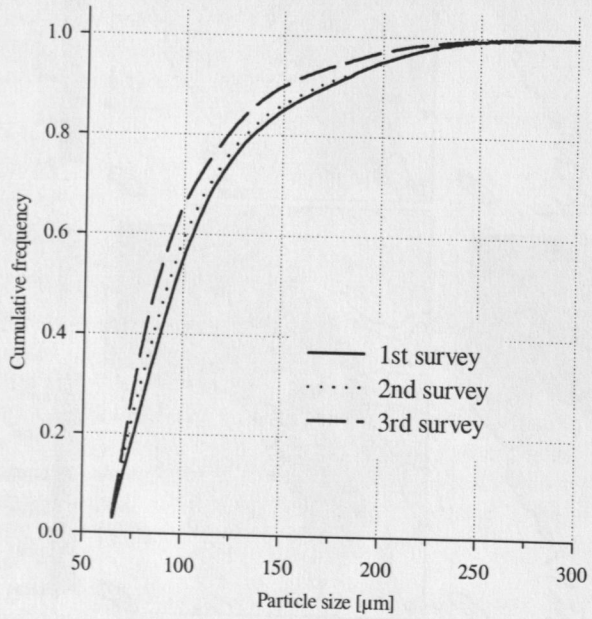

Fig.C4: cumulative size frequency of counted microzooplankton particles based on average counts per channel and survey. There is a small but inconsequential tendency of decreasing plankton size with survey

Abundance of microzooplankton (Fig.C1:d) was lowest during the 1st survey with average counts of 41,100 particles/m³. During the 2nd survey, data revealed increased concentrations on the western side of the bay and at the mouth, similar to the changes in fluorescence. With 79,700 particles/m³ on day 211, average microzooplankton concentration was significantly higher ($P<0.001$) than during both previous surveys. However, there still remained a detectable east-west gradient in zooplankton abundance (Fig.C1:d). The observed differences in the mean abundance did not substantially affect the relative size composition of microzooplankton, although there was a weak tendency of decreasing particle size from the 1st to 3rd surveys (Fig.C4)

For capelin sampled by the IYGPT trawls a bimodal total length distribution was found (Fig.C5). The smaller cohort had a mode length of 90-95mm TL, and was considerably less abundant in the samples than the larger cohort with a mode length of 125-130mm TL. Given that all capelin over 24mm are representatively sampled by the IYGPT trawls (Anderson and Dalley 1995), the reason for the low abundance of the smaller cohort is not known. Average capelin length in the samples was 118 mm TL (SD=23.4 mm, n=3342).

Resolved vertically, acoustic returns indicated high densities of capelin near the surface from dusk until dawn. Mean depth of capelin backscatter (Fig.C7) was above or close to 50m depth one hour prior to midnight until 7 a.m., while at other hours capelin stayed considerably deeper (between 81m-113m). In addition, acoustic data obtained during IYGPT trawls (Fig.B2) indicated that capelin schools occurred more dispersed in

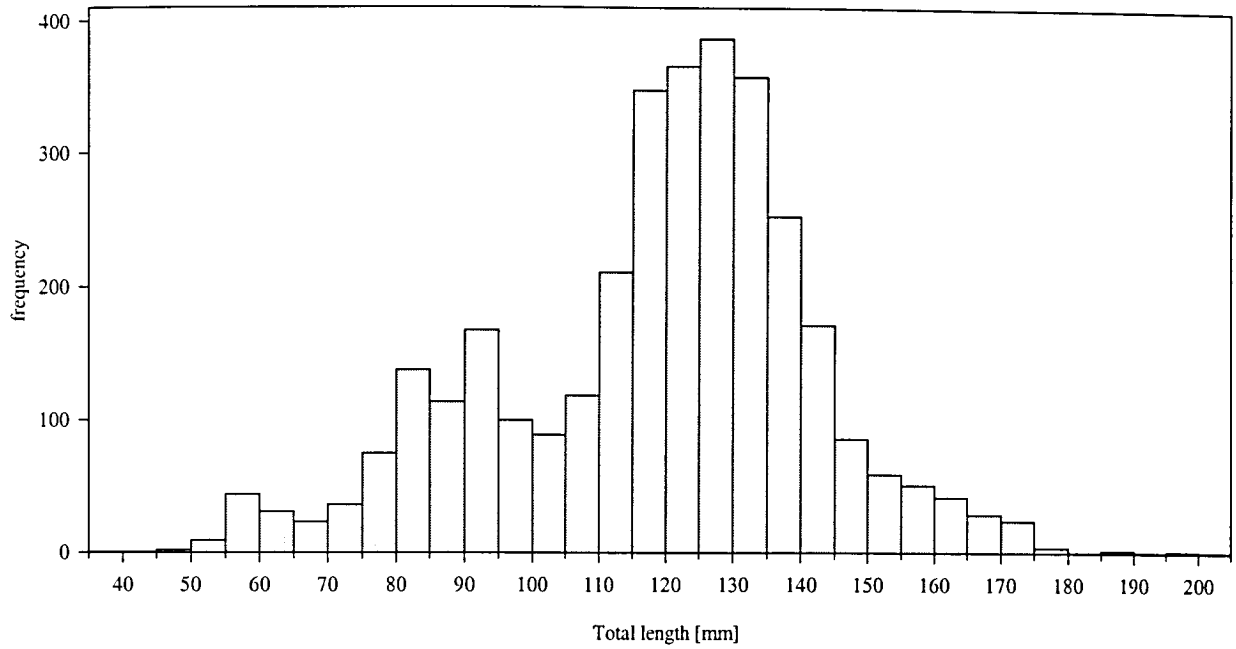

Fig.C5: Total length-frequency distribution of juvenile capelin (*Mallotus villosus*) sampled during 26 IYGPT trawls in July 2000 in Trinity Bay (mean TL=118 mm, SD=23.4, n=3342)

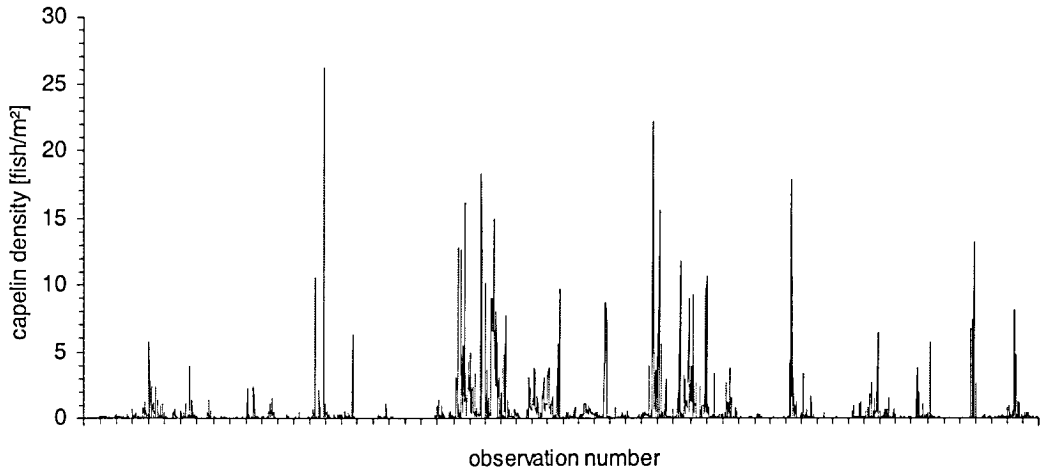

Fig.C6: Hydroacoustic estimation of whole water column content of capelin along the 1st survey transsect. Each data point represent one 100m horizontal integration bin (n=3064). The plot depicts the high variability among consecutive horizontal bins, where high values of capelin abundance are seen as „density spikes" among the majority of very low density estimates

the surface layer (Fig.C8:a-b), unlike when seen on the bottom around noon or in mid-water depths (Fig.C8:c-d), where they tend to form much denser aggregations. Dispersion is commonly assumed to be a characteristic pattern of pelagic fish schools foraging in surface waters (Fran Mowbray, North-West Atlantic Fisheries centre, A1C 5X1, St.John's/NF, Canada, personal comment). Based on this and the mean backscatter depth, it was surmised that throughout the study period average feeding time of capelin in the ichthyoplankton layer was at least five hours daily.

Hydroacoustic integration along survey transects yielded whole water column content estimates of capelin expressed by capelin/m². As addressed in Appendix 1, estimates over one capelin/m² were considered high density areas, because this level roughly corresponds to the entire surface layer (0-40m) searched completely by capelin predators once per day. This does not imply an encounter rate of 100%, as both larvae and capelin predators are moving around.

High density areas >1 capelin/m², however, accounted for only 9% of all continuously obtained observations (14,500) along survey transects, and were typically seen as "density spikes" produced by heavily aggregated capelin schools (Fig.C6). Cumulative acoustic catches (Fig.C9) showed 68% of all abundance values laying between 0-0.1 fish/m² with no major changes between surveys. As expected for schooling fish like capelin, variability between consecutive 100m echo bins was very high and explained a considerable portion of

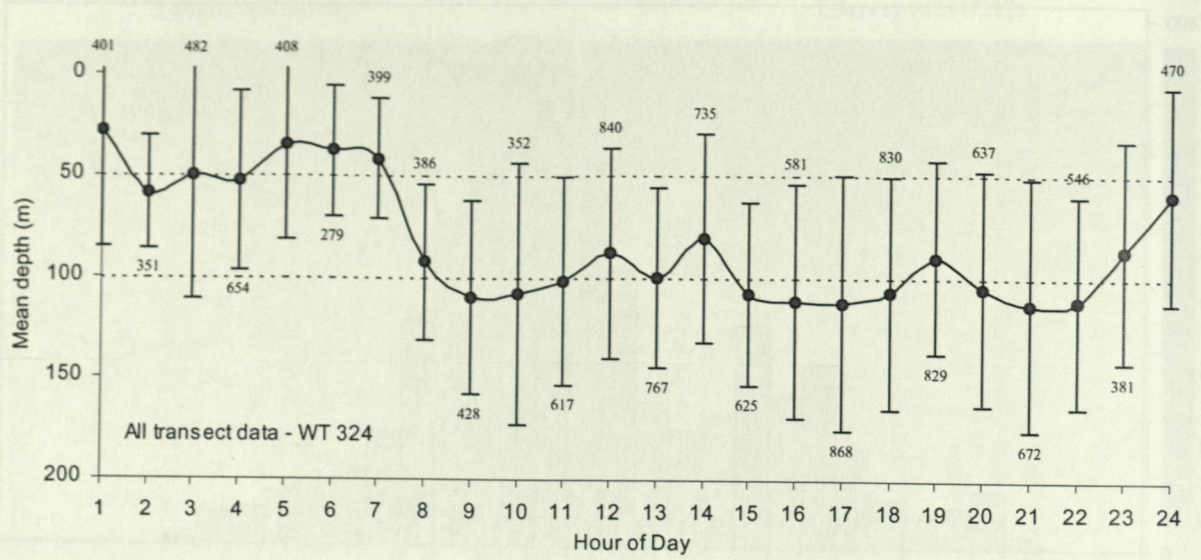

Fig.C7: Mean depth and standard deviation of capelin backscatter between 20-300m, obtained from 13,538 horizontal integration bins (100m) along survey transects. N-values per hour are given above or below the error bars. Capelin are seen to stay above or close to 50m predominantly between one hour prior to midnight and 7 a.m. (dotted lines are 50m and 100m reference levels)

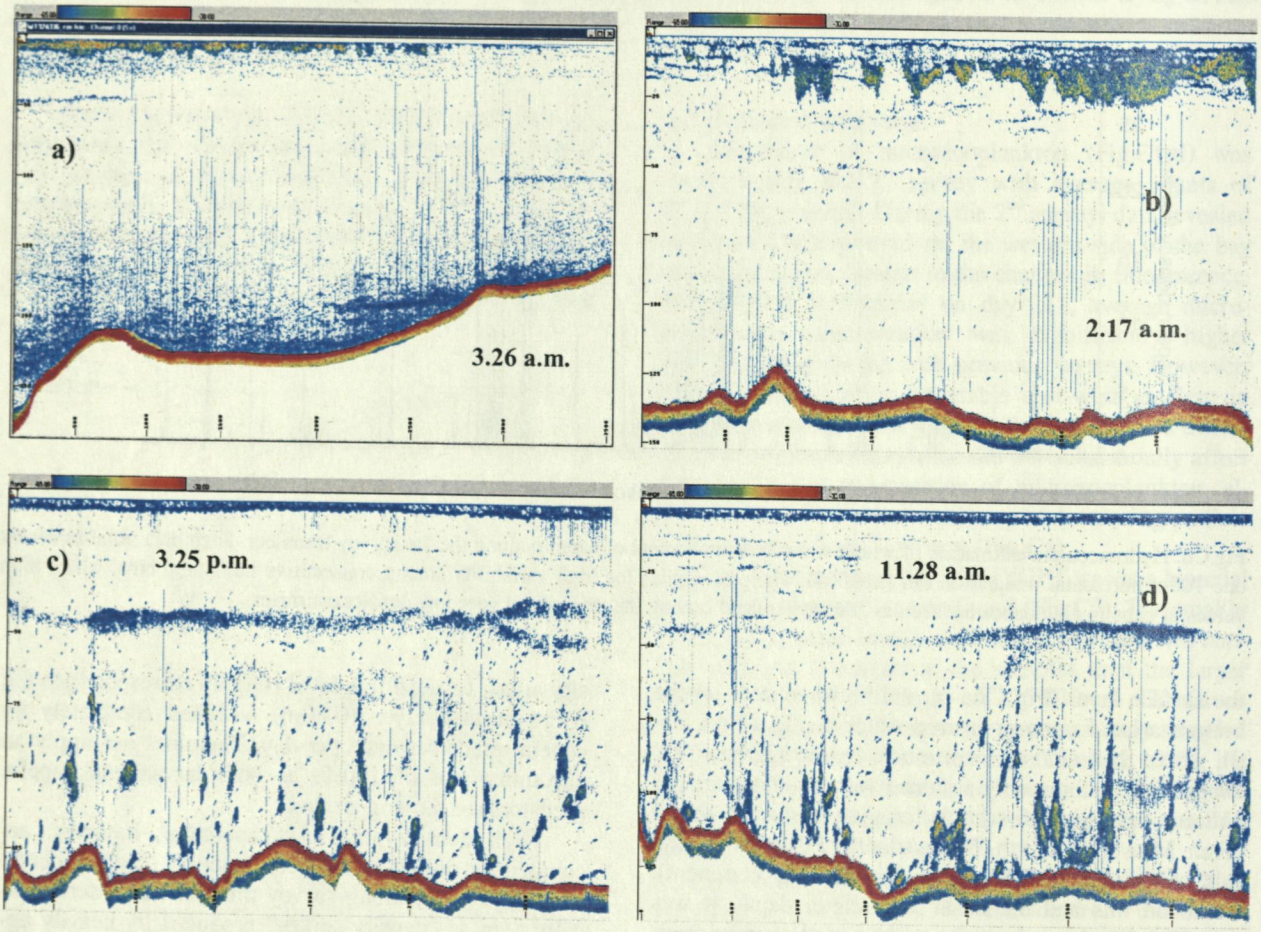

Fig.C8: Examples of acoustic capelin catches during IYGPT trawls: a), b) – dispersed green-yellowish aggregations are interpreted as capelin schools foraging in the surface layer at night. c), d) dense aggregations are observed in mid-water depths or on the bottom around noon. (horizontal scale: distance in metres, vertical scale: depth in metres). b-c are taken during the same 24h IYGPT trawl cycle, whereas a) is depicting the situation at a different site. The thick, red-green-blue band is the acoustic image of the bottom, while bluish areas are primarily backscatter noise. Time is Local Time (=GMT – 3.5 hours)

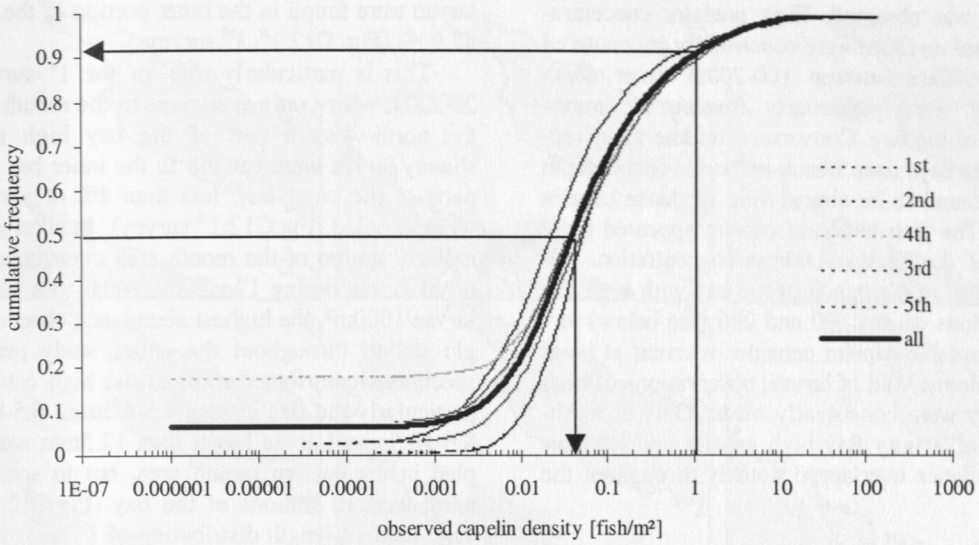

Fig.C9: Cumulative observed capelin density in July, 2000, along all five survey transects. Solid reference lines indicate that 50% of the whole water column content estimates were below 0.04 capelin/m². 91% of all observations were less than 1 capelin per m², which was defined as high density capelin area.

the overall variance in capelin distribution. To decide whether our hydroacoustic estimates were sufficient to disclose possible large scale spatial differences in capelin abundance, a semi-variogram was employed to estimate the variance of observations as a function of their spatial distance [km] (Fig.C10). The positive slope of the empirical variogram model indicates that, despite the existence of high amounts of small scale variability

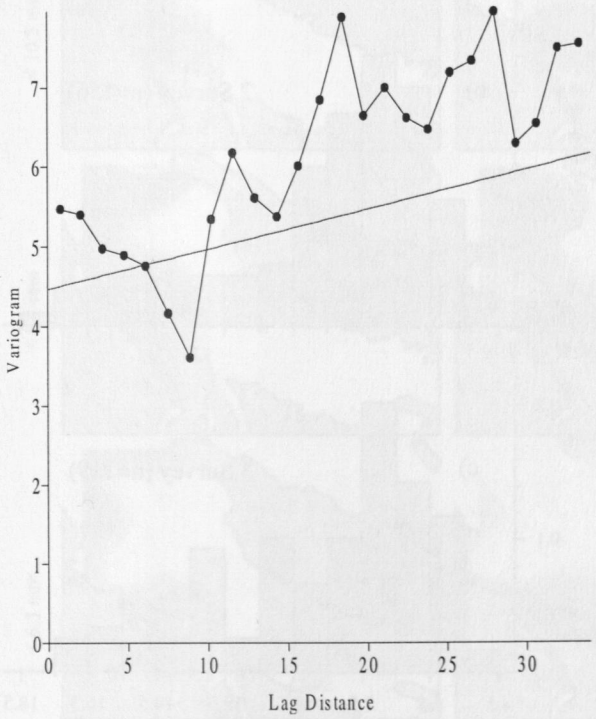

Fig.C10: Semi-variogram calculating the variability as a function of distance. The positive slope of the empirical variogram model indicates that despite the existence of high amounts of small scale variability (nugget effect), large scale features also exist.

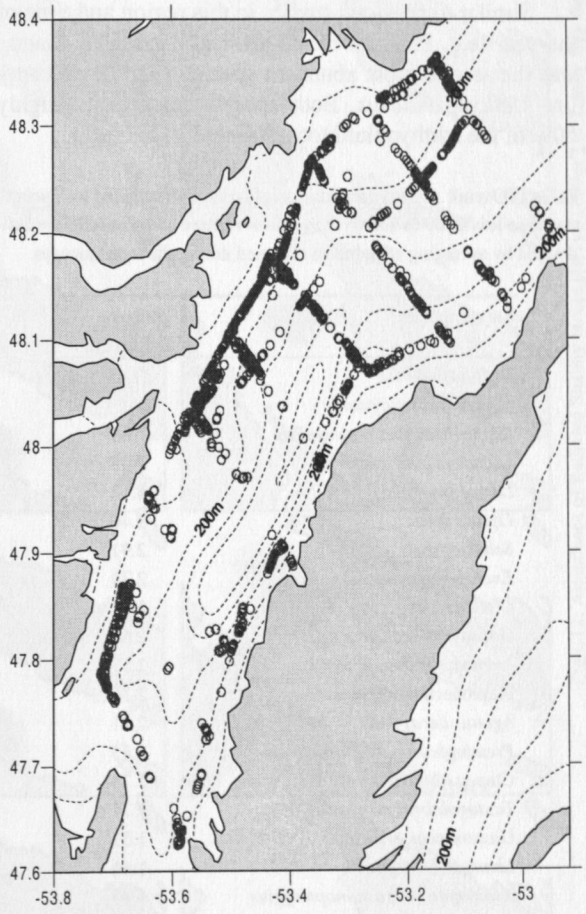

Fig.C11: Hydroacoustic observations of whole water column contents >1 capelin/m² during all 5 transects surveyed in July 2000 in Trinity Bay. Dense aggregations were found predominantly between 100-200m and in the north-western area of the bay.

(nugget effect), large scale features also exist.

Most remarkably, a close correspondence between capelin density and the bathymetrical structure of the

study area was observed. High predator concentrations (>1 fish/m² n=1306) were consistently encountered in shallower waters between 100-200m water depth (Fig.C11) and were particularly frequent at north-western areas of the bay. Conversely, middle inner sections, where the bays deep trench is located (max. depth 630m), were found to be almost void of dense capelin aggregations. The distribution of capelin appeared to be independent of the ichthyoplankton concentration. For example, stations at the mouth of the bay with high larval concentrations on day 200 and 206 (see below) virtually lacked notable capelin densities whereas at inner bay stations, almost void of larvae, observations of high capelin density were consistently made. Only at north-western parts of Trinity Bay high capelin and ichthyoplankton abundance overlapped notably throughout the study period.

Larval distribution

Similar to previous studies in this region and time of the year (e.g. Pepin *et al.* 2000), larval radiated shanny was the second most abundant species after larval capelin, *Mallotus villosus*. Both species comprised roughly 50% of the ichthyoplankton community (Table 1).

Table 1: Overall species composition of larval fish sampled by Tucker trawls in July 2000 in Trinity Bay. Mean relative abundance [%] was derived by averaging all samples obtained during the three surveys.

Larval species	Relative abundance
Mallotus villosus	27.81
Ulvaria subbifurcata	20.29
Hippoglossoides platessoides	7.86
Stichaeus punctatus	5.08
Lumpenus spec.	4.12
Liparis spec.	3.46
Sebastes spec.	2.91
Enchelyopus cimbrius	2.79
Cottidae	2.78
Gadus morhua	2.68
Ammodytes spec.	2.53
Pleuronectidae	2.26
Agonus decagonus	2.21
Pseudopleuronectes americanus	1.83
Clupea harengus	1.73
Tautogolabrus adspersus	1.71
Gasterosteus aculeatus	1.57
Limanda ferruginea	1.46
Aspidophoroides monopterygius	1.45
Cyclopterus lumpus	1.41
Unidentified larvae	2.04

During all three surveys, the spatial shanny distribution was found to be very heterogeneous ranging from zero to almost 50 larvae/1000m³. High concentrations over 10 larvae/1000m³ occurred in dense clusters limited to a few stations, whereas low concentrations were found over large portions of the bay. Very few shanny larvae were found in the inner portion of the bay (below 47.9 N) (Fig. C12:1st-3rd surveys).

This is particularly true for the 1st survey on day 200/201, where only at stations in the mouth area and in the north-western part of the bay high numbers of shanny larvae were caught. In the inner bay and central parts of the outer bay, less than 4% of all individuals were sampled (Fig.C12:1st survey). In contrast, the most easterly station of the mouth area contributed one third of all larvae during 1st survey, equal to a value of 48.2 larvae/1000m³, the highest abundance observed at a single station throughout the entire study period. Small specimens contributed most to the high concentrations, particularly the size classes 4.5-6.5mm, 6.5-8.5mm, and 8.5-10.5mm. Larvae larger than 12.5mm were not sampled in the eastern mouth area, but to some extent at north-western stations of the bay (Fig.C12:1st survey). The standard-length distribution of 1st survey larvae was highly skewed to the right (Fig.C13:a), with larvae be

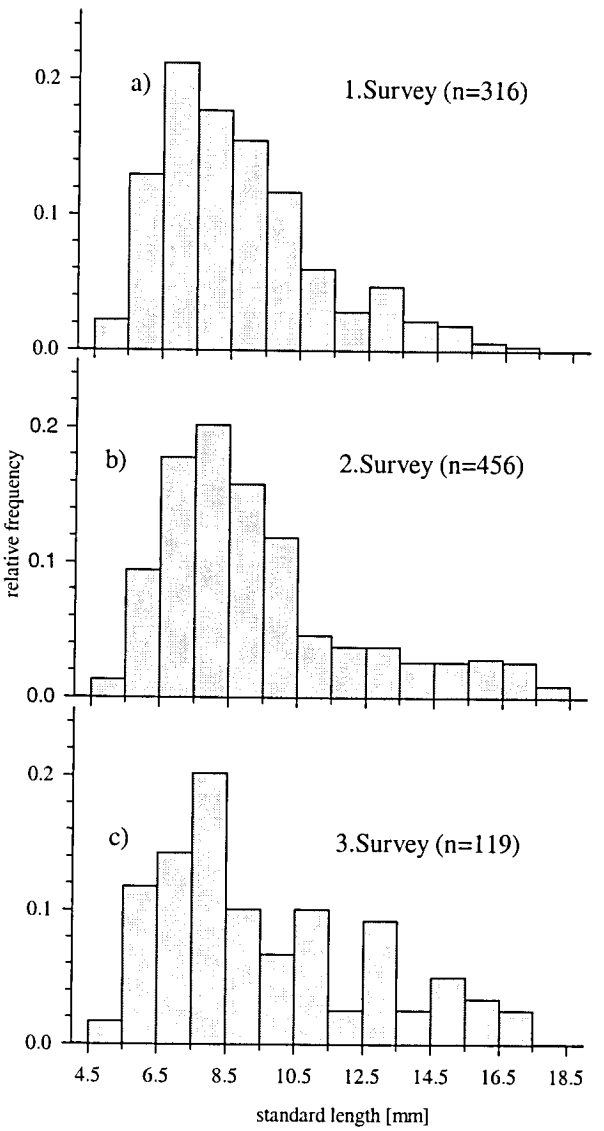

Fig.C13: Relative length-frequency distributions of larval shanny sampled during the three subsequent surveys in Trinity Bay, July 2000.

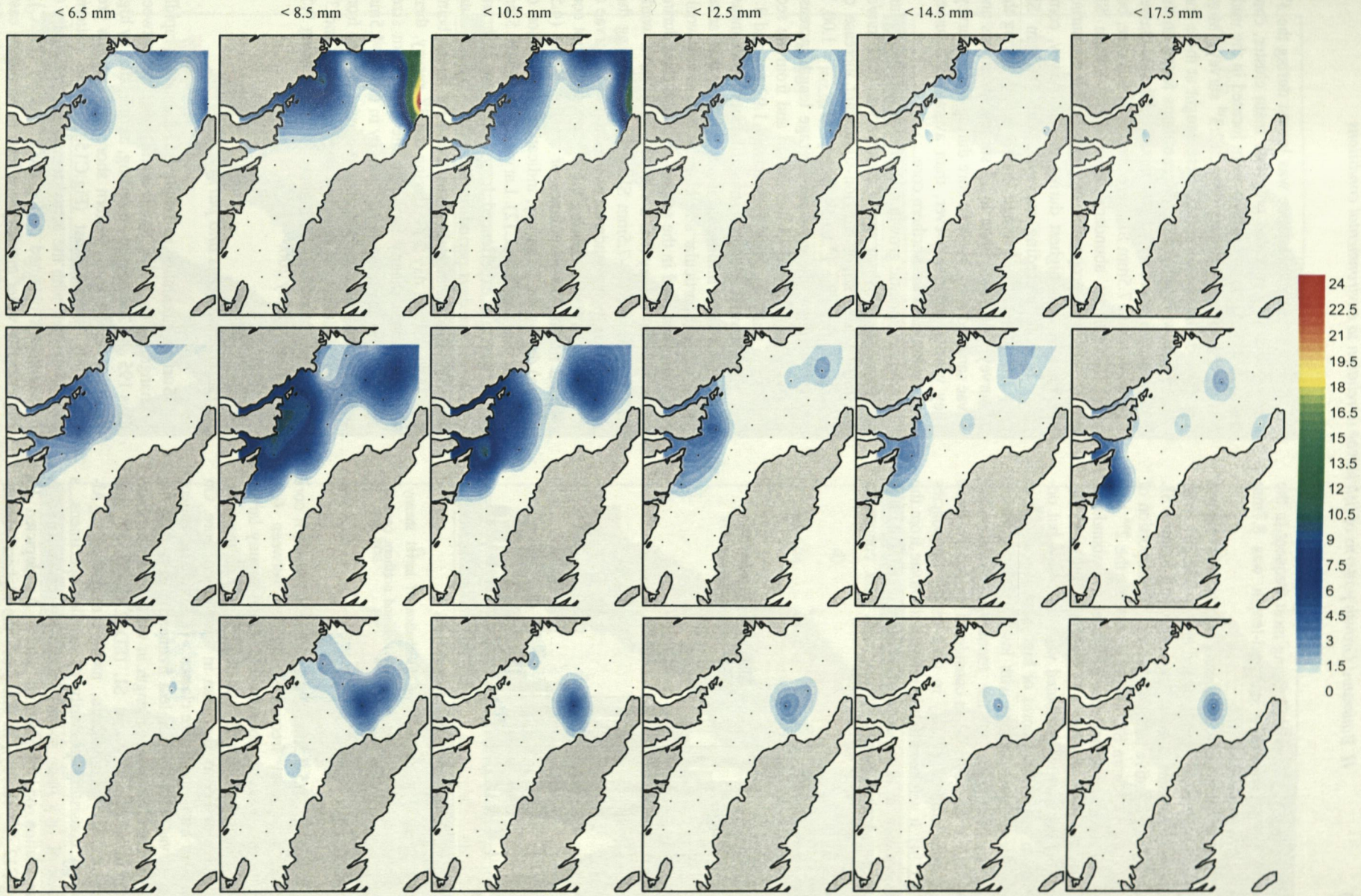

Fig.C12: Abundance of Radiated Shanny larvae [larvae/1000m³] in Trinity Bay during three surveys in July, 2000.

tween 6.5-7.5mm SL being most frequent in the sample (mode). Average standard-length was 8.7mm (SD=2.37mm, n=316).

Overall abundance of shanny larvae was highest during the second sampling period on day 206/207, with specimens measuring most frequently 7.5-8.5mm SL (Fig.C13:b). Relative to the 1st survey, the proportion of small larvae <7.5mm SL was lower during the 2nd survey, but there was an increase in the relative abundance of larger larvae measuring >13.5mm SL. However, larvae were not evenly distributed within the bay, but occurred in two distinct cores of high abundance: one at the western shore and one with lower peak concentrations located north, at the mouth of Trinity Bay (Fig.C12:2nd survey). When considered separately, these two cores differed notably in their length frequencies (Fig.C14). It was seen that in relation to larvae from the western core the distribution of northern core larvae was shifted to higher length classes, with peak concentra-

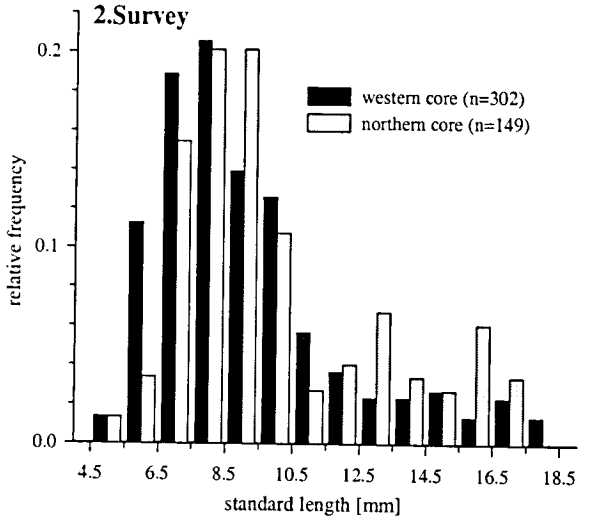

Fig.C14: Relative length-frequency distribution of larval shanny sampled during the 2nd survey in the western and northern core of high larval abundance

tions between 7.5-9.5mm SL. In contrast, western core larvae were most frequently sampled between 6.5-8.5mm SL. Relative abundance of small shanny larvae measuring 5.5-6.5mm SL was much higher on the western shore of Trinity Bay than in the northern core. On the other hand, in all size classes >11.5mm SL, western core larvae were sampled less frequently. Reflecting the size differences, average length in western and northern core larvae was 9.14mm SL (SD=2.82, n=302) and 9.91mm SL (SD=3.02mm, n=149) respectively. Although consisting primarily of smaller specimens, a patch of very large shanny larvae was encountered at one station on the western shore. As depicted by Fig.C12 (2nd survey), in this patch the highest concentrations of larvae between 14.5-17.5mm SL occurred throughout the study period.

Larval shanny abundance was lowest during the 3rd survey. Sampling revealed only one main cluster, consisting of three stations, which were located in the mid-east portion of the outer bay (Fig.C12:3rd survey). More than 50% of the shanny larvae were caught at these stations. There were no dense concentrations found on the bay's western shore or at the mouth. All size-classes from 4.5mm to 17.5mm SL were present in this core, but larvae were most abundant between 7.5-8.5mm SL (Fig.C13:c). The proportion of large larvae measuring >12.5mm SL was highest during the 3rd survey, compared to both preceding surveys. With 9.67mm SL (SD=3.1mm, n=119), average shanny length during the 3rd survey was greater than in 1st survey specimens and larvae sampled at the western core during the 2nd survey. They were smaller, however, than average 2nd survey larvae sampled at the northern core.

Average somatic growth rate of radiated shanny larvae, based on length at age of capture was 0.32 mm/d, and there was a slight but non-significant increase of growth rate from the 1st to 3rd surveys ($F_{s[2,339]} = 1.00$, $P > 0.5$). Therefore, the expected average length increase of larvae from the first to the second and from the second to the third sampling period was 1.92mm and 1.6 mm, respectively. Because standard length was measured to the nearest millimeter, it was assumed that larvae belonging to a particular size-class at one survey would have been measured in the second next size-class during the subsequent survey (i.e. a 4.5-5.5mm SL larva would have been in the 6.5-7.5mm SL size-class). Using this estimates, the high abundance of 6.5-8.5mm SL larvae at western shore stations during the 2nd survey did not correspond to the low abundance of smaller larvae (4.5-6.5mm) during the 1st survey, indicating a production of larvae in this area (Fig.C12). Larvae being 6.5-10.5mm SL on day 200 experienced losses between 21% and 67% in the six days period between the 1st and 2nd surveys. The highest mortality was found for larvae being 8.5-9.5mm SL on day 200. During the 3rd survey, there were also more shanny larvae in the 6.5-7.5mm size-class than larvae during the 2nd survey in the 4.5-5.5mm size-class. Losses in the larger size-classes ranged from 10% to 72% during the five days between the 2nd and 3rd surveys, but mortality was highest for larvae being 9.5-10.5mm SL on day 206.

Circulation patterns and particle drift

Surface circulation in Trinity Bay responded rapidly to changing wind fields. Stable south-westerlies between days 195 and 204 caused upwelling, as indicated by high densities on the bays western shore and currents predominantly to north-east (Fig.C15a). These patterns were consistent with the actual temperature and salinity measurements obtained during the 1st survey (Fig.C1). High density water masses were seen to propagate eastward covering about two thirds of the bay on day 203 (Fig.C15c), the day prior to the sudden relaxation of offshore winds. At the eastern shore, the predicted cur

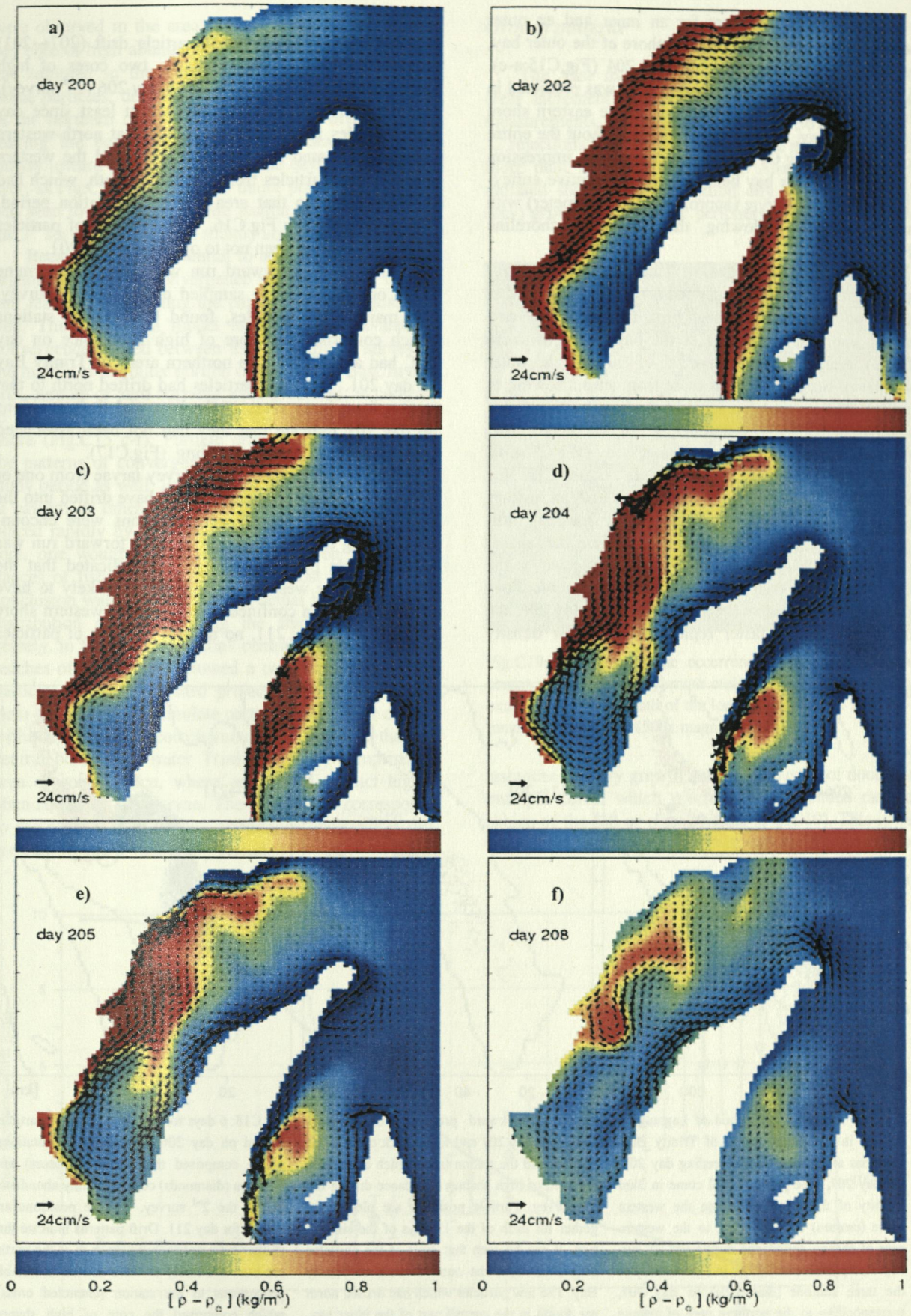

Fig.C15: density fields modeled by the nonlinear CANDIE model (expressed as density anomaly with respect to initial stratification)

rents were different for an inner and an outer portion of the bay. At the eastern shore of the outer bay, currents flowed outwards until day 204 (Fig.C15:a-c). After day 204, an opposite, inward flow was predicted in this area (Fig.C15:d-f). In contrast, at the eastern shore of the inner bay, flow was inwards throughout the entire study period (Fig.C15b-f). This created the impression of the whole inner bay behaving like a retentive anticyclonic (clockwise) gyre (approx. 40km in diameter) with strong currents following the U-shaped shoreline (Fig.C15a-f).

The modeled changes of surface circulation responding to the diminishing winds on day 204 seemed to consist of three major features. First, the appearance of a narrow and fast coastal jet at the bays western shore (Fig.C15c-e). Second, a reversal of flow at the outer portions of the bays eastern shore from an outflowing to and inflowing current (Fig.C15d-f). Finally, there is a steadily increasing proportion of lighter water that overlayed the denser upwelled water body (Fig.C15d-f). This is consistent with the CTD-data obtained on day 206, indicating no signs of upwelling and an inward movement of warmer and fresher water masses, most pronounced at north-western stations, where the coastal jet was developing (Fig.C1, 2nd survey). However, at the inner bay, where cold and high salinity waters were observed to still dominate the surface layer on day 206, the model indicated a faster replacement by low density waters.

Backward projections of particle drift (207←201) supported the impression that the two cores of high shanny abundance, encountered on day 206 (2nd survey), had been environmentally separated at least since day 201. Particles found back on day 207 at north-western stations originated from the inner bay and the western shore, unlike particles from the bays mouth, which had stayed roughly in that area for the simulation period. This is depicted by Fig.C16, where origins of particles from both sites are seen not to overlap on day 201.

An 11 day backward run was used to determine likely origins of larvae sampled during the 3rd survey. The majority of particles, found back at the stations which comprised the core of high abundance on day 211, had already been in northern areas of Trinity Bay on day 201. Very few particles had drifted north to that station from inner areas of the bay, and their positions on day 201 indicate that they had not been associated with the area of coastal upwelling. (Fig.C17).

To determine whether 2nd survey larvae from one or both cores of high abundance could have drifted into the area, where high shanny concentrations were encountered during the 3rd survey, a six days forward run was used. Particle positions on day 211 indicated that the majority of the western core larvae was likely to have drifted north in a confined area along the western shore (Fig.C18). On day 211, no notable portions of particles

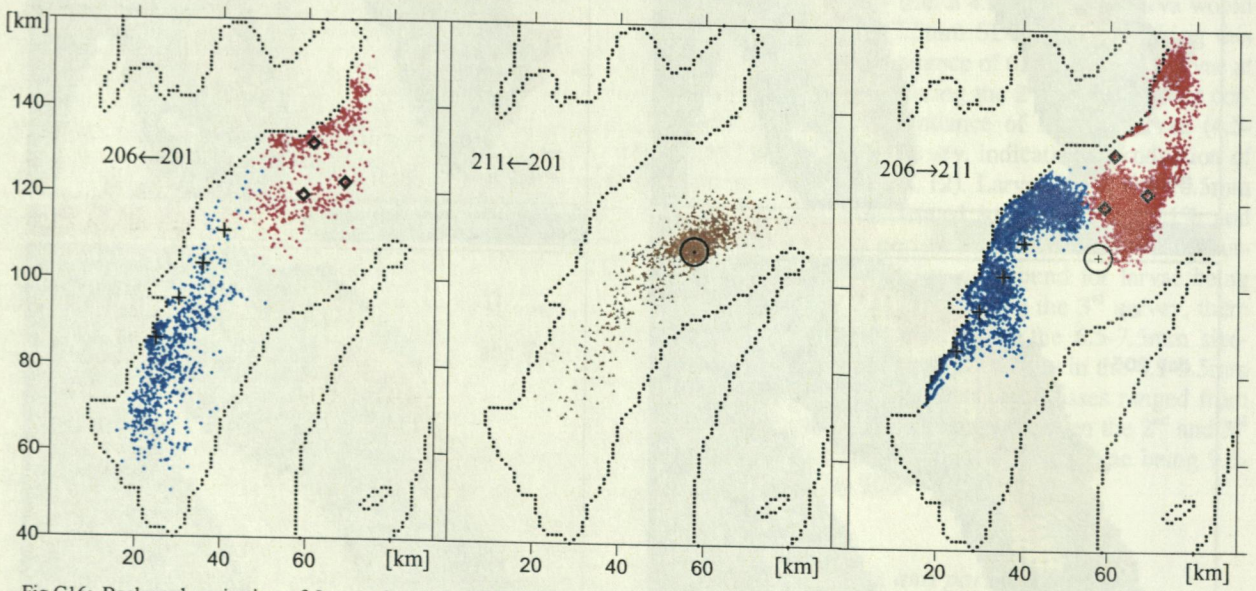

Fig.C16: Backward projection of Lagrangian drifters in the model space of Trinity Bay. Positions are shown for the seeding day 201. On day 207, blue particles will come in 3km vicinity of the four stations on the western shore (crosses) corresponding to the western core of shanny abundance during the 2nd survey. Red particles will come in 3km vicinity of the three stations (diamonds) on day 207, corresponding to the northern core of shanny abundance. Note that the areas of particle origins do not overlap.

Fig.C17: Backward projection of particles seeded on day 201 and found back on day 212 3km around the station (star) which comprised the core of high shanny abundance during the 3rd survey. Particle positions are plotted together for each of the 11 days of the simulation. It can be seen that most of the particles originated from the outer reaches of Trinity Bay. The few particles which had drifted north are found in the central part of the inner bay, which may indicate that they were not associated with the upwelled water from the western shore.

Fig.C18: 6 days forward projection of particles seeded on day 206 one km around stations, which comprised the western (crosses) and northern (diamonds) core of shanny abundance during the 2nd survey. Particle positions are shown for day 211. Drift patterns indicate that neither larvae of the western, nor of the northern core are likely to have drifted in notable proportions to the station (encircled cross), which comprised the core of high shanny abundance during the 3rd survey.

were observed in the area corresponding to the 3rd survey core of high abundance. The same was true for larvae sampled in the northern core during 2nd survey. Some particles, derived from the most westerly station of the northern core, were seen to have drifted north, leaving the bay, whereas other particles had moved slowly toward the central part of the bays mouth. However, as Fig.C18 illustrates, no major portion of particles was seen to come close to the station, which comprised the 3rd survey core of high shanny abundance.

Because of their potential to accumulate planktonic organisms, areas of convergence are particularly important features determining the patterns of larval distribution. The circulation model indicated that an area of convergence existed between the 2nd to the 3rd survey in the middle of the outer portion of the Trinity Bay. In this area, minute or zero currents were predicted, in contrast to the strong currents on the bays western or eastern shore (Fig.C15 c-f). Particle drift projections reflected the patterns of convergence and divergence during the study period as well. For example, most particles seeded at eastern or inner bay stations were bound to be displaced rapidly by the predicted strong currents. Therefore, one would expect very low or even zero abundances of fish larvae at those innermost stations. This conclusion was supported by the actual ichthyoplankton distribution observed during the study period. Conversely, in forward projections central parts of the outer reaches of Trinity Bay showed a consistent retention of particles. In the backward projections this area had a clear tendency to accumulate particles from other origins within the bay. This corroborated the impression that the central portions of outer Trinity Bay did comprise an area of convergence, where one would predict higher abundances of fish larvae. The conclusion corresponds to the core of high shanny abundance observed in this area during the 3rd sampling period.

Growth patterns

The vast majority of otoliths revealed relatively clear increments resulting in sufficiently reproducible measurements. Re-readings (119 out of 361) led to only 12 rejections in cases where increment numbers differed more than 10% between counts. Also, the otoliths of radiated shanny did not exhibit any secondary (accessory) growth zones in the periphery. However, in some instances primary growth centres consisted of double or multiple cores, which precluded the intended random choice of the left or right sagittae (Fig.C19). This is because increment widths had to be measured consistently

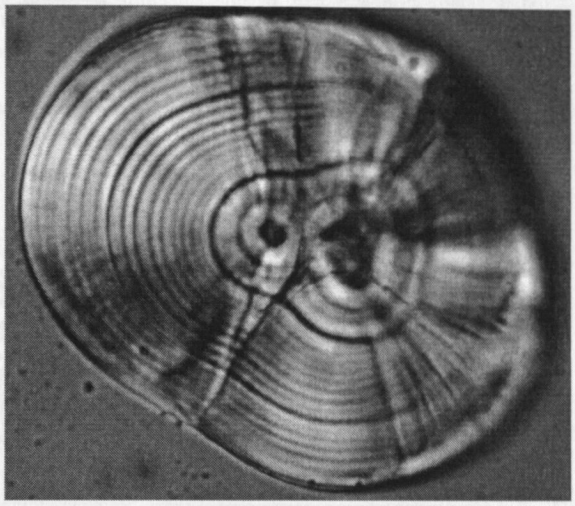

Fig.C19: Example for the occurrence of a double growth centre in *Ulvaria subbifurcata* otoliths. Because there is no exact midpoint, the path of the longest axis cannot be determined with certainty (500x magnification)

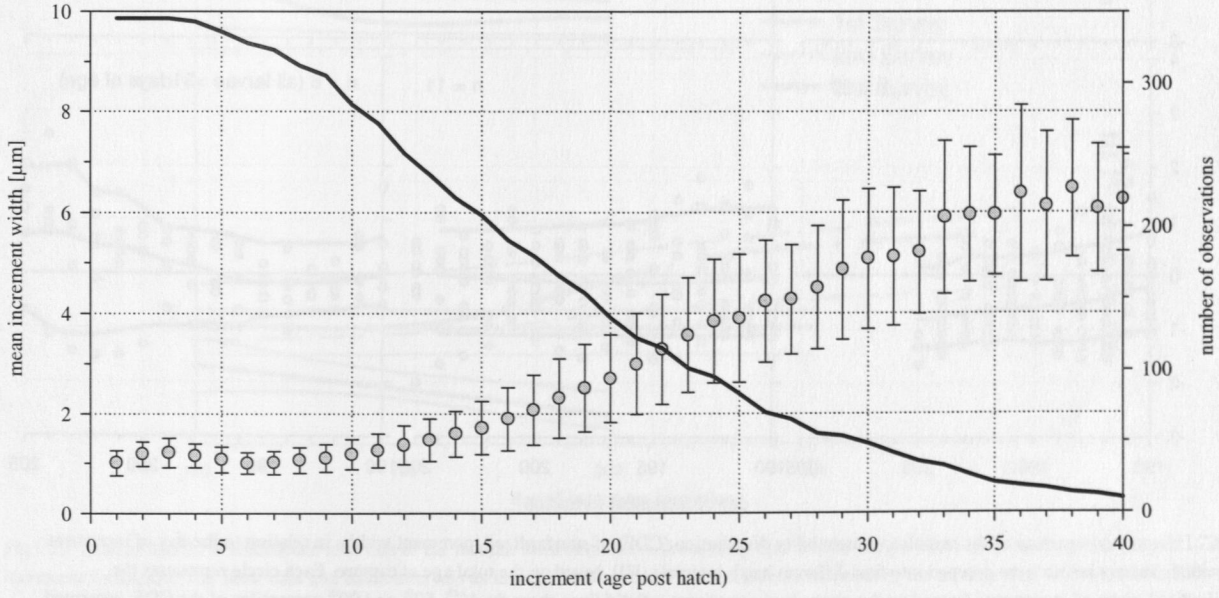

Fig.C20: Mean, standard deviation and observation numbers of increment widths from sagittal otoliths of Radiated Shanny larvae. Increasing means and variances are evident after approximately 10 days of age. There is a significant ($P < 0.001$) decrease in increment widths after day three until day six post hatch.

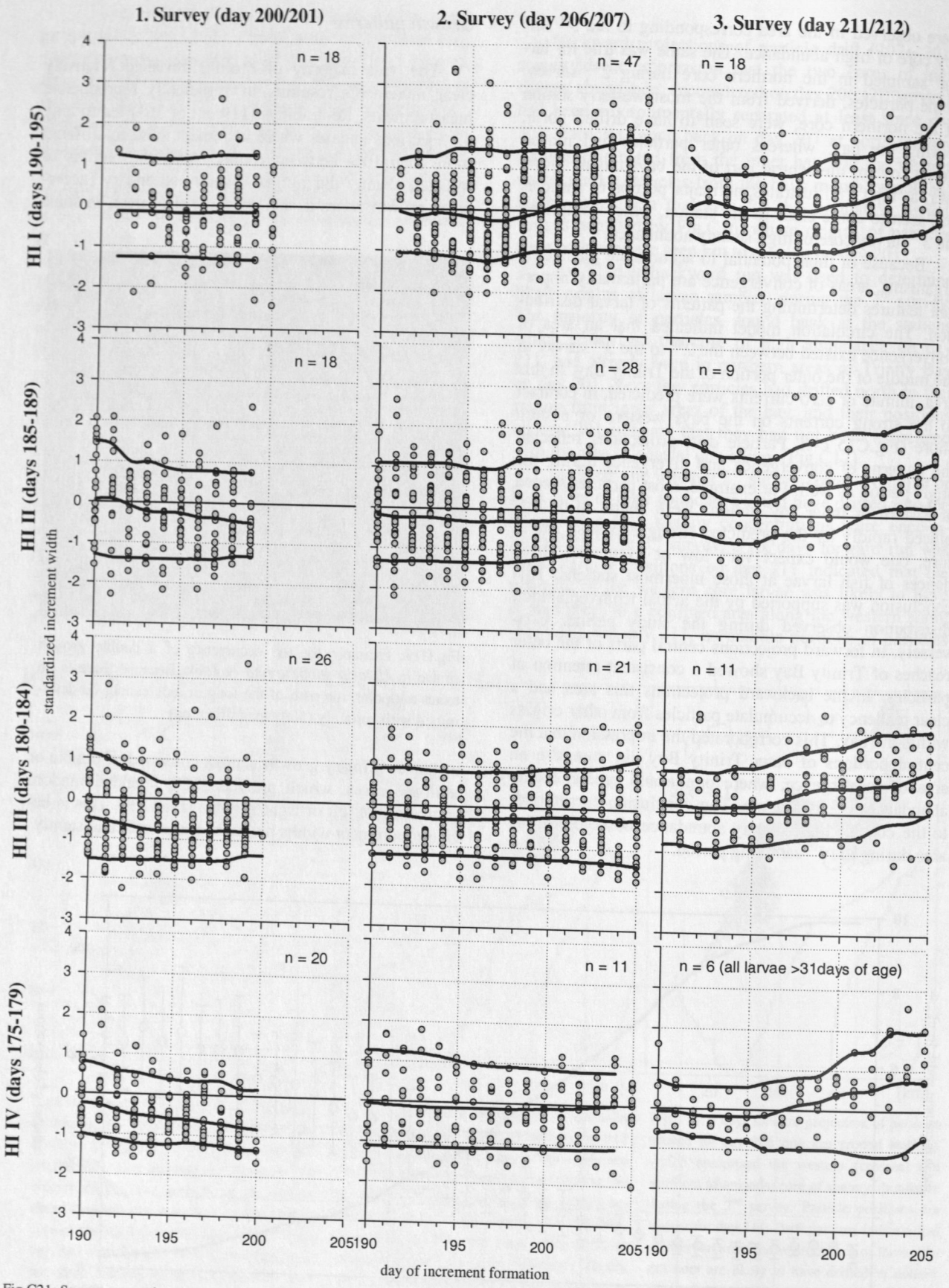

Fig.C21: Survey comparison of the cumulative probability distribution (CDF) of standardized increment widths in relation to the day of increment formation. Shanny larvae were grouped into four different hatch intervals (HI), based on the total age at capture. Each circle represents the standardized width of increment i formed on the given day in specimen j. Solid lines show the 10th, 50th, and 90th percentiles of the CDF, estimated using a local non-parametric density estimator with varying bandwidths. N-values in each plot refer to number of specimens used to build the CDF of increment widths. Note that due to different days of hatch and sampling, the number of points per day may vary within a plot.

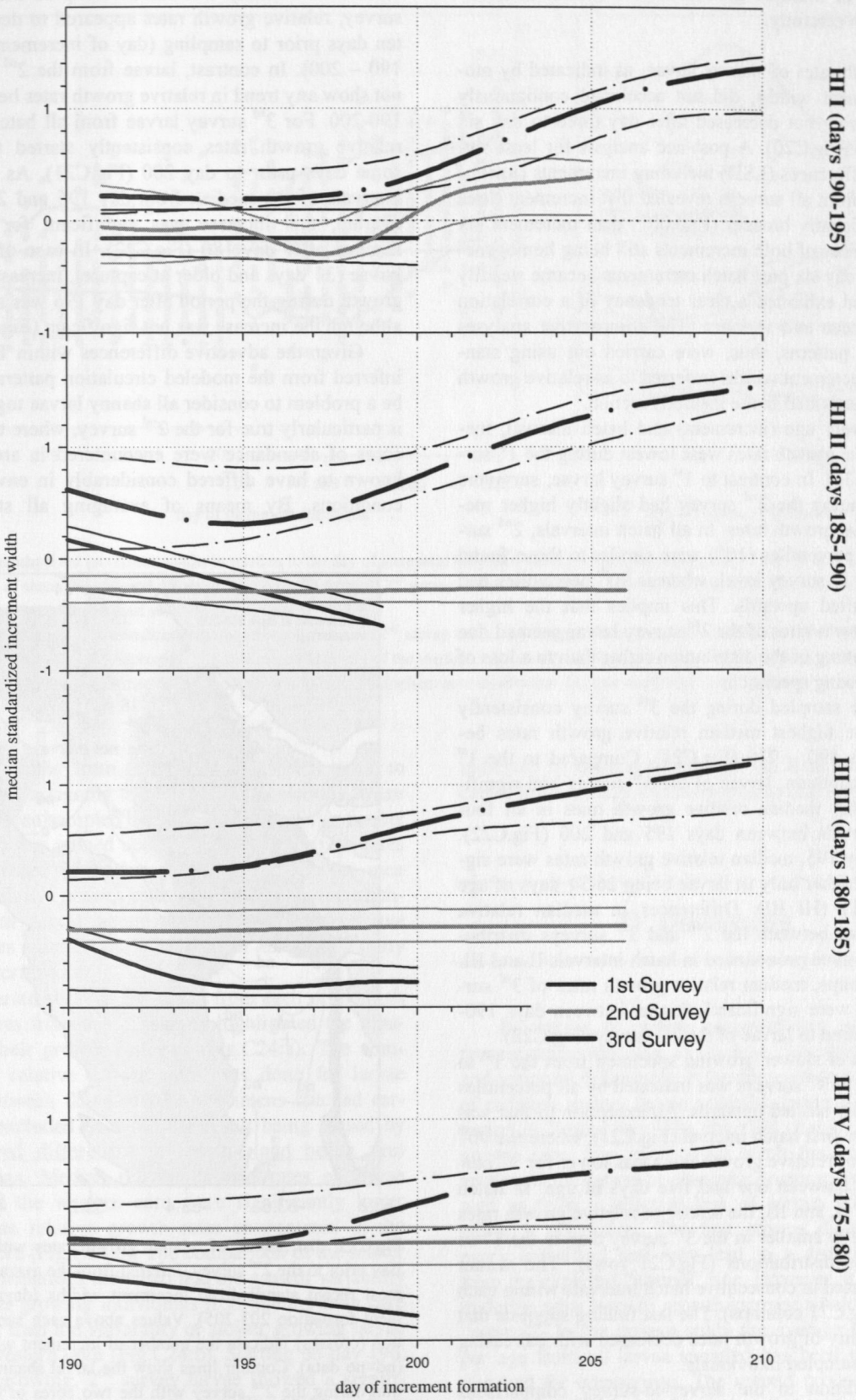

Fig.C22: Median and 95% confidence intervals of the median from cumulative probability distributions of growth rates in relation to the day of increment formation. The same data and hatch intervals as in Fig.C21 were used. The confidence intervals of the median were estimated from 500 randomizations of the data. Median standardized increment widths differ significantly if confidence intervals do not overlap.

along the longest otolith axis, which in the case of double or multiple growth centres cannot be determined with certainty.

Growth rates of shanny larvae, as indicated by otolith increment widths, did not accelerate continuously from hatching but decreased after day three to day six post hatch (Fig.C20). A post-hoc analysis for least significant differences (LSD) including increments (µm) of specimen from all surveys revealed that increment three was significantly broader ($P<0.001$) than increment six with variances of both increments still being homogeneous. After day six post hatch increments became steadily broader and exhibited a clear tendency of a correlation between mean and variance. The comparative analyses of growth patterns, thus, were carried out using standardized increment widths (referred to as relative growth rates), as described in the methods section.

For every age (increment) and hatch interval, median relative growth rates were lowest during the 1st survey (Fig.C21). In contrast to 1st survey larvae, survivors sampled during the 2nd survey had slightly higher median relative growth rates. In all hatch intervals, 2nd survey lower percentiles (10th) were similar to those found during the 1st survey level, whereas 90th percentiles had visibly shifted upwards. This implies that the higher relative growth rates of the 2nd survey larvae seemed due to a broadening of the distribution rather than to a loss of slower growing specimens.

Larvae sampled during the 3rd survey consistently showed the highest median relative growth rates between days 190 – 210 (Fig.C21). Compared to the 1st survey distribution, larvae of the 3rd survey had significantly higher median relative growth rates in all four hatch intervals between days 195 and 200 (Fig.C22). Prior to day 195, median relative growth rates were significantly higher only in larvae being 26-31 days of age on day 211 (HI III). Differences in median relative growth rates between the 2nd and 3rd surveys distributions were most pronounced in hatch intervals II and III. In both groups, median relative growth rates of 3rd survey larvae were significantly higher between days 190-205, compared to larvae of the 2nd survey (Fig.C22).

A loss of slower growing specimen from the 1st to 3rd and 2nd to 3rd surveys was indicated by all percentiles being visibly shifted upwards. An exception to that was found in the first hatch interval (Fig.C21), where the 90th percentile of relative growth rates was lower for 3rd survey larvae between one and five days of age. In hatch intervals I, II, and III, the scatter of relative growth rates was generally smaller in the 3rd survey than in the 1st or 2nd surveys distributions (Fig.C21 rows). The scatter also decreased in consecutive hatch intervals within each survey (Fig.C21 columns). The last finding suggests that the variability of growth rates decreased with increasing age of the sampled individuals.

In addition to the survey-to-survey comparisons among larvae, Fig.C21 also provides information about the trend, the distributions of relative growth rates exhibited for individuals from each hatch interval (i.e. based on a comparison of standardized increment widths within individuals). For larvae sampled during the 1st survey, relative growth rates appeared to decrease over ten days prior to sampling (day of increment formation 190 – 200). In contrast, larvae from the 2nd survey did not show any trend in relative growth rates between days 190-200. For 3rd survey larvae from all hatch intervals, relative growth rates consistently started to increase some days prior to day 200 (Fig.C21). As confidence intervals of the median from day 195 and 211 did not overlap, this increase was significant for all larvae hatched after day 180 (Fig.C22). In case of the oldest larvae (31 days and older at capture), increasing relative growth during the period after day 196 was still evident although the increase was not significant (Fig.C22).

Given the advective differences within Trinity Bay, inferred from the modeled circulation patterns, it might be a problem to consider all shanny larvae together. This is particularly true for the 2nd survey, where two distinct cores of abundance were encountered in areas already known to have differed considerably in environmental conditions. By means of averaging all standardized

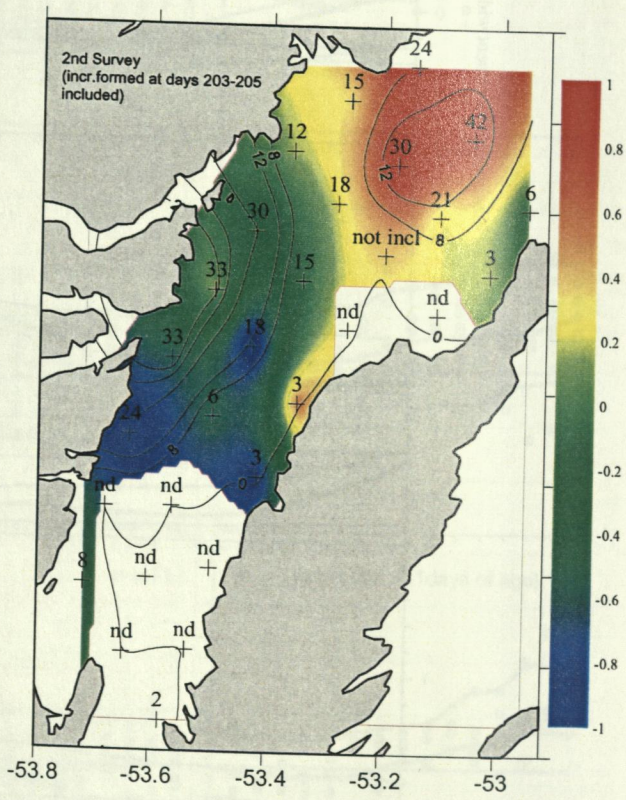

Fig.C23: distribution of relative growth rates within Trinity Bay prior to the 2nd survey, inferred from the average of the 3 most recent standardized increment widths (days of increment formation 203-205). Values above each sampling station (crosses) indicate the number of increment widths used. (nd=no data). Contour lines show the larval shanny distribution during the 2nd survey with the two cores of high abundance. High growth rates are seen to coincide with the northern core, lower growth rates with the western core of abundance. Kridging was used for the interpolation between data

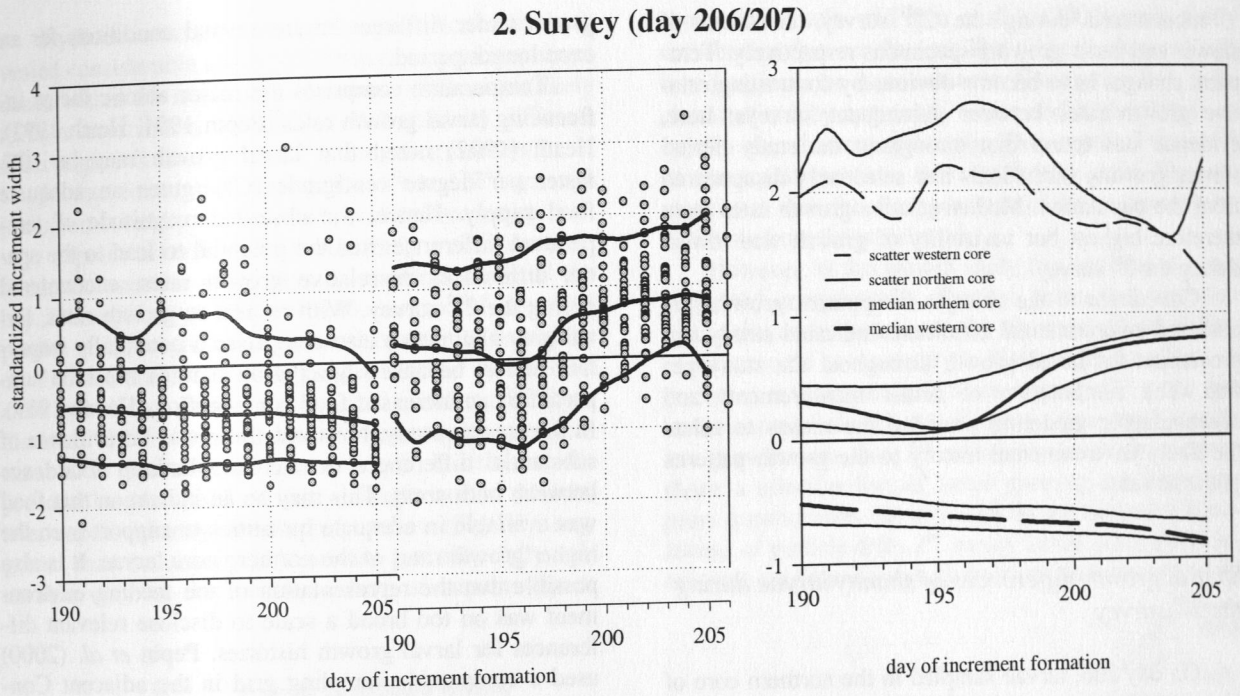

Fig.C24: a) Standardized increment widths in relation to the day of increment formation for larvae sampled during the 2nd survey in the western and northern core of shanny abundance. Otolith data were used from all 2nd survey individuals between 5-26 days of age. Solid lines show the 10th, 50th, and 90th percentiles of the CDF of standardized increment widths.
b) Comparison of median standardized increments widths between 2nd survey cores, and comparison of the scatter (difference 90th – 10th percentiles of the CDF). Thin solid lines represent 95% confidence intervals of the median, estimated from 500 randomizations of the data. Median standardized increment widths are assumed to be significantly higher in the northern core distribution, because confidence intervals do not overlap.

increment widths from three days (203-205) prior to sampling and assigning these averages to stations where larvae had been sampled on day 206 (2nd survey), further information was gained about how relative growth rates were distributed in the bay. In Fig.C23 it can be seen that high relative growth rates coincided with the northern core of larval abundance whereas low relative growth rates matched the other core of larvae on Trinity Bay's western shore.

A separate analysis for larvae from each of the high density cores from the 2nd survey highlighted the separation in their growth histories (Fig.C24:a). The comparison of relative growth rates was done for larvae hatched between day 180-200: specimens hatched earlier were excluded to avoid the result being biased by the observed differences in length- (and hence age) compositions. Median relative growth rates of larvae sampled at the western core were significantly lower than median relative growth rates encountered in the northern core (Fig.C24:b). The comparison of the scatter of both distributions indicated that the growth variability of the faster growing individuals from the northern core was higher than the variability of slower growing larvae from the western core (Fig.C24:b). Starting on day 196, the faster growing, 2nd survey larvae showed a significant increase of relative growth rates (Fig.C24:b), which may imply a somehow improved environment for growth. Conversely, larvae sampled at the western core of abundance exhibited steadily decreasing growth rates, indicated by median relative growth rates being significantly lower on day 205 compared to day 190.

D. Discussion

By means of otolith microstructure analysis, the present study was able to disclose considerable spatial and temporal differences in the apparent growth patterns of radiated shanny larvae sampled during a two weeks period in Trinity Bay. The observed changes in relative growth rates may in principle result from a direct response of the larvae to changing growing conditions as well as from a selective loss of certain growth types within a population. The first process directly affects every individual and may lead to a growth differing from the expected "normal" rate. However, it is difficult to define what level of growth increase would have been "normal". In the present study the average growth rate per age from all larvae sampled has been used as the standard for comparison. The second process does not change an individuals growth, but may select for certain growth rates within a cohort of larvae during development. Regional differences have been shown by the fact that a western and a northern core of larval abundance,

encountered during the 2nd survey, consisted of slower and faster growing specimens respectively. Temporal changes have become obvious by contrasting relative growth rates between subsequent surveys; here, evidence was found that throughout the study period slower growing individuals had selectively disappeared from the population. Median relative growth rates were therefore highest but variability of growth was lowest during the 3rd survey.

Concurrent to the changes in apparent growth, the observed environmental conditions indicated steady improvement for larval growth throughout the study period. The combination of actual measurements and oceanographic modeling provided the means to relate the likely environmental history to the growth patterns of the larvae.

Spatial growth differences of shanny larvae during the 2nd survey

On day 206, larvae sampled in the northern core of high abundance possessed significantly higher relative growth rates than larvae occurring at the western shore of Trinity Bay. Whether environmental factors can be held responsible for the observed differences depends on the time the larvae had developed in spatially separated areas and on the degree to which these areas had differed in environmental characteristics. Because it was shown that growth rates reflect the influence of a past rather than the recent environment (Pepin *et al.* 2001), it is critical to describe the conditions encountered by the larvae prior to the 2nd survey. Backward projections of particle drift corroborated the separate development of both groups of larvae between the 1st and 2nd surveys. The drift simulations suggested that larvae sampled in the northern core had already been present in the mouth area on day 201, unlike larvae from western shore stations, which originated from inner or western areas of the bay. Measurements obtained during the 1st and 2nd surveys revealed that these two regions had differed substantially in several environmental factors. Offshore winds induced upwelling of cold water on the bays western shore, where average temperatures in the surface layer were more than 2°C lower than in northern areas. The circulation model indicated that these features had persisted at least until day 204, when offshore winds relaxed. Even though upwelling had vanished by time of the 2nd survey, cold water masses were seen to cover the entire inner bay, partly including the western shore stations of high larval abundance. It is now concluded, thus, that larvae sampled on the western shore had been associated with the cold, upwelled water for at least six days prior to sampling on day 206. In contrast, larvae sampled in the northern core are likely to have developed in the mouth area of the bay, which was not seen affected by coastal upwelling. No data are available prior to the 1st survey, however, the circulation model indicated that upwelling features had already existed before day 200. Therefore, it is possible that larvae had grown under different environmental conditions for an even longer period.

Temperature comprises the major abiotic factor influencing larval growth rates (Pepin 1991, Heath 1992). Heath (1992) noted that larval growth may be 10% faster per degree centigrade (C°), given an adequate food supply. Hence, the observed magnitude of temperature differences had the potential to lead to the spatial differences in relative growth rates, encountered during the 2nd survey. With respect to growth rates, larval prey abundance also comprises a potentially important factor, because higher growth rates must be supported by an increased food consumption (Houde 1989). In the present study, however, there was no evidence of substantial differences in microzooplankton abundance between both areas. This may be an indication that food was available in adequate quantities to support even the higher growth rates of the northern core larvae. It is also possible that the representation of the feeding environment was on too broad a scale to disclose relevant differences for larval growth histories. Pepin *et al.* (2000) used a comparable sampling grid in the adjacent Conception Bay and found no strong relationship between prey abundance and larval growth rates. The authors suggested that events at the very small scale of the individual have yet to be adequately described but may be more important in determining an individual's growth in relation to prey availability.

Due to intrinsic differences in the growth potential (Parma and Deriso 1990), it is likely that larval fish will exhibit not a single but a continuous spectrum of individual responses to improving environmental conditions. Initially, thus, one would predict not only higher average growth rates but also a higher growth variability, resulting from increasing ambient temperatures. In the case of the 2nd survey cores of abundance, growth variability was indeed higher in the northern core, where shanny larvae had experienced more favorable growth conditions. By contrasting relative growth rates between cores, it was also observed that the lower percentiles of the northern core distribution were shifted up in relation to the western core distribution. However, lower percentiles of the western core are comparable to those encountered during the 1st survey (see figures C21 and C24:a). This indicates that a loss of slower growing individuals between the 1st and 2nd surveys occurred predominantly in the northern core of shanny abundance. Previously, it has been shown that larval mortality rates are positively correlated with ambient temperature (Pepin 1991), partly because of a decreased starvation potential for larvae under higher temperature regimes (Clemmesen *et al.* 1997). It may be reasonable to assume that a higher overall mortality rates will also cause a faster selective loss of less viable individuals. Given the environmental history of the northern core larvae, it is suggested that improved growing conditions led to more variable growth rates and a faster selective loss, and thus facilitated the ability to detect patterns of selective mortality in this group of shanny larvae.

Hydroacoustic integration of capelin backscatter revealed considerable spatial differences in predator abundance within the study area. Are these differences likely to have contributed to the observed spatially different relative growth rates of the 2nd survey distributions?

It was found that during the 1st and 2nd surveys (complemented by the first dedicated hydroacoustic survey) capelin schools were consistently more abundant along the western shore than in northern areas of the bay. Between days 200 and 206 one would therefore predict a higher predation pressure by capelin for larvae on the western shore, compared to larvae in northern areas of the bay. From an individual-based model Paradis *et al.* (1996) concluded that larvae may be most vulnerable to predators if larval length is 10% of the predator length. Based on this, a comparison of the relative capelin/shanny length-frequencies (Fig.D1) suggested that the shanny larvae were probably fully vulnerable only to the smaller cohort of capelin (mode length 90-95mm TL). This cohort, however, was far less abundant in the IYGPT samples than larger juvenile capelin (mode length 125-130mm TL). Because of the dome-shaped relationship between larval size and vulnerability to predation, Cowan *et al.* (1996) proposed that larvae should grow through a predator-specific "window" of vulnerability. This implies that prior to the point, where the majority of larvae has reached a threshold length, larvae of a bigger size at age (i.e. of higher growth rates) are more vulnerable to predation. During the study period, the majority of shanny larvae had not yet reached a threshold length corresponding to 10% of the mode-length of the bigger capelin cohort. While still growing into the vulnerability "window", faster growing shanny larvae may thus have been selectively removed by foraging capelin. Therefore, due to the surmised differences in predation pressure, a selective loss of faster growing specimens appears possible on the bays western shore. The results of Pepin *et al.*'s (2000) study partly corroborate this conclusion. The authors observed two broad regions, the inner and outer Conception Bay, to be characterized by apparently lower and higher levels of capelin abundance respectively. They reported that drift of shanny larvae from the inner to the outer bay was associated with the disappearance of faster growing individuals from the population.

However, in the present study this conclusion is not supported unequivocally. First, to prove that predation by capelin added notably to the observed growth differences it would be necessary to disentangle the effects of predation and temperature. More importantly, given that larvae sampled during the 1st survey possessed equally low growth rates than 2nd survey larvae on the western shore, a selective loss of faster growing specimens appears questionable. As indicated by the backward simulations of particle drift, 2nd survey larvae from the western core originated most likely from western and inner areas of Trinity Bay. However, no larvae had been sampled in this area during the 1st survey precluding an appropriate comparison of the relative growth rate distributions between surveys. Like in Pepin *et al.*'s (2000) study in Conception Bay, only this would have provided true means to substantiate the impression of a selective loss of faster growing individuals.

The CTD data revealed a very close correspondence of water temperature and salinity throughout the study period. Cold water appearing on the western shore (1st survey) or at the inner bay (2nd survey) was always of a higher salinity, whereas warmer water masses were consistently less saline. Therefore, larvae sampled in the western and northern core during the 2nd survey had not only experienced different water temperatures but had also been associated with different salinities. From the physiological point of view, a higher ambient salinity should entail a higher osmotic stress for larval fish

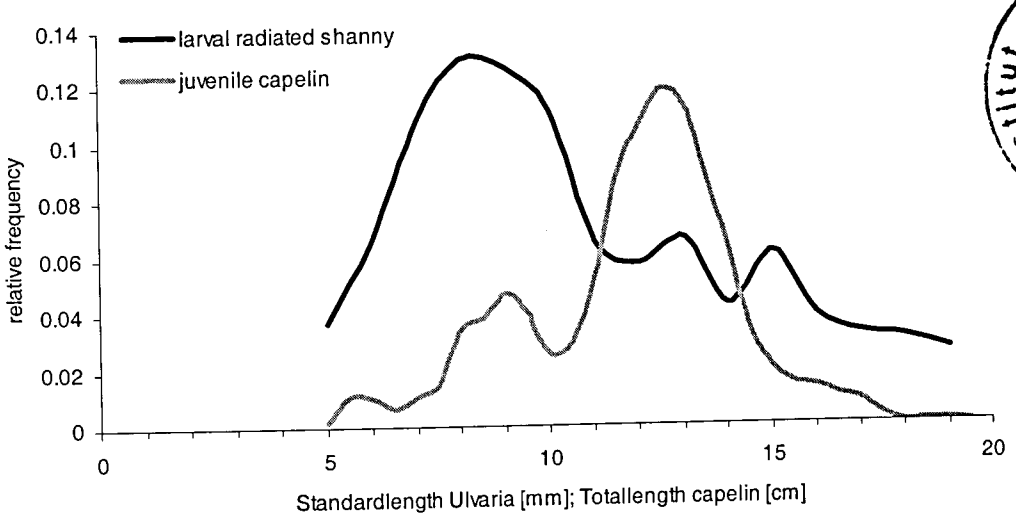

Fig.D1: Size-overlap of juvenile capelin and larval Radiated Shanny. If larvae are most vulnerable to predators at 10% of the predator's length (Paradis et al. 1996), then most shanny larvae had not yet grown into the preferred size-range of the present capelin schools.

(Helfman *et al.* 1997). Instead on growth, larvae in higher salinity waters may thus have to spend a higher proportion of metabolic energy to maintain their internal osmotic balance. Studies, primarily with focus on aquaculture, have corroborated this general dependence (e.g. Henne *et al.* 2001, Estudillo *et al.* 2000, Huang *et al.* 2000). However, the range of salinities tested in such studies does not correspond to the differences normally experienced by larvae in the open sea. In laboratory experiments, Alderdice and Velsen (1971) investigated the combined effects of salinity and temperature on the early development of Pacific Herring, *Clupea pallasi*. They found that herring eggs and larvae have a broad tolerance to varying salinities (euryhalin), but a much smaller tolerance to temperature (stenothermal). Given that maximum salinity differences in Trinity Bay during the 1st and 2nd surveys did not exceed 2 psu, it is concluded that salinity differences were too minute to contribute to the observed spatial differences in growth rates. This is consistent with Laprise and Pepin (1995), who did not notice effects of salinity gradients on larval fish in the adjacent Conception Bay.

Temporal changes in larval growth patterns

In this study, shanny larvae sampled during the 3rd survey showed consistently higher median relative growth rates than larvae of the previous two surveys. Evidence was found that this increase was due to a selective loss of slower growing individuals from the population. In all hatch intervals, this was indicated by the 10th percentiles of the 3rd survey CDF's being visibly shifted upwards, and by the smaller scatter in the last survey distributions. A smaller scatter refers to a lower variability of growth rates among the surviving shanny larvae. Because random removal of individuals would change neither the mean nor the variance of a given trait (Miller 1997), the less variable relative growth rates are therefore a signal that selective mortality has occurred during the course of the study.

Given the fact that faster growth translates into a bigger size at age, the present result of higher survival rates for faster growing individuals would be consistent with the pattern of generally decreasing mortalities with increasing size (Peterson and Wroblewski 1984, Miller *et al.* 1988). It would be consistent, too, with the so called "bigger is better" hypothesis (Litvak and Leggett 1992, Conover and Schultz 1997) and its implicit corollary of "getting bigger faster is better" (Houde 1987). Also, faster growth has been hypothesized to shorten the duration of the most vulnerable larval stages ("stage-duration" hypothesis, Leggett and DeBlois 1994). In correspondence, Folkvord *et al.* (1997) studied larval herring mortality in two large mesocosms without predators, and reported a selective loss of slower growing individuals from the population. The authors found this loss most pronounced in larvae older than 20 days post hatch and only partly ascribable to the disappearance of specimens, which had not or not successfully initiated feeding. Consistent with this, in the present study selective mortality was most apparent in larvae of the second and third hatch intervals, but less clear in oldest or youngest specimens.

However, increased survival of higher growth rates appears to be contradictory to a higher vulnerability of faster growing larvae to predation by capelin, as discussed above. It also seems inconsistent with the results of Pepin *et al.* (2000) in Conception Bay, where evidence was presented for a selective loss of faster growing individuals from the population, although some of the patterns were not unequivocal.

In the present case, measured environmental characteristics in conjunction with the modeled drift of the 3rd survey larvae were used to address the problem. The majority of 3rd survey specimens was sampled in a rather small area located in the central part of outer Trinity Bay. This area was not affected by coastal upwelling, and temperature in the surface layer had always been high throughout the study period. In addition, capelin abundance was consistently lower in this area than, for example, on the western shore of the bay. However, it depends on the advective history of the larvae, whether they had been associated with such favorable conditions prior to the sampling day.

Backward projections of particle drift indicated that most of the 3rd survey larvae had indeed developed in central outer reaches of the bay for the last 10 days (start of simulation on day 201). Few larvae might have drifted north from inner parts of the bay, yet the model suggested that they had not been associated with cold, upwelling water from the western shore. Importantly, central inner parts of the bay were found to be of particular low capelin densities. It is therefore concluded that between days 200-211 larvae sampled during the 3rd survey had developed in warm waters and probably experienced a lower predation pressure by foraging capelin schools. Furthermore, all surviving larvae had probably benefited from increasing prey densities, for microzooplankton levels showed a steady increase during the course of the study.

If an individual's growth is affected by ambient temperature and food density (Heath 1992) it was to be expected that shanny larvae of the 3rd survey exhibited higher growth rates compared to larvae from the 2nd survey, which had partly experienced poorer growing conditions. Because no environmental data are available prior to day 200, the conditions encountered by the 1st survey larvae cannot be inferred.

However, by studying a given growth rate distribution of field sampled larvae, it appears to be complicated to consider the two effects of changes in individual growth rates and selective loss of growth types separately. In the present case, selective mortality was inferred from increased lower percentiles from one survey to the next for the same cohort of larvae, but improved growing conditions (temperature increase, prey abundance) strongly suggest absolutely higher growth rates as well. The observed distribution of the 3rd survey larvae was therefore likely to be the result of both proc-

esses, acting in the same direction, but there were no means to assess the relative importance of the two processes.

Larval distribution

A major point of criticism to the above conclusions may be found in the spatially different patterns of larval shanny abundance. While during the 1st survey larvae occurred predominantly at the mouth of the bay, 2nd survey cores of abundance were located at the western shore and northern areas. Deviant from both previous surveys, 3rd survey larvae were found in central outer reaches of the study area. The important point, however, is that model simulations of particle drift suggested rather separate advective histories for each of the observed larval patches. For example, surface circulation between days 200 and 206 did not allow for notable portions of 1st survey larvae to drift into areas of high abundance during the 2nd survey. This is also true for the 3rd survey, where larvae seemed to have no relation to the majority of the 1st and 2nd surveys specimens.

The underlying rationale of otolith microstructure analysis, as applied here, is to compare individuals of the same age at the same time, although larvae had been sampled at different surveys. In a strict sense, this approach assumes that specimens are repeatedly sampled from the same initial larval population. In a laboratory tank or mesocosm, this assumption may be safely satisfied, hence subsequent samplings would truly characterize the population at different times (e.g. Folkvord *et al.* 1997). In the field, larvae may drift or disperse and will therefore be sampled at different stations, given that they remain inside the study area. However, if the drift patterns are known, then larvae of subsequent sampling periods will be comparable as well. The main difficulty of the present study was, therefore, that the encountered larval patches apparently had not been connected by a common advective history. This might have been particularly problematic in the case of the 2nd survey, where shanny larvae had spatially different growth rates. Compared to the 3rd survey, a selective loss of slower growing specimens was found, however, one is left to question to which of the two 2nd survey cores this selective loss could be related more appropriately.

In any case, it is critical not to over-interpret the circulation model (Pepin *et al.* 2001), for its accuracy will likely be limited by a number of factors. For example, it has yet to be determined until what age the dispersion of larval fish may be modeled by passively drifting particles without a systematic bias. This will depend on larval swimming speeds relative to the current speed of the ambient water parcel. If larval swimming activity cannot be assumed negligible but random around a passively drifting object, then particle drift may still adequately approximate larval drift. Of equal importance may be how dispersion of particles is included in the model. In the present case, the drifters were given a random walk component to their displacement at every time step, regardless of their previous direction. In reality, however, it is likely that the path of a drifter will be influenced by its previous speed and direction. Therefore, it is possible that the application of "no-memory" particles may have led to partly an underestimation of the magnitude of larval dispersion.

As reported by LeDrew and Green (1975), average size at hatch for larval radiated shanny is 6.58 mm TL (range 6.0-7.21mm), which is consistent with this field study, where 6.5-7.5mm SL larvae comprised the most frequent size-class during the 1st survey. However, throughout the entire study period there was also a considerable proportion of larvae smaller than 6.5 mm SL present in the ichthyoplankton layer (0-40m). This indicated a constant influx of newly hatched specimens with a range of hatch lengths broader than previously thought.

The found average somatic growth rate of 0.32 mm/day is in close correspondence to 0.29 mm/day, reported by Pepin *et al.* (2000) for shanny larvae in Conception Bay. Based on this, the expected average length increase between surveys was approximately 2mm SL. This estimate was used to gain some insights into patterns of larval production and mortality throughout the course of the study. It was seen that production was highest between the 1st and 2nd surveys for very small larvae, particularly on the bays western shore. It was assumed that the majority of larvae between 7.5-8.5mm SL, observed during the 2nd survey, had already hatched during the 1st sampling period. However, no correspondingly high values of larval abundance were encountered in the top 40m of this area during the 1st survey. It was noticed that the appearance of high numbers of larvae on day 206 co-occurred with the disappearance of coastal upwelling in this area. Similar findings were reported by Frank and Leggett (1982, 1985) for newly hatched capelin larvae in Bryant's Cove, Conception Bay. The authors surmised that a shift from offshore to onshore winds may trigger the emergence of capelin larvae from the gravel into the pelagic layer. Frank and Leggett (1982) demonstrated that a wind-induced water mass replacement is connected with higher food levels and a lower abundance of invertebrate predators (no vertebrate predators were considered). Therefore a release of larvae during periods of onshore winds would be beneficial for larval growth and mortality. The authors proposed that this pattern could be adaptive, and may be valid as well for other larvae of demersal spawning species (e.g. radiated shanny). In the present case, it can be concluded that due to upwelling on the bays western shore, colder temperature had caused a delayed hatch or a delayed ascension of shanny larvae to the surface layer. Both possibilities explain the low abundance of small larvae during the first sampling period in this area.

From forward projections of particle drift it was learned that 2nd survey larvae probably had not drifted away from the western shore between days 206-211.

Particles were seen to accumulate onshore during this period, suggesting that larvae might have come in too shallow waters to get sampled by the 3rd survey trawls. Nevertheless, the apparent paucity of shanny larvae was unexpected in this area and may not be fully explained by patchy abundance or drift. Is it therefore possible that shanny mortality was much higher on the western shore than indicated by the gross comparison of length-distributions between the 2nd and 3rd surveys? The two major agents of larval mortality are generally recognized to be predation and starvation (Bailey and Houde 1989). However, in the present case, a mass starvation of larvae was unlikely, given the observed increase in food abundance and the short time between both sampling periods. Provided that predation was the major source of mortality, the pattern of shanny mortality observed in this study would lend some evidence to the proposal of Paradis *et al.* (2001), advocating capelin as the dominant planktivorous predator in the region. The idea is supported by the high capelin densities, which were consistently observed at the western shore of the bay. Contradictory findings to this conclusion involve high abundances of other larval species during the 3rd survey in this area (notably larval capelin) and a similar disappearance of 2nd survey larvae from the northern core of shanny larvae, which had probably experienced lower levels of predation pressure.

Size-specific mortality between surveys, as calculated from the relative length-frequency distributions, was also found to be suggestive of capelin predation. In particular, it was noticed that relative losses were highest for larvae measuring 8.5-12.5mm SL. Based on the average length-age relationship of all sampled specimens, it was estimated that larvae of this length had been older than 14 days. At this age and length, the majority of shanny larvae can be assumed actively feeding (Dower *et al.* 1998). Because starvation is known to be a potential source of high mortality only during the transitional stage between endogenous and exogenous feeding (Heath 1992), predation should have caused the observed high losses in older shanny larvae. As stressed above, larvae of this length were probably sufficiently vulnerable only to predation by capelin. However, the major caveat to this conclusion was the apparently different advective history of larvae caught during subsequent surveys.

In contrast to the length-frequencies, the study of relative growth rate distributions yielded little conclusive evidence for capelin predation. As discussed above, this can be ascribed partly to a limited size- and spatial overlap between predators and larvae, and to the limited ability to compare shanny larvae between surveys. It was thus attempted to describe more qualitatively the spatial patterns of predator abundance during the course of the study.

To characterize the predator environment, hydroacoustic integration of capelin backscatter was used earlier by Pepin *et al.* (2000) in the adjacent Conception Bay. The authors observed only few consistent patterns of capelin distribution and proposed that this was due partly to inadequate temporal scales (surveys separated by one week) and the relative small size of the study area (1000km²). In the present case, the description of the predator environment was probably enhanced, because of the two additional dedicated hydroacoustic surveys and the broader spatial scale of Trinity Bay (3000km²). However, owing to the high variability between horizontal echo bins, it still seems difficult to assign representative values of capelin abundance to a given point or sampling station. More important, although of increasing complexity, would be how to move from abundance values to estimates of individual encounter probabilities.

Due to the enhanced survey design, the present study revealed some consistent patterns in the spatial distribution of capelin schools. In particular it was shown that high capelin densities occurred predominantly in waters shallower than 200m. This finding may have some implications for larvae differing in their advective histories. For example, fast growing 3rd survey larvae were seen to have developed primarily in areas deeper than 200m for the preceding 10 days, whereas the drift of other shanny larvae had been confined to the shallower areas of the western shore. In this area, capelin densities were consistently higher throughout the study period.

If two areas, like the central part and the western shore of Trinity Bay, differ notably in predator abundance, it may be reasonable to assume a spatially different predation pressure for larval fish. From the total length distribution of the sampled specimen it was inferred that the majority of shanny larvae had not yet reached 10% of the predator length. Therefore, if predation by capelin was size-selective, then faster growing specimens, being bigger at a given age, should have been removed selectively from the population. This prediction is in contrast to the observed loss of slower growing specimens from the population during the study period. One is left to question, whether even in areas of high capelin abundance the predation pressure was sufficient to evoke detectable changes in the shanny growth rate distributions. Taken into consideration the high mortality rates on the bays western shore, a too low predation pressure appears rather unlikely. However, the major obstacle to a conclusion about the impact of capelin on the growth distributions was the limited ability to compare larvae between subsequent surveys.

The selective impact of foraging capelin schools on the ichthyoplankton community may also be limited by the time of the day, during which the fish are feeding in the surface layer. In the Newfoundland area, capelin schools are seen in surface waters only at night hours, but are distributed at deeper depths during the day (Shackell *et al.* 1994, this study Fig.C6). In spite of that, ambient light levels have rarely been considered to affect a visual predator's foraging behavior, and to date nothing is known about how size-selective predation may change under fluctuating light intensities. However, most of the variables determining the probability of an encounter clearly depend on the performance of the

predator's sensory system (Gerritsen and Strickler 1977). For example, it is reasonable to assume a decreasing encounter radius with diminishing light levels. In addition, also a predators ability to select for larger or more pigmented larvae may be lower.

As Cowan *et al.* (1996) pointed out, laboratory studies have been limited to few predator species, and to date no such study has yet investigated the predation by capelin under experimental conditions. The findings of Cowan *et al.* (1996) also suggested that the dome-shaped vulnerability of larvae to fish predators (Bailey and Houde 1989) may not apply to filter-feeding planktivorous fish. Because the feeding repertoire of capelin is known to include biting, picking, and filter-feeding (Huse and Toresen 1996), it may be necessary to determine, which method is primarily used during the nightly foraging in the surface layer. Given the different characteristics, it is possible that the capelin-specific patterns of size-selective predation will differ from better investigated predators (e.g. sticklebacks, Litvak and Leggett 1992). It is suggested to address these questions in a subsequent meso- or macrocosm study (see below) using capelin as predators of larval fish under realistic light intensities.

Circulation and biological production

Environmental measurements (CDT) were in close correspondence to the modeled circulation patterns and revealed that Trinity Bay comprises a highly dynamic system, which responds rapidly to variations in wind forcing. In view of Templeman's (1966) water replacement theory, the encountered changes in surface temperature and salinity appear as very typical for that area and time of the year. In particular, Templeman (1966) proposed that prevailing offshore winds can cause a local disruption of the summer stratification, which is characterized by a thin surface layer of warm and low salinity waters and a thicker intermediate layer of cold water underneath. This is consistent with the situation observed during the 1st survey, where offshore winds caused upwelling of intermediate cold water masses on the bays western shore. Upwelling was adequately reflected by the circulation model, showing increasing densities with respect to the initial density fields.

In support to Templeman's theory, Frank and Leggett (1982) demonstrated that short and unpredictable periods of onshore winds are likely to cause a reversion of water replacement. Resulting from inverse Ekman forcing, warmer and lighter waters will rapidly overlay the heavier intermediate water, which can be measured as a quick increase in nearshore water temperature. In the present case, strong offshore winds (>20m/s) relaxed abruptly on day 204, but a real shift of wind directions did not occur. However, consistent with the theory, upwelling features had vanished 48 hours later, when the 2nd survey was conducted. Warmer surface water, which had always been present in the central and outer parts of the bay, quickly replaced the cold water masses in north-western areas. The observed temperature increase was similar to the results of Frank and Leggett's (1982) study in Conception Bay. In the model space, a narrow coastal jet of light (and presumably warm) water was predicted in response to the diminishing winds. This is in close correspondence to a pronounced temperature increase, measured on the bays north-western shore. Deviant from expectation, however, was that cold and high salinity water masses covered the entire inner bay on day 206, including areas where warm water masses had been present on day 200. Meteorological measurements indicated that wind forcing was probably too weak and variable after day 204 to allow for an upwelling of this magnitude in the inner bay. The observations were also inconsistent with the model predictions, advocating a faster replacement of high density waters in that area. However, these differences are considered to be of minor importance, because shanny abundance in the inner bay was generally very low.

During the second half of the study period, meteorological observations revealed that winds had blown from variable directions and at consistently low speeds. As a consequence, cold and dense water was not seen anymore in the surface layer on day 211, and warm and light waters covered the entire study area. This situation, which was adequately reflected by the modeled density fields, is consistent with Templeman's (1966) water replacement theory for onshore wind conditions.

In this study, upwelling of cold intermediate water was suggestive of being detrimental for the growth of larvae, which had developed on the bays western shore. However, measurements of fluorescence and microzooplankton abundance also suggested beneficial effects of upwelling patterns. In general, upwelling is recognized to enhance the primary production because of a constant influx of nutrients into the phototrophic layer. This in turn is likely to stimulate the secondary production. The observed rapid increase of fluorescence, most pronounced in north-western areas of the Trinity Bay, clearly indicated a developing phytoplankton bloom. The fact, that this bloom was apparent in the 2nd instead of the 1st survey, is likely to be the result of a delayed response of phytoplankters to enriched nutrient levels. Microzooplankton levels were highest during the 3rd survey and mimicked the patterns of fluorescence during the 2nd survey. Therefore, larvae surviving until day 211 are likely to have experienced steadily increasing prey concentrations. In combination with increased surface temperatures, this was seen supporting the faster growth of the 3rd survey larvae.

The applied oceanographic model assumed that water circulation in Trinity Bay was driven entirely by the effects of local wind forcing. The observed close correspondence between actual measurements and the model forecasts therefore substantiates that variable wind fields explain most of the variability in surface circulation in this coastal area. Given the overall reliability of the model it is assumed that drift projections of particles were adequate as well. Apparently, however, the model provided little help in predicting previous

(backward runs) or future patterns (forward runs) of larval shanny abundance throughout the study period. Hence, one is left to question, whether this was the result of unrepresentative drift simulations, too high larval mortalities, or a patchy distribution on spatial scales, unresolved by the used sampling grid. However, the model provided valuable information of the likely advective histories of the larvae sampled during each of the three surveys. Without this knowledge, it would not have been possible to draw conclusions on the growing conditions the larvae had encountered along their way.

General conclusions and perspectives

Considerable emphasis has been put on the development of daily growth patterns in order to further understand the complexity of processes, which act to determine larval growth and survival in the open sea. The major benefit of this effort is the ability to compare the state (e.g. growth rate) of individuals of the same age at the same time, between different sampling periods. This ability may comprise a promising tool to determine whether and how surviving individuals differ from the "average" larva. In this field study, it was learned that this approach was useful to discuss how environmental influences, like ambient temperature, can alter shape and magnitude of growth rate distributions in surviving larvae. It was also learned that the environmental history provided meaningful answers to the observed selective loss of slower growing individuals throughout the study period. The ability to detect selective mortality patterns seems to be enhanced in areas with better growing conditions. As a further result, spatial differences in shanny growth rates were observed on a small scale of tens of nautical miles (2nd survey). This may add to the present understanding of spatial growth variability in coastal embayments.

With respect to predator abundance highly detailed information was accumulated, which primarily confirmed the high amount of small scale variability inherent to the distribution of pelagic schooling fish. Broad regions of consistently higher (western shore) and lower capelin abundance (central deep areas) could be characterized, however, to better understand the importance of fish predators it will be necessary to move beyond such descriptions. Despite the sophisticated, highly resolving means available now to assess fish density, severe difficulties still persist in determining an individuals probability to be encountered and attacked by a fish predator. New approaches for field studies are therefore in demand. Improvements may come from modeling approaches (IBM's), including predation and more realistic parameters of the entirety of variable larval traits (e.g. Rice *et al.* 1993, Cowan *et al.* 1996, Paradis and Pepin 2001). Ultimately, however, as Paradis and Pepin (2001) have pointed out, all conceptual models will need to be evaluated by field observations. Alternatively, progress in understanding vertebrate predation can be made in meso- or macrocosm studies, which include fish predators of different sizes and/or species. Mesocosms are generally perceived as valuable links between field observations and laboratory experiments, for they provide semi-natural conditions and allow for some degree of environmental control (Øiestad 1990, Folkvord *et al.* 1997).

In order to reach the above conclusions, the present study had to be based on considerable financial, personal, and material efforts. Only a spatially and temporally intensive sampling program provided the appropriate resolution to describe larval abundance and environmental conditions throughout the study period. Only the preliminary meticulous effort to identify and sort the ichthyoplankton samples enabled subsequent analyses of larval shanny otolith microstructure. The concomitant processing of hydroacoustic data, counts of microzooplankton particles, and the development of the dynamic circulation model, were further pre-requisites to the attempt to find meaningful reasons for the observed growth patterns. And yet, in light of this effort, the conclusions that could be drawn appear to be rather cautious. This was seen to be partly a consequence of unexpected patterns of larval abundance, a high small-scale variability of the predator environment, but also of a limited number of otolith data. Faced with this, one might easily be tempted to demand denser sampling grids, a higher temporal resolution, more otolith measurements, or other parameters to be assessed. For example, it may be speculated whether an additional sampling between the 2nd and 3rd surveys would have enhanced the ability to detect the effects of capelin predation on the larval growth rate distributions. However, from the authors strictly personal view, limited human and financial resources in research programs may impede such demands in future studies. Therefore, to elaborate upon the existing and the alternative frameworks, and to develop new approaches in the field of larval ecology, may comprise the major challenge for fishery scientists in the near future.

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G. Appendix

In order to define a level of capelin density (expressed as capelin per m^2 sea surface) that might be regarded as "high" in view of the potential predation impact on the ichthyoplankton, the following calculation was made. By assuming a rather low average swimming speed of half a body length (BL) per second and an encounter radius of one body length, the water volume (V) effectively searched by one predator was expressed by:

$$V\ [m^3] = 0.5\ BL[m/s] * BL^2 * \pi * t[s]$$

The equation indicates that a predator of 11cm total length would search almost $40m^3$ during a 5 hours feeding period. Since mean capelin size in July 2000 was 11.8 cm (stdev=2.3 cm, n=3342 Fig.C5) it was concluded that a whole water column content of one observed capelin/m^2 sea surface can effectively search the top 40 m during its daily feeding period. This layer usually contains more than 95% of the present ichthyoplankton (Pepin *et al.* 1995). The estimate of the daily feeding time of five hours was derived from the mean depth of capelin backscatter between 20 – 300 m depths for each of the 100 m horizontal integration bins (13,500).

Accordingly all areas where the whole water column capelin content exceeded 1 fish/m^2 were considered areas of "high" capelin densities.

Erklärung

Hiermit erkläre ich, daß ich die vorliegende Arbeit selbständig angefertigt habe und keine anderen als die angegebenen Hilfsmittel verwendet habe.

Mit der Archivierung dieser Arbeit in die Fachbibliothek des Biologiezentrums, des Institutes für Meereskunde (IfM) sowie der Universitätsbibliothek der Christian-Albrechts-Universität zu Kiel (CAU) bin ich einverstanden.

Kiel, den 12.3.2002

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