Linking Individual Patterns of Feeding and Growth with Implication for Survival in the Ecology of Larval fish

By

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ABSTRACT

In an attempt to understand the processes governing recruitment variability in marine fish populations, a number of proxies for larval survival probabilities have been proposed. The most popular of these are an individual's length-at-age and its growth rate prior to capture, both of which are presumed to be positively correlated with survival probability. The goal of this study was to use measurements of larval growth rates and gut contents (from the same individuals) to determine the best proxy for larval feeding ability, and to identify the "characteristics of survivors". Contrary to expectations, it is shown that (i) early larval growth rate is the best predictor of future feeding success, and (ii) that high early growth may increase individual survival probabilities by simultaneously increasing foraging success while reducing encounter rates with predators. These results also suggest that there is indeed a link between larval survival and prey availability in the field.

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CHAPTER 1

Introduction

1.1 Recruitment dynamics of marine fish populations – History and Theory

Understanding the processes that regulate interannual variability in recruitment has remained the central focus of fisheries oceanography for the past 90 years. In the fish population ecology literature, recruitment is usually defined as the addition of new members to the population through reproduction. More specifically, individuals that manage to survive the larval stage and metamorphose into juveniles are considered to have successfully recruited to the population, and are generally termed "survivors". This focus on the transition from larva to juvenile is based on the widely held belief that year-class strength in marine fish populations is established by the abundance of individuals that survive to the end of the larval stage (Hjort, 1914; Leggett and Deblois, 1994).

During their early life history stages (*i.e.* egg and larval stages), marine fish experience extremely high mortality rates (Bailey and Houde, 1989). For this reason, innumerable laboratory and field studies have attempted to quantify patterns of larval mortality, with varying degrees of success (Ware, 1975; McGurk, 1986; Delafontaine and Leggett, 1987; Beyer, 1989; Houde, 1989). Consequently, however, most studies have generally ignored other factors that may contribute to recruitment variability, such as maternal and/or genetic effects on larval growth and survival. Furthermore, it has been also recognized that more accurate mortality estimates are required in order to quantify the relative importance of the various factors that are believed to regulate larval survival (Heath, 1992; Pepin, 1993; Dower *et al.*, 2000; Pepin, 2004). The extremely high mortality rates during the early life history stages have since led scientists to the idea that the survival of individual larvae is influenced not only by luck (*i.e.* whether an individual encounters a suitable range of environmental conditions during its larval stage), but also by individual variability in *viability* (Rice *et al.*, 1993). Thus, identifying the "characteristics of survivors" has recently emerged as a key theme in fisheries oceanography. The popularity of this approach is based on the notion that quantifying individual variability in viability will provide a better understanding of the mechanisms that regulate larval survival, as opposed to simply trying to estimate the larval mortality rates directly (as most early studies did) (Fritz *et al.*, 1990; Letcher *et al.*, 1996).

The three main sources of larval mortality are widely held to be starvation, predation and advective losses. Of these starvation has received, by far, the most attention to date. Early in the twentieth century, Hjort (1914) proposed that interannual variability in the amount of food available to larval fish at the time when they initiate exogenous feeding (*i.e.* following yolk-sac absorption) resulted in interannual variability in larval survival and, hence, year-class strength. Hjort termed this transition to exogenous feeding the "critical period", and proposed that in years when there was insufficient food during this transition most of the larvae starved, producing a weak year class. Despite the popularity of the theory, however, little direct evidence for Hjort's critical period has ever been found (Leggett and Deblois, 1994).

Elaborating on Hjort's idea, Cushing's (1975) "match-mismatch" hypothesis proposed that the overall degree of overlap between the hatching of fish larvae and the blooming of their zooplankton prey was the key factor determining variability in larval survival. Years when the two distributions "matched" produced good feeding conditions for the larvae (and, thus, strong year-classes), while "mismatch" years resulted in poor larval feeding conditions (and, consequently, weak year-classes). Although intuitively attractive, in practice (and especially under field conditions) it was almost impossible to determine what constituted a match and what constituted a mismatch (reviewed by Leggett and Deblois, 1994). In fact, Leggett and Deblois even cite examples where the same data are used by different authors; one claiming a "match" in a given year, the other claiming a "mismatch".

A third starvation-based theory was proposed by Lasker (1975) to explain interannual variability in recruitment. His "stable ocean" hypothesis held that strong year-classes resulted in years during which there were a sufficient number of calm periods, during which stratification acts to concentrate the prey of larval fish near the surface (thereby enhancing their feeding success). According to the hypothesis, if the mixed layer is deepened and stratification is broken down repeatedly (*e.g.* due to storm winds and/or intense upwelling), then the density of food for the larval fish decreases resulting in poor feeding conditions and a weak year-class.

In addition to starvation, other sources of larval mortality have been put forth. Beginning in the mid 1970s, interannual variability in predation rates on larval fish (*e.g.* by larger fish, gelatinous zooplankton, *etc.*) was proposed to contribute significantly to recruitment variability (Hunter, 1976; Bailey and Houde, 1989). Although the impact of predation on recruitment variability has not yet been fully resolved (mainly due to the logistical constraints on observing and measuring predation on larval fish in the field) numerous studies have demonstrated that predation mortality generally declines throughout larval ontogeny, perhaps implying that larval predation mortality is size-dependent (Bailey and Houde, 1989; Pepin, 1991; Leggett and DeBlois, 1994; Paradis *et al.*, 1996; Houde, 1997). This is currently an area of active research within fisheries oceanography.

The final factor proposed to play a major role in regulating year-class strength is advective loss. The "member-vagrant" hypothesis of Sinclair and Iles (1989) holds that interannual variability in the transport and retention of larvae by currents may control larval survival and recruitment. They argued that the successful transport of larvae to, and the retention of larvae in, suitable nursery grounds (*i.e.* areas with retentive currents, sufficient food and perhaps lower numbers of predators) leads to years of strong recruitment, in which many larvae survive to become "members" of the population. In contrast, years in which currents carry larvae away from such areas lead to poor recruitment, during which the larvae are lost to the population and become "vagrants".

Although there is ample evidence of this phenomenon for certain species (*e.g.* Atlantic herring), the extent to which the member-vagrant hypothesis applies to fish populations in general remains to be seen.

In summary, although starvation has received far more attention than either predation mortality or advective losses, all three factors likely play a role in determining year-class strength. Despite this, however, clear evidence for a causal relationship between larval survival (or growth) and prey abundance *per se* (hereafter referred to as 'the causal relationship') has only rarely been found in field studies (Leggett and Deblois, 1994). In part, this may be the result of using inappropriate measures of prey availability (Fortier *et al.*, 1995). Fish larvae are gape-limited predators, and generally change their main prey items as they grow (Pepin and Penney, 2000). However, until recently, most field studies have equated simple measures of *total* zooplankton abundance or total zooplankton biomass with prey availability (Betsill and Van den Avyle, 1997; Meekan *et al.*, 2003). However, we now know that not all size classes of zooplankton are equally consumed by all larvae of different ages. Thus, variations in larval feeding success (and perhaps larval growth and survival) may be linked to variations in prey quality (*e.g.* prey of a suitable size) as well as mere quantity.

Although a demonstrated causal relationship between prey abundance *per se* and larval survival has been elusive, interest in this topic remains strong. For instance, the "growth-mortality" hypothesis (Anderson, 1988) has been proposed as a means of combining the roles of starvation and predation into one integrated framework. The basic idea is that among larvae of the same age, larger individuals should have higher survival probabilities than smaller individuals, because larger larvae can swim faster, thereby presumably gaining an advantage both in obtaining prey and evading predation (Hunter, 1981; Miller *et al.*, 1988; Bailey and Houde, 1989; Fuiman, 1993). Two additional consequences predicted under this proposal are that: (i) larger larvae should be exposed to fewer predators than smaller larvae (Leggett and DeBlois, 1994), since body size is inversely proportional to abundance (Sheldon *et al.*, 1972; 1973; Platt and Denman, 1978), and (ii) larvae that are larger at age (*i.e.* faster growing) will undergo metamorphosis at younger ages than slow growing individuals, thereby reducing the time spent in the highly vulnerable early life history stages. Together, these two predictions have come to be known, respectively, as the "bigger-is-better" hypothesis (Miller *et al.*, 1988) and the "stage duration" hypothesis (Chambers and Leggett, 1987, Houde, 1987). These hypotheses are strongly supported by laboratory studies demonstrating that abundant prey levels lead to higher growth rates of larval fish (Leggett and DeBlois, 1994), and that larval susceptibility to predators is size-dependent (Bailey and Houde, 1989; Fuiman and Margurran, 1994; Paradis *et al.*, 1996).

Consequently, the "growth mortality" hypothesis (and its variants) has gained in popularity from the growing empirical evidence of non-random selection on size and/or growth rate (Miller *et al.*, 1988; Bertram, 1996; Meekan and Fortier, 1996; Hare and Cowen, 1997; Sogard, 1997). As a result, large length-at-age and high larval growth rates are increasingly being used as proxies for predicting individual larval survival (Werner and Gilliam, 1984; Winemiller and Rose, 1993; Sogard, 1997). Despite this, however, the implicit assumption that length-at-age actually confers a measurable survival advantage has not been well tested. Furthermore, although the 'growth mortality' hypothesis has been proposed as "new", it is worth noting that all of the previously discussed hypotheses implicitly assume that increased prey abundance leads to larger body size (and high growth rates) and, thus, increased survival probability. Therefore, a critical understanding of the relationship between larval feeding success and growth (and the question of whether length-at-age is indeed a valid proxy for survival), would help to identify factors regulating larval survival and to better understand the characteristics of the survivors in prey-predator relationships.

1.2 Growth and survival of larval fish and their prey

As remarked above, efforts to establish a causal relationship between fluctuating prey availability and the interannual variability in survival of larval fish have long been sought (Hjort, 1914; Cushing, 1975). However, although laboratory studies clearly show that the growth and survival of larval fish increases with zooplankton abundance (Leggett and Deblois, 1994; Welker *et al.*, 1994), results from field studies remain far less conclusive (Pepin, 2004). A similar situation exists in studies of cascading effects in food chains. In marine ecosystems, it is widely held that physical forcing (*e.g.* nutrient supply) leads the bottom-up control of phytoplankton and zooplankton production (Venrick *et al.*, 1987; Brodeur and Ware, 1992; Beamish, 1993; Polovina *et al.*, 1995; Roemmich and McGowan, 1995). However, it is still unclear to what extent (or whether) variability in such bottom-up effects transfers directly to higher trophic levels. For instance, examining a 20 year time-series of zooplankton and larval fish data McGowan *et al.* (1998) found only a very weak correlation between annual anomalies in larval fish abundance and zooplankton abundance.

Results of this sort naturally lead one to question the very existence of a causal relationship between prey availability and survival (or growth) of larval fish. However, at least one recent study (Platt *et al.*, 2003) has demonstrated quite a strong correlation between the timing of the spring bloom (as estimated from remotely sensed ocean colour data) and interannual variations in larval survival. Why, then, has a direct relationship between prey availability and larval survival not been found in the field? Sampling issues would seem to be one possible answer. Most of the field studies which have failed to find a strong link between zooplankton abundance and larval fish survival have employed traditional plankton nets to estimate prey availability. In most of these cases *total* zooplankton biomass (or total wet weight, or total displacement volume) was used as the proxy for estimating the amount of prey available to the larvae. For instance, when Crecco and Savoy (1984) determined the total abundance of zooplankton from plankton net samples, they found that the mortality of larval American shad (*Alosa sapidissima*) was seemingly unrelated to prey abundance. However, when larval gut fullness was measured instead, a strong correlation between larval survival and year-class strength emerged (Crecco and Savoy, 1987). These results indicate that zooplankton abundance *per se* is a poor proxy for estimating prey availability for larval fish, and that a new approach is needed (Pepin, 2004).

Although the zooplankton collected by a plankton net typically include a wide range of sizes and species, not all of these potential prey items are available to (or are selected by) larval fish. For instance, it is well known that as larval fish grow the average size of their prey increases (Pepin and Penney, 1997). Thus, the zooplankton from a given net tow might constitute very different levels of prey availability to larvae of different ages. For instance, a sample containing large numbers of adult copepods might constitute good feeding conditions for older larvae (which consume adult copepods), but poor feeding conditions for very young larvae (which consume copepod nauplii). Furthermore, until relatively recently, most field studies also used rather coarse meshed nets (*e.g.* >180μm), which typically miss the smaller size-fraction of the zooplankton (which also just happen to be the size range of greatest importance to young larvae). This may explain, in part, the conflicting results between lab and field studies of larval feeding and why studies of larval survival have only rarely found strong correlations with estimates of prey availability based on the total (or average) zooplankton abundance.

Gut content analysis offers an alternative means of exploring links between prey availability and patterns of larval growth and survival. For instance, Dower *et al.* (2002) found that radiated shanny (*Ulvaria subbifurcata*) larvae collected from coastal Newfoundland in 1995 had significantly greater volumes of food in their guts than did *Ulvaria* larvae collected from the same area in 1997, despite the fact that *total* prey concentrations were almost fivefold higher in 1997. The difference was that, although fewer in number, the prey consumed by the 1995 larvae were significantly larger than in 1997 and thus that larval feeding conditions (at least as evidenced by gut contents) were actually better in the year with the lower total zooplankton biomass. This indicates that we need to identify the actual prey items from among the all zooplankton available to the larvae, (and that gut content analysis can help to facilitate this).

The fact that larvae ingest both more and larger prey as they grow suggests that larval gut contents may serve as snapshots of individual larval feeding ability and perhaps even as measures of relative “fitness” (*i.e.* as measured by feeding success) among larvae of the same age. Ringuette *et al.* (2002) showed that the amount of food ingested by larval mackerel (*Scomber scombrus*) had a stronger relationship with larval survival than with fish length, even though the latter is widely accepted as a proxy for larval survival (or “fitness”). Comparing data across several years, they found that mackerel larvae had significantly higher gut fullness in 1982 than in any of 1985, 1987 or 1996, and that the 1982 cohort was the strongest. However, the average size of the mackerel at the end of each year was smallest in 1982. This not only indicates that gut contents may serve to indicate individual larval “fitness”, but also emphasizes the need of better understanding whether size (*i.e.* relative length-at-age) is indeed the best proxy for estimating individual larval survival.

1.3 Proxy measures for larval survival

Fisheries scientists and managers have long sought effective proxies to estimate larval survival and, thus, to help predict year-class strength of marine fish populations. Based largely on predictions from the “bigger-is-better” paradigm, length-at-age (or growth rate) has been used as the main proxy in recent years. However, although the “bigger-is-better” paradigm has achieved wide acceptance (Sogard, 1997), considerable evidence and theoretical arguments to the contrary also exist (Fuiman, 1989; Litvak and Leggett, 1992; Pepin *et al.*, 1992; Conover and Schultz, 1995; Kolok and Oris, 1995; Gregory and Wood, 1998; Billerbeck *et al.*, 2001; Lankford *et al.*, 2001; Pepin *et al.*, 2003). These studies suggest that, because bigger larvae have to search a larger volume of water to capture sufficient prey, they have greater energetic requirements. Thus, their increased foraging activity (*i.e.* coupled with longer searching time and faster swimming speeds), together with the fact that larger larvae are also more conspicuous to visual predators, may increase the rate at which larger larvae encounter predators (Cowan and Houde, 1992; Gallego and Heath, 1997).

Whereas length-at-age may provide an integrated measure of condition, other proxies for estimating survival probabilities have been based on short term measures of growth state or condition. These short term measures can be categorized into two groups. First, early growth rate (*i.e.* during the early part of the larval period) has been proposed as a potential proxy for larval survival. For instance, Bergenius *et al.* (2002) found that monthly variations in the recruitment of larval doctorfish (*Acanthurus chirurgus*) to a Caribbean reef were strongly correlated with their growth rates during the first weeks post-hatch. Similar results from studies on brown trout fry (Mosegaard *et al.* 1988, Mosegaard 1990, Titus and Mosegaard 1991) argue that although high growth during the first weeks post-hatch is not necessarily correlated with future large body size (Mosegaard *et al.*, 1988), it may be an indicator of high metabolic rate, fast growth and enhanced survivorship. Second, a number of studies have proposed that measures of recent condition (or growth rate) of larval fish in the days immediately prior to capture provide useful proxies for individual larval survival. These have variously included measures based on nucleic acid ratios (*i.e.* RNA:DNA) (Buckley, 1984; Clemmesen, 1988; 1994; Ferron and Leggett, 1994), lipid profiles (Lochman *et al.*, 1995), and measures of the average growth across the outermost few daily rings of larval otoliths (Maillet and Checkley, 1990; Suthers, 1998).

Assuming we accept that each of these measures is a valid proxy for larval condition (and hence provides a useful predictor of individual survival probabilities), then given a set of larvae each proxy should generally diagnose the same individuals as having the highest probability of survival. If, however, the results do not agree it still merits determining which candidate proxy provides the most reliable estimate of larval survival. Such a comparative study could also provide significant insight into understanding the processes regulating larval survival.

Despite this, such comparative studies have rarely (if ever) been attempted. For such a study to be valid, all measurements for the various candidate proxies would need to be taken from the same individual larval fish. For the past 20 years, otolith microstructure has been used to estimate the age and growth trajectories of individual larval fish in numerous studies (reviewed by Campana and Thorrold, 2001). In fact, fish otoliths have often been compared to the "black-box" flight data recorders of airplanes, insofar as they provide an integrated time-series of the environmental variability experienced by an individual throughout its life (and particularly during the larval stages, when daily growth rings can be distinguished). Thus, I propose that the various proxies for larval survival based on measurements of larval otolith microstructure could provide the appropriate material for such a comparative study.

Although condition measures are widely used as proxies for larval survival, what is generally reported in the literature are simply the differences in larval growth or condition observed among individual larvae (or groups of individuals). In most cases, the actual processes (or factors) that determine larval survival are not examined explicitly. However, for any proxy to be truly useful it is important to understand the underlying mechanism that links observed differences in the proxy measure to presumed differences in survival probability. Given that starvation and predation are held to be the major sources of mortality to larval fish, differences in larval survival probabilities are likely linked to individual variability in swimming ability, which could affect both foraging success and predator avoidance (Fritz *et al.*, 1990; Gallego and Heath, 1997; Fuiman and Cowan, 2003). Therefore, it will be necessary to understand whether any observed differences in the otolith-based proxy measures of survival are indicative of differences in the swimming and perceptive ability among individuals of the same age. Thus, in addition to the otolith-based proxies, an instantaneous measure of individual "ability" is required.

Comparisons of the amount and composition of the prey in the guts of larval fish can provide snapshots of individual foraging ability, insofar that feeding success integrates both an individual's swimming ability and its ability to both perceive and capture prey (Browman and O'Brien, 1992; Munk, 1992). However, it remains to be determined whether individuals with high feeding ability can also better avoid predators, because increased swimming activity should increase encounter rates with predators (Bailey and Houde, 1989; Cowan and Houde, 1992; Winemiller and Rose, 1993; Gallego and Heath, 1997). Only then can we determine the best proxy for larval survival, and ask how and what factors regulate larval survival and what the characteristics of the survivors are.

1.4 Objectives

The primary objective of this thesis is to better delimit the "characteristics of survivors" with respect to their ability to succeed in feeding and avoiding predators and, in doing so, to further explore the link between prey availability and larval growth and survival. To do this, I have used radiated shanny (*Ulvaria subbifurcata*) larvae collected in coastal Newfoundland during the summer of 2000. In Chapter 2, I first determine which otolith-based condition measure provides the best proxy for larval feeding ability (*i.e.* among the various proxies that have been suggested for larval survival). Chapter 2 thus includes an explicit test of the "bigger-is-better" hypothesis as it relates to larval feeding success. In Chapter 3, I attempt to elucidate the characteristics of potential survivors among larvae of the same age-class as reflected in their feeding patterns, and discuss how this fits with predictions from optimal foraging theory. Finally, in Chapter 4 I consider further the reasons why a causal relationship between prey availability and larval survival in the field has remained elusive, and offer some directions for future research.

CHAPTER 2

Comparing the relative importance of early larval growth, length-at-age, and recent larval growth to measures of feeding success: Bigger is not necessarily better.

2.1 Introduction

The main sources of mortality of larval fish are believed to be starvation and predation, because their small size and incomplete development limit their ability to avoid and evade predators and to perceive and capture prey (Bailey and Houde, 1989; Leggett and DeBlois, 1994). However, mortality rates of larval fish generally decline during larval ontogeny (Houde, 2002), while individual survival probabilities (as indicated by an individual's rank within the population) appear to persist throughout an individual larva's life (Pepin *et al.*, 1999). It has also been suggested that the extremely high mortality rates during the larval stage implies that individuals surviving to the juvenile stage are exceptional not only in terms of their luck (*i.e.* in terms of having encountered a suitable range of environmental conditions during the larval stage) but also in terms of their ability to survive (Rice *et al.*, 1993). These results may therefore indicate that the survival of individual larvae is not merely the result of random processes. However, the factors that contribute to an individual's ability to survive remain unclear.

In recent years, length-at-age (or growth rate) has been proposed as a proxy measure for an individual's survival probability because of its presumed influence on both prey capture and predator avoidance (Werner and Gilliam, 1984; Winemiller and Rose, 1993). Larger larvae are believed to have an advantage in capturing prey (Drost, 1987) and escaping predators (Fuiman, 1993) because they generally have better developed body musculature and fins and, consequently, more developed locomotor and sensory systems. However, although there is considerable empirical evidence in support of the "bigger-is-better" concept (Bailey and Batty, 1984; Blaxter, 1986, Miller *et al.*, 1988; Bertram, 1996; Meekan and Fortier, 1996; Hare and Cowen, 1997; Sogard, 1997; Allain *et al.*, 2003, Oozeki *et al.*, 2003), there is also considerable empirical evidence to the contrary

(Fuiman, 1989; Litvak and Leggett, 1992; Pepin *et al.*, 1992; Kolok and Oris, 1995; Conover and Schultz, 1995; Gregory and Wood, 1998; Billerbeck *et al.*, 2001; Lankford *et al.*, 2001; Pepin *et al.*, 2003). For instance, contrary to the "bigger-is-better" hypothesis, it has been shown that early growth (during the first weeks of the larval stage) may be a better indicator of an individual's chance of survival to recruitment than is its size at age (Mosegaard *et al.*, 1988; Mosegaard, 1990; Titus and Mosegaard, 1991). In addition, recent larval growth (*i.e.* during the days immediately prior to capture) has been also suggested as a useful proxy for an individual's survival probability (Clemmesen *et al.*, 1997; Suthers, 1998) and feeding activity (Maillet and Checkley, 1990; Ferron and Leggett, 1994). Despite the fact that several proxies for larval survival have now been proposed, to date no study has undertaken to compare these proxies under realistic field conditions.

Even if these various proxies might be indicative of individual survival probabilities, it is still unclear whether a high growth rate also equates to an enhanced ability to capture prey and avoid predators. A recent experiment by Fuiman and Cowan (2003) assessed individual variability in swimming skills and startle response among 100 red drum (*Sciaenops ocellatus*) larvae of the same size (7.7 ±0.19 mm total length). Individual ability varied considerably, with only about 2 % of the larvae performing well in repeated trials. This implies that size-at-age alone may not be indicative of an individual's survival probability, and that individual variability in ability may be at least as (if not more) important. Furthermore, given the possibility that larger body size may attract more attention from visual predators (Litvak and Leggett, 1992), understanding the nature of the relationship between individual ability and growth is fundamental to understanding the mechanisms underlying variability in survival.

Foraging ability varies among larval fish of the same age, presumably due to variations in perceptive ability, response time and attack ability (Browman and O'Brien, 1992), in addition to physical limitations due to body length differences (Pepin and Penney, 1997).

Therefore, comparisons of gut contents among individuals could serve as snapshots of feeding ability and perhaps as an instantaneous measure of “fitness”. However, a longer term measure of “fitness” is also needed to understand individual ability in terms of growth history until the time of capture. I have chosen to use measurements of otolith microstructure as the long term measure of “fitness”, because the larval otolith records an individual’s daily growth trajectory. The combination of these two data sets (*i.e.* gut contents and otolith microstructure) from the same individuals can provide useful insights into understanding the nature of the relationship between individual ability and growth and determining the best indicator of the ability to survive among the proxies suggested. Here, I hypothesize that if the various suggested growth and size measures (*i.e.* length-at-age, early larval growth rate, and recent growth rate prior to capture) are all valid proxies for larval survival probability, then all of the proxies should show similar results when applied to a single collection of individuals. If this turns out not to be the case, then it still merits determining which measure is the best proxy. To do this, I examined the gut contents of larval fish (in terms of both the number and the size distribution of prey ingested) grouped according to otolith-based measurements of (i) size-at-age, (ii) early larval growth rate, and (iii) recent growth rate prior to capture. Perhaps surprisingly, although fisheries oceanographers have studied larval gut contents and otolith microstructure for more than 20 years, to date no study has ever combined these two approaches on the same set of individuals.

2.2 Materials and methods

2.2.1 Sample collection

Larval radiated shanny (*Ulvaria subbifurcata*) were collected from 21-29 July 2000 in Trinity Bay (48°N, 53°W; Fig. 1), Newfoundland. This species was chosen because its larvae are quite robust, as well as being numerically dominant in the ichthyoplankton community of the east coast of Newfoundland (Dower *et al.*, 1998; 2002; Pepin and Penney, 2000). Larvae were collected using a 4 m^2 Tucker trawl equipped with an over size cod-end (20 cm diameter, 30cm length) and fitted with sections of 1000, 570, and

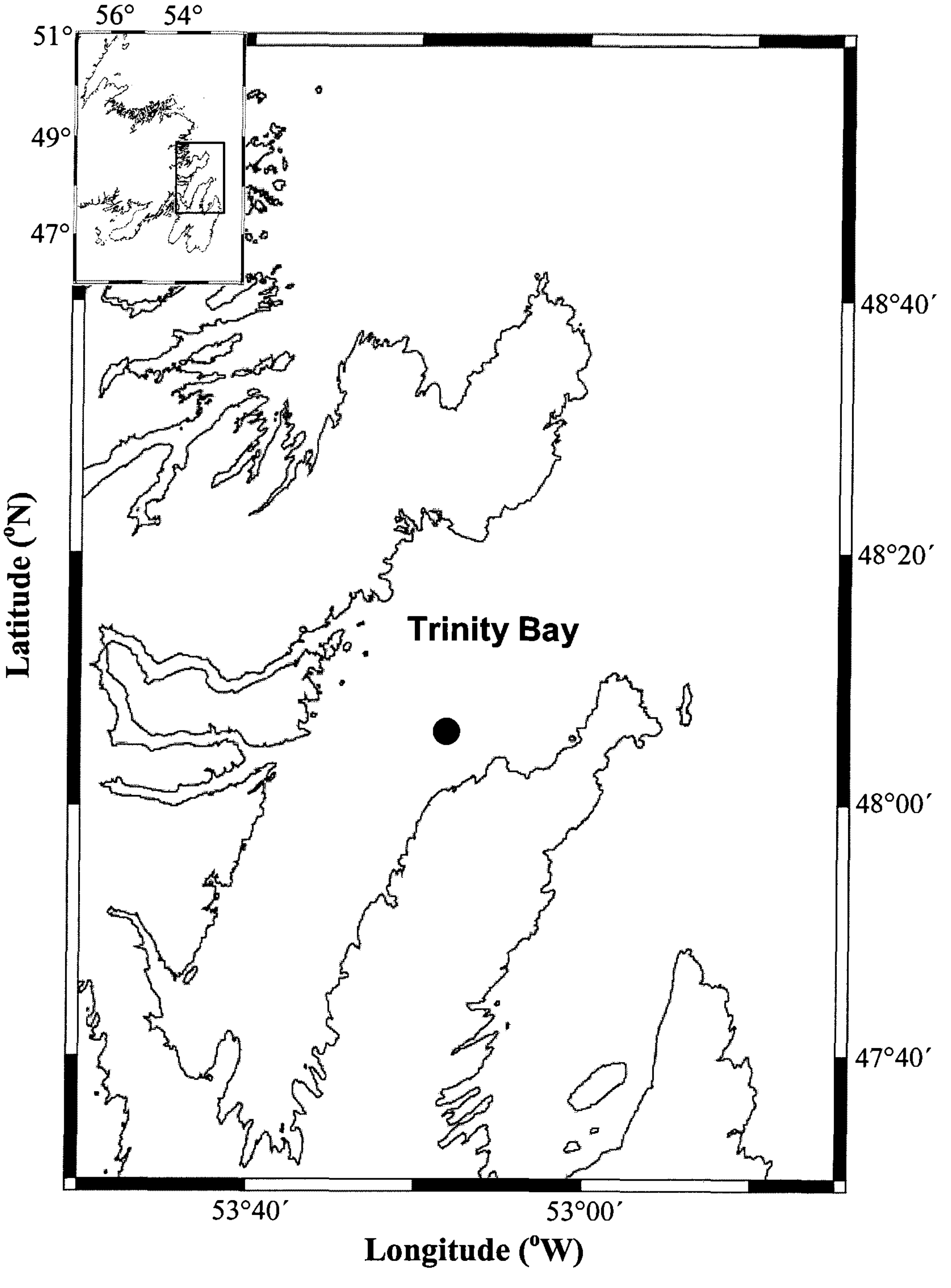

Figure 1. Map of Trinity Bay, Newfoundland. Solid circle indicates location of the sampling site.

333 μm mesh nitex (Pepin and Shears, 1997; Dower *et al.*, 2002). Oblique tows were made to 40m depth, as this depth horizon usually contains virtually all of the ichthyoplankton community in coastal Newfoundland (Pepin and Shears, 1997). Once the net had been washed down on deck, the *U. subbifurcata* larvae (*Ulvaria*, hereafter) were immediately sorted from the rest of the sample and then individually labeled and recorded on videotape using a Pulnix TM-7CN CCD video camera mounted on a Wild M3C dissecting microscope to avoid changes in body length following preservation (Pepin *et al.*, 1998). Individual larvae were then transferred to 95% ethanol in 1.5-mL microcentrifuge tubes for later analysis. In order to compare feeding ability amongst individuals, and to minimize any potential bias due to different environmental conditions, the larvae (n = 197) were collected at a single site on Trinity Bay and during daylight hours only.

2.2.2 Laboratory methods

The total length (TL) of each larval fish was measured to the nearest 0.1 mm using an optical imaging system (Scion Image®, Scion corp.). Larval guts were then excised and the individual prey items in each gut were videotaped and measured to the nearest 0.01 mm using an ocular micrometer on a Leica MZ6 binocular microscope with digital camera attachment. Since virtually all of the prey consisted of crustacean zooplankton, the length measured was the length of the prosome and the width was taken at the widest point. Empirical length-width relationships for the various prey types were subsequently derived using a sub-sample of items collected in the guts. The resultant relationships were used to derive equivalent ellipsoid volumes (mm^3) for individual prey items in the larval guts. To examine the change in the composition of the larval diet according to increasing age, prey items were categorized as either nauplii, copepodites, adult copepods, or "other". The "other" category was excluded from all subsequent analyses because my objective was to examine age-dependent effects on the consumption of specific prey items, and because the "others" (a heterogeneous collection of fish and invertebrate eggs, plus other unidentifiable fragments) accounted for only about 5% of all prey ingested.

Sagittal otoliths were extracted from 191 *Ulvaria* larvae from which gut content data had already been extracted. Otoliths were embedded in epoxy resin, ground to near the sagittal plane with a series of graded silicon carbide papers (1000 and 1200 grits), and polished with alumina powder of 0.3 μm diameter (Lee and Kim, 2000). The hatch mark in the saggital otolith of *Ulvaria* had been previously defined, and the daily periodicity of increment deposition validated (Fig. 2), by Fisher (2000). All otoliths were measured under a Leica DMLS compound microscope (1000X) connected to a Nikon Coolpix 995 digital camera (3.34 mega pixels).

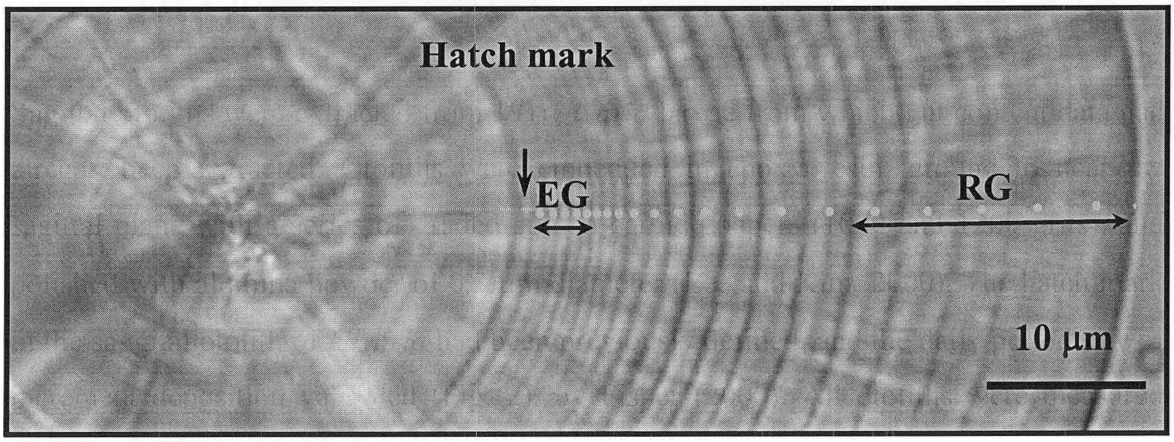

Figure 2. A portion of a sagittal otolith from a 20 day old *Ulvaria subbifurcata* larva, as viewed under a light microscope at a magnification of 1000 X. Twenty individual growth increments are visible beyond the hatch mark. The EG region represents growth during the first five days post-hatch. The RG region shows growth over the five days immediately prior to capture.

The width of each increment was measured by marking the outer edge of that increment along the longest axis of each otolith. Because of the potential for measurement error (Pepin *et al.*, 2001), each otolith was read three times, and the width of each increment was measured twice. If the age estimated on the second and third readings differed from the first or second, the specimen was excluded from the analysis. If the width of an increment on the second measurement is differed by more than 5% of that on the first measurement, the measurement was considered incorrect. If the number of the incorrect measurements was more than 10% of total number of the measurements in the otolith, the specimen was excluded from further analysis (a total of 10 individuals were excluded on this basis).

2.2.3 Data analyses

Visual inspection of the otolith-based age data showed no time-dependent variation in age composition of the larval fish (i.e. there was a wide distribution of ages represented among the larvae capture on each sampling day). Thus, the larvae were pooled across sampling times for all subsequent analyses.

Length-at-age: To test one element of the "bigger-is-better" hypothesis, I hypothesize that if larval growth rate or length-at-age is a good predictor of swimming and prey capturing abilities, then larvae whose length-at-age (LAA) is higher than average (hereafter referred to as LAA_{long}) should ingest more prey than will larvae of the same age but which are shorter than average (hereafter referred to as LAA_{short}). That is, my purpose is not to see whether older larvae ingest more prey but to see whether larger larvae at same age ingest more prey. However, the growth rate of an individual larval fish and the amount of food in its gut are both known to be age- and length-dependent variables. Therefore, age-dependent variation should be eliminated. To do this, each larva was categorized as having a length-at-age that was either longer or shorter than average on the basis of the residuals estimated from a regression of total length (TL) against age ($TL=0.42*Age+3.21$, $r^2=0.89$, $P<0.001$, Fig. 3a).

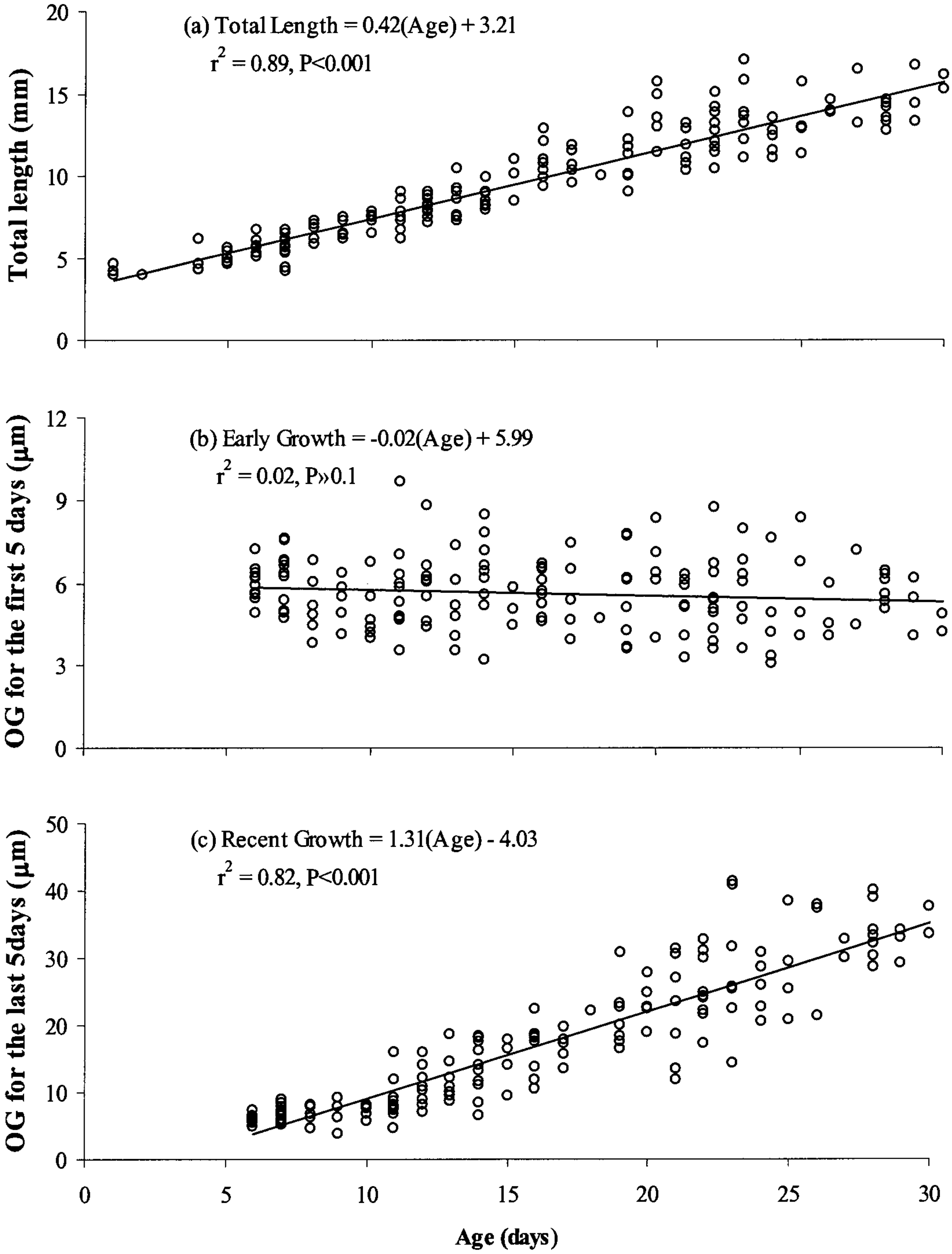

Figure 3. Linear regressions of (a) total length (mm), (b) otolith growth (OG) for the first five days (µm) and (c) otolith growth for the five days prior to capture (µm), each versus larval age (days). Residuals from these regressions were used to group the larvae on the basis of LAA, EG and RG (see text for details).

The larvae were then grouped in 5-day age intervals, which was the minimum interval possible that still permitted statistically reasonable sample sizes in each age class.

The effect of age-dependent variation in prey volume ingested was removed as follows. Prey volume data were first log-transformed to obtain a normal distribution of residuals (Fig. 4). The residuals were then estimated from the linear regression of log-transformed prey volume (PV) data against age ($\ln(PV)=0.16*Age-5.27$, $r^2=0.65$, $P<0.001$). The residuals were found to be randomly distributed with respect to age (linear regression, $r^2\ll0.01$, $P\gg0.1$).

To determine whether length-at-age had a significant effect on feeding success the residual prey volume in larval guts was compared between the LAA_{long} and LAA_{short} groups (both within and across age-classes) using a two-way ANOVA with length-at-age and age-class as the independent variables. Within age-classes, differences in residual prey volume between LAA_{long} and LAA_{short} groups were tested using t-tests with Bonferroni-adjusted probabilities.

***Early larval growth rate*:** To test whether growth rate during the first five days post-hatch affects larval foraging ability, I focused on those larvae that were more than five days old at the time of capture. Larvae were categorized as having either high (EG_{high}) or low (EG_{low}) early growth on the basis of the residuals estimated from a regression of otolith growth for the first five days post-hatch (OG) on age ($OG =-0.02*Age+5.99$, $r^2=0.02$, $P\gg0.1$, Fig. 3b). Larvae were then grouped across 5 day age intervals. Both the EG_{high} and low EG_{low} group designations were independent of length and age. Visual inspection of the data also showed that there was no time-dependence in the distribution of the EG_{high} and EG_{low} groups (i.e. the EG_{high} and low EG_{low} larvae were distributed randomly across the sampling period).

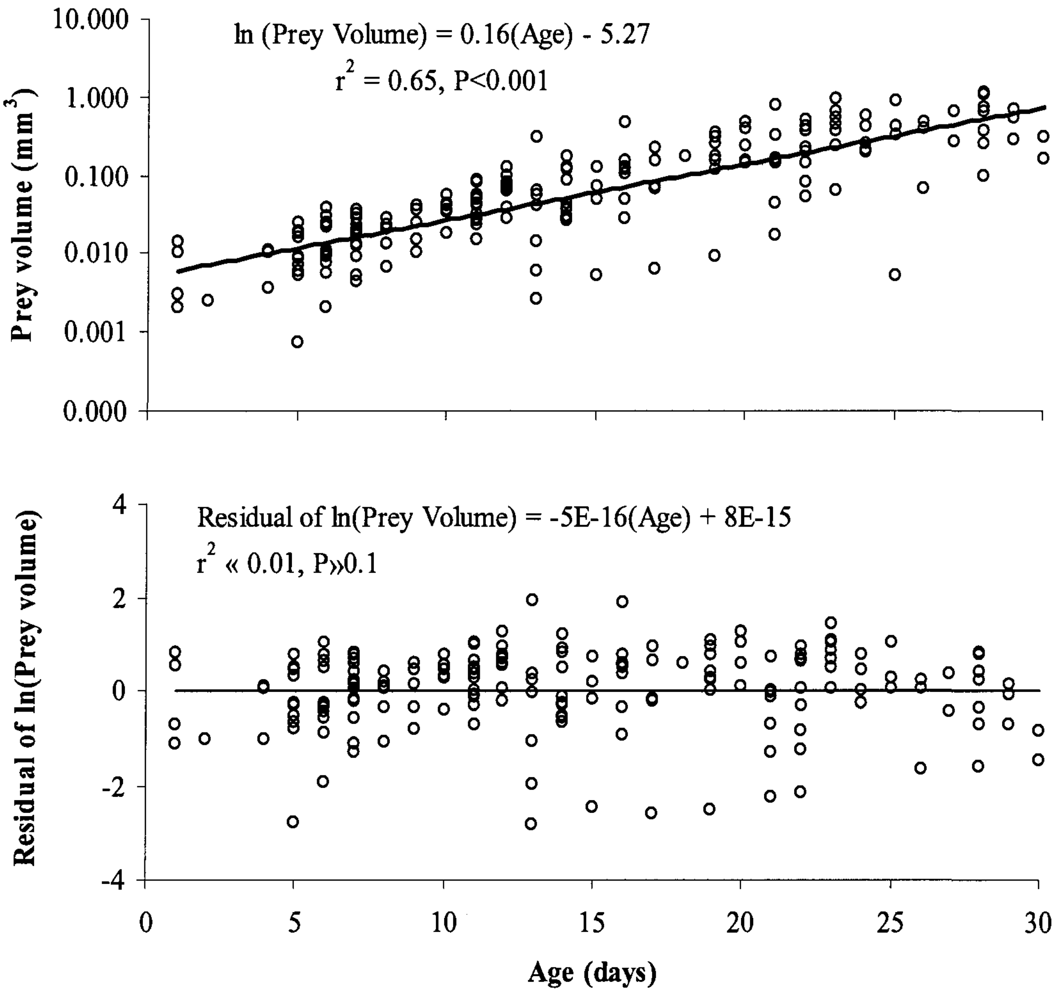

Figure 4. Linear regression of Prey Volume vs. larval age (top panel), and the residuals from the regression (bottom panel).

Age-dependent variation in prey volume in guts was removed as above. Residual prey volume in guts was compared between the EG_{high} and low EG_{low} groups (both within and across age classes) using a two-way ANOVA with growth states for the first five days and age-classes as independent variables. Within each age-class, differences in residual prey volume between EG_{high} and low EG_{low} groups were tested using t-tests with Bonferroni-adjusted probabilities.

Recent growth rate: To test whether growth during the five days prior to capture is indicative of larval foraging ability, I again considered only those larvae more than 5 days old at the time of capture. To eliminate age bias, individual larvae were categorized as having either high or low recent growth rate on the basis of residuals from a regression of otolith growth over the 5 days before capture and age ($OG=1.31*Age-4.03$, $r^2=0.82$, $P<0.001$, Fig. 3c). Age-dependent effects were removed as above and the residual gut contents of the two groups was compared (within and across age-classes) using a two-way ANOVA with recent growth and age class as the independent variables. Within each age-class, differences in residual prey volume between RG_{high} and RG_{low} groups were tested using t-tests with Bonferroni-adjusted probabilities.

2.3 Results

2.3.1 Ontogenetic switch in larval diets

The composition of the larval diet changed considerably with age (Fig. 5). The diets of the youngest larvae were dominated by copepod nauplii (235±60 µm, mean length±SD). By age 20 days, however, the main prey item had switched to copepodites and adult copepods (322±66 µm, 529±124 µm, respectively). This alteration in diet indicates that larval feeding ability improves with their age and size (*i.e.* larger prey being both less abundant and harder to capture).

2.3.2 Effect of length-at-age on gut fullness

When grouped by length-at-age, the LAA_{long} groups were significantly larger than LAA_{short} groups at all age-classes except the 1-5 day age class (Table 1). When pooled across age-classes, larvae that were larger at age contained significantly more food in their guts than individuals that were smaller at age (two-way ANOVA: length effect, $F_{1,180}=13.149$, $P<0.001$, Fig 6a). Comparing age-classes we see that the LAA_{long} larvae contained more food per gut than the LAA_{short} larvae in three of the six age classes: 1-5d, 16-20d and 21-25d (Bonferroni adjusted t-tests, $t_{16,\,0.05}=2.136$, $P=0.034$; $t_{26,\,0.05}=2.209$, $P=0.025$; $t_{31,\,0.05}=4.158$, $P<0.001$, respectively, Fig. 6b). Results of a two-way ANOVA on the residual gut volumes indicates a significant interaction between age and length effects ($F_{5,180}$=3.508, P=0.005, Table 2a). This seems to be due to the tendency of the difference in prey volumes between the LAA_{long} and LAA_{short} groups to be quite variable with age. However, there was no statistically significant difference among the residual gut volumes ingested by different age-classes (two-way ANOVA: age effect, $F_{5,180}$=1.092, P=0.367, Table 2a), indicating that, overall, the difference between the prey volumes ingested by the LAA_{long} and LAA_{short} groups was not affected by age-dependent variation. In other words, even though there were significant differences in some age-classes, overall there was no consistent pattern in the differences between the LAA_{long} and LAA_{short} groups.

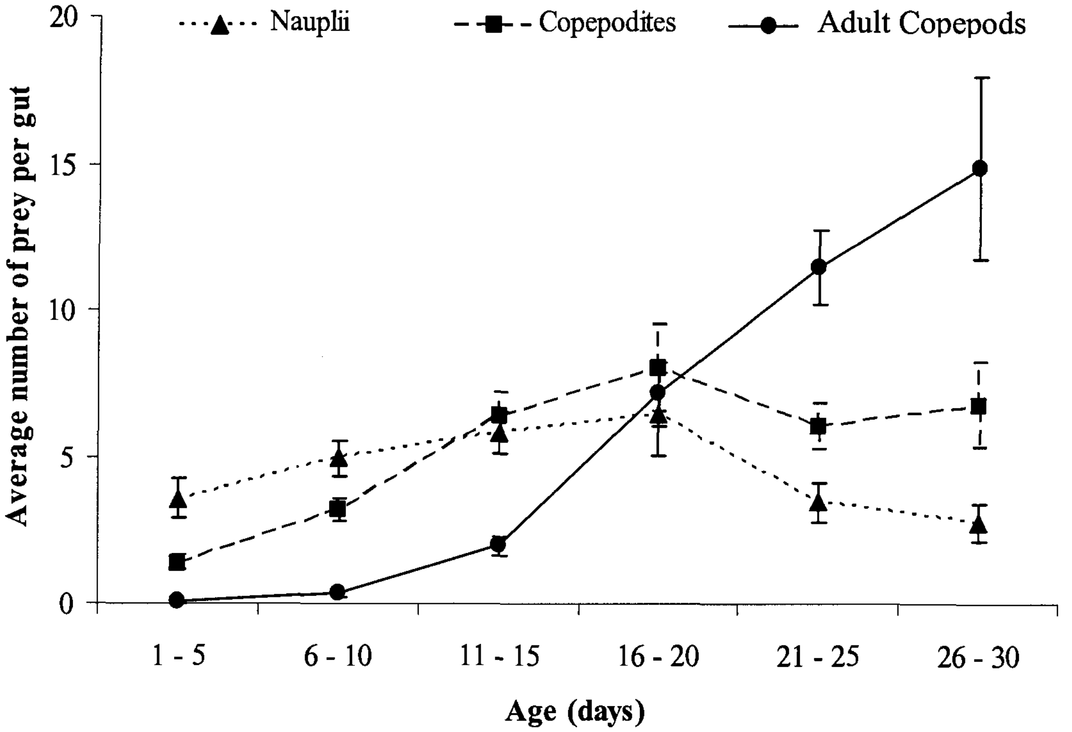

Figure 5. Contributions of nauplii, copepodites and adult copepods to the diets of the different age-classes of *Ulvaria subbifurcata* larvae. Error bars are ±1 SE.

Table 1. Average length of larval *Ulvaria subbifurcata* when grouped as a function of (a) length-at-age, (b) early larval growth, and (c) recent larval growth. * indicates that mean length of groups is different at the alpha = 0.05 level. Note that individuals younger than 6 days old were removed in analyses of (b) and (c).

(a) Grouped by length-at-age

Age	LAA_{short}			LAA_{long}			LAA_{long} - LAA_{short}	P-value*
	n	length (mm)	sd.	n	length (mm)	sd.	(mm)	
1-5d	7	4.58	0.35	11	5.06	0.76	0.48	NS
6-10d	23	5.68	0.68	20	6.84	0.57	1.17	<0.001
11-15d	29	7.80	0.75	13	9.40	0.83	1.60	<0.001
16-20d	10	9.90	0.67	18	12.20	1.51	2.29	<0.001
21-25d	17	11.65	0.81	16	13.95	1.29	2.29	<0.001
26-30d	13	13.86	0.70	4	15.99	0.95	2.13	<0.001

(b) Grouped by early growth (first five days of post-hatch)

Age	EG_{low}			EG_{high}			EG_{high} - EG_{low}	P-value*
	n	length (mm)	sd.	n	length (mm)	sd.	(mm)	
1-5d	-	-	-	-	-	-	-	-
6-10d	21	6.35	0.93	22	6.10	0.79	-0.25	NS
11-15d	20	8.06	1.06	22	8.51	1.06	0.46	NS
16-20d	13	10.44	0.82	15	12.19	1.83	1.75	0.004
21-25d	20	12.09	1.25	13	13.80	1.48	1.70	0.001
26-30d	9	14.16	1.07	8	14.58	1.34	0.42	NS

(c) Grouped by recent growth (five days prior to capture)

Age	RG_{low}			RG_{high}			RG_{high} - RG_{low}	P-value*
	n	length (mm)	sd.	n	length (mm)	sd.	(mm)	
1-5d	-	-	-	-	-	-	-	-
6-10d	12	6.78	0.98	31	6.00	0.71	-0.78	NS
11-15d	29	8.06	0.97	13	8.83	1.14	0.77	NS
16-20d	13	11.10	1.18	15	11.62	2.03	0.52	NS
21-25d	18	11.97	0.98	15	13.73	1.63	1.76	<0.001
26-30d	8	13.99	0.99	9	14.69	1.30	0.70	NS

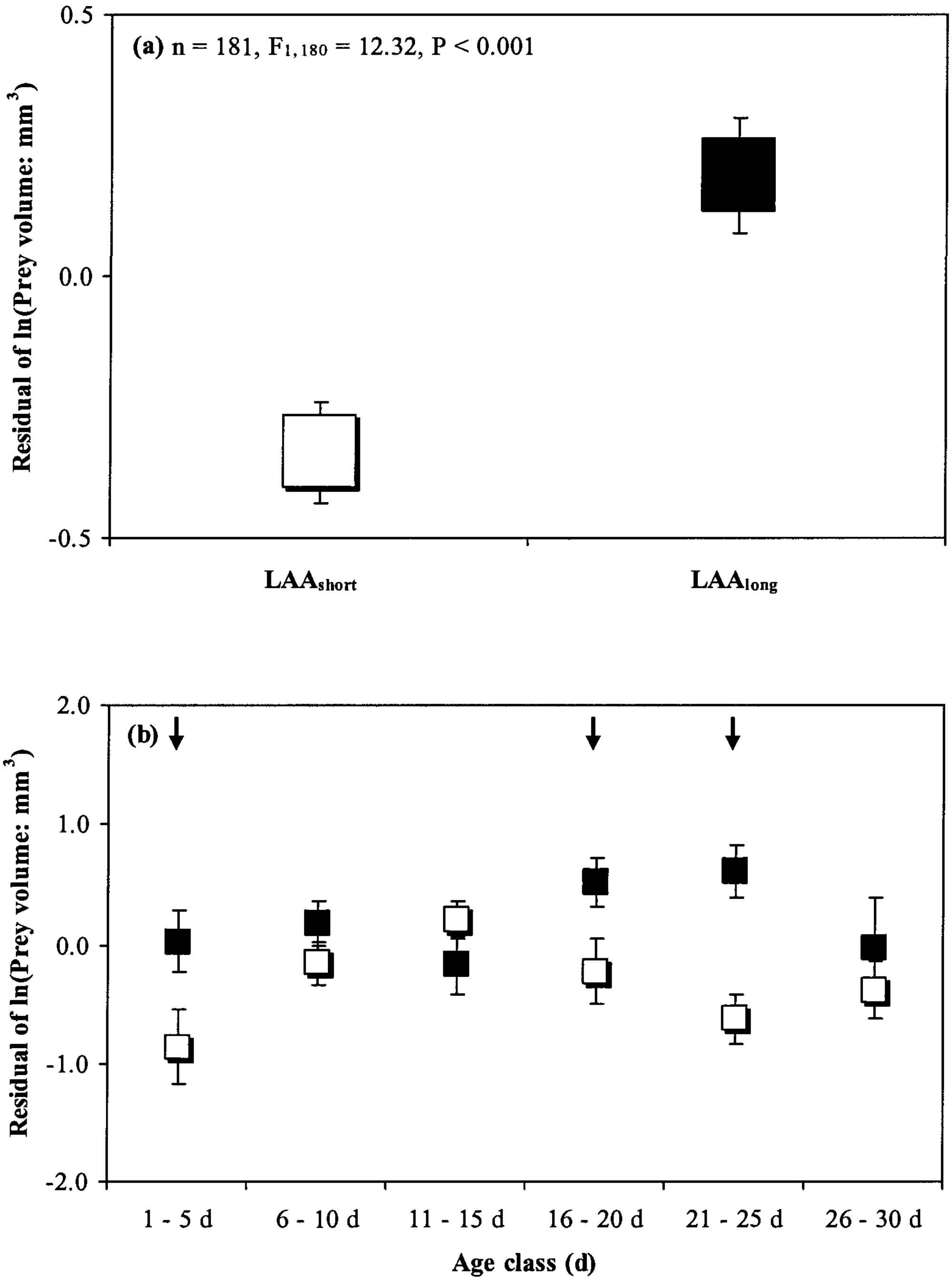

Figure 6. Mean residual prey volume (mm^3) in the guts of larval *Ulvaria subbifurcata* for LAA$_{long}$ (black) and LAA$_{short}$ (white) groups: (a) pooled across age-classes (result of one-way ANOVA reported in the panel), and (b) within age-classes. Arrows indicate significant differences between groups within an age-class. Error bars in both panels are ±1 SE.

Table 2. Results of two-way ANOVAs on prey volume in the guts of larval *Ulvaria subbifurcata*. Factors were (a) length-at-age and age class, (b) early growth and age class, and (c) recent growth and age class. The smaller sample sizes for the ANOVAs on early growth and recent growth (n = 163 as opposed to n = 181) result from the fact that larvae less than 5 days old were excluded from these particular analyses. See text for details.

(a) LAA_{short} vs. LAA_{long} (n = 181)

Source of Variation	df	SS	MS	F	P
Age class	5	3.986	0.797	1.092	0.367
Growth group	1	9.600	9.600	13.149	<0.001
Age class x Growth group	5	12.805	2.561	3.508	0.005
Residual	169	123.388	0.730		
Total	180	151.303	0.841		

(b) EG_{low} vs. EG_{high} (n = 163)

Source of Variation	df	SS	MS	F	P
Age class	4	2.819	0.705	0.942	0.441
Growth group	1	14.494	14.494	19.382	<0.001
Age class x Growth group	4	5.502	1.375	1.839	0.124
Residual	153	114.419	0.748		
Total	162	135.768	0.838		

(c) RG_{low} vs. RG_{high} (n = 163)

Source of Variation	df	SS	MS	F	P
Age class	4	3.624	0.906	1.085	0.366
Growth group	1	0.990	0.990	1.185	0.278
Age class x Growth group	4	1.430	0.358	0.428	0.788
Residual	153	127.743	0.835		
Total	162	133.674	0.825		

2.3.3 Effect of early larval growth on gut fullness

When grouped by otolith growth for the first five days post-hatch, the EG_{high} larvae contained significantly more food in their guts than did the EG_{low} larvae (two-way ANOVA: early growth effect, $F_{1,162}=19.382$, $P<0.001$, Fig. 7a). When divided by age-class, the EG_{high} larvae ingested more prey at all ages than did the EG_{low} larvae, although differences only became statistically significant after age 15d (Bonferroni adjusted t-tests, 16-20d, $t_{26,0.05}=2.622$, $P=0.010$; 21-25d, $t_{31,0.05}=3.321$, $P=0.001$; 26-30d, $t_{15,0.05}=2.039$, $P=0.043$). The magnitude of the difference in prey volume between the EG_{high} and EG_{low} groups increased with age (Fig. 7b). There was no significant interaction between age and early growth effects (two-way ANOVA, $F_{4,162}=1.839$, $P=0.124$) nor any significant difference among the residual gut volumes across the different age-classes (two-way ANOVA: age effect, $F_{4,162}=0.942$, $P=0.441$, Table 2b).

2.3.4 Effect of recent larval growth on gut fullness

When grouped by recent otolith growth (*i.e.* over the five days prior to capture), the RG_{high} larvae generally ingested more prey than did the RG_{low} larvae (Fig. 8). However, none of the observed differences were statistically significant, neither within (Bonferroni adjusted t-test, $P>0.250$, Fig. 8b) nor across age-classes (two-way ANOVA: recent growth effect, $F_{1,162}=1.185$, $P=0.278$, Fig. 8a). There was also no significant interaction between age and recent growth effects (two-way ANOVA, $F_{4,162}=0.428$, $P=0.788$) nor any significant difference among the residual gut volumes across the different age-classes (two-way ANOVA: age effect, $F_{4,162}=1.085$, $P=0.366$, Table 2c).

2.4 Discussion

2.4.1 Comparing proxies for larval survival

Both length-at-age and early growth rate had significant effects on larval gut fullness. When pooled across age-classes, larvae that were relatively large at a given age contained more food in their guts than did larvae that were relatively small at age (Fig. 6a), and larvae with high early growth rates contained more food than did larvae with low early

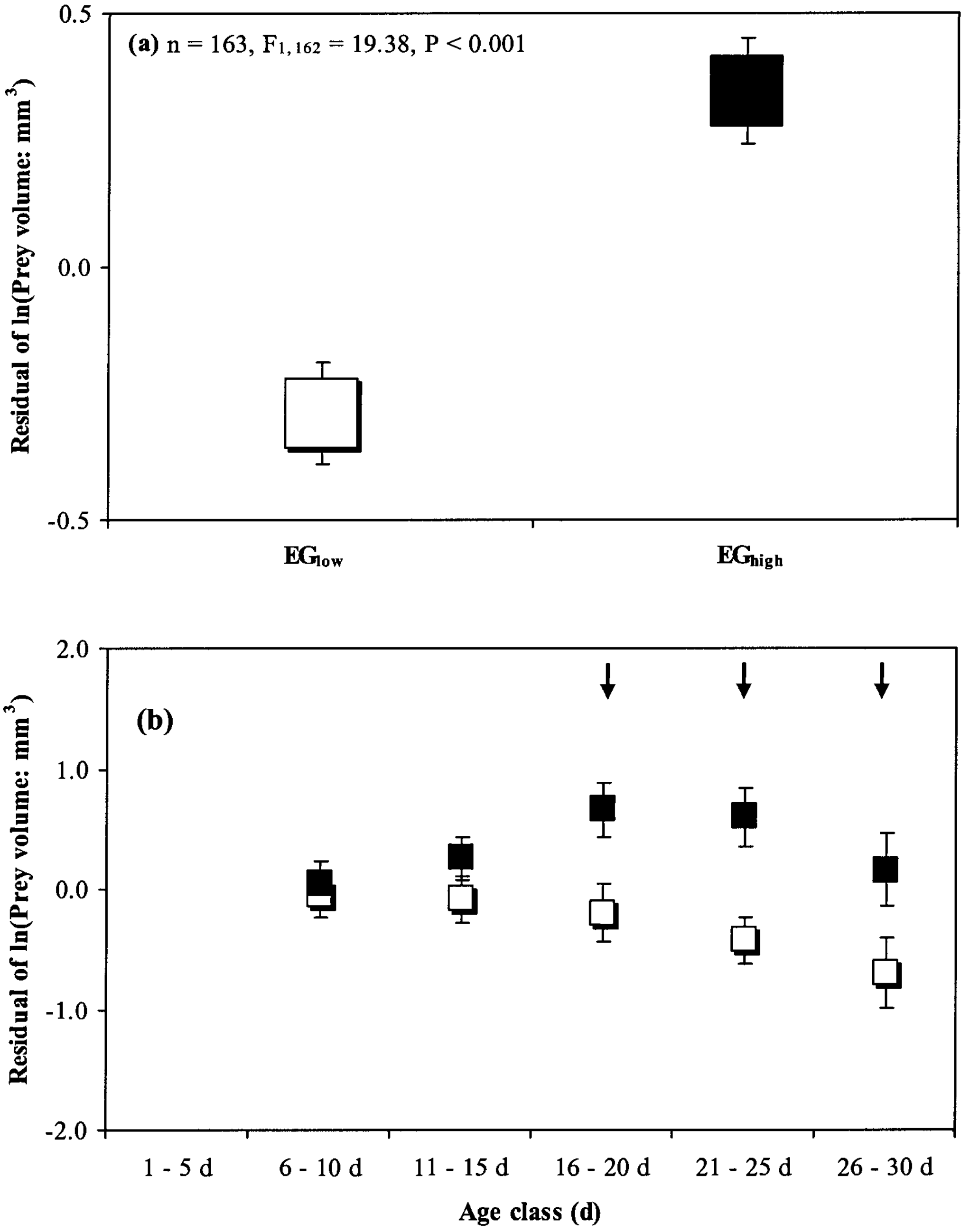

Figure 7. Mean residual prey volume (mm^3) in the guts of larval *Ulvaria subbifurcata* for EG_{high} (black) and EG_{low} (white) groups: (a) pooled across age-classes (result of one-way ANOVA reported in the panel), and (b) within age-classes. Arrows indicate significant differences between groups within an age-class. Error bars in both panels are 1 SE.

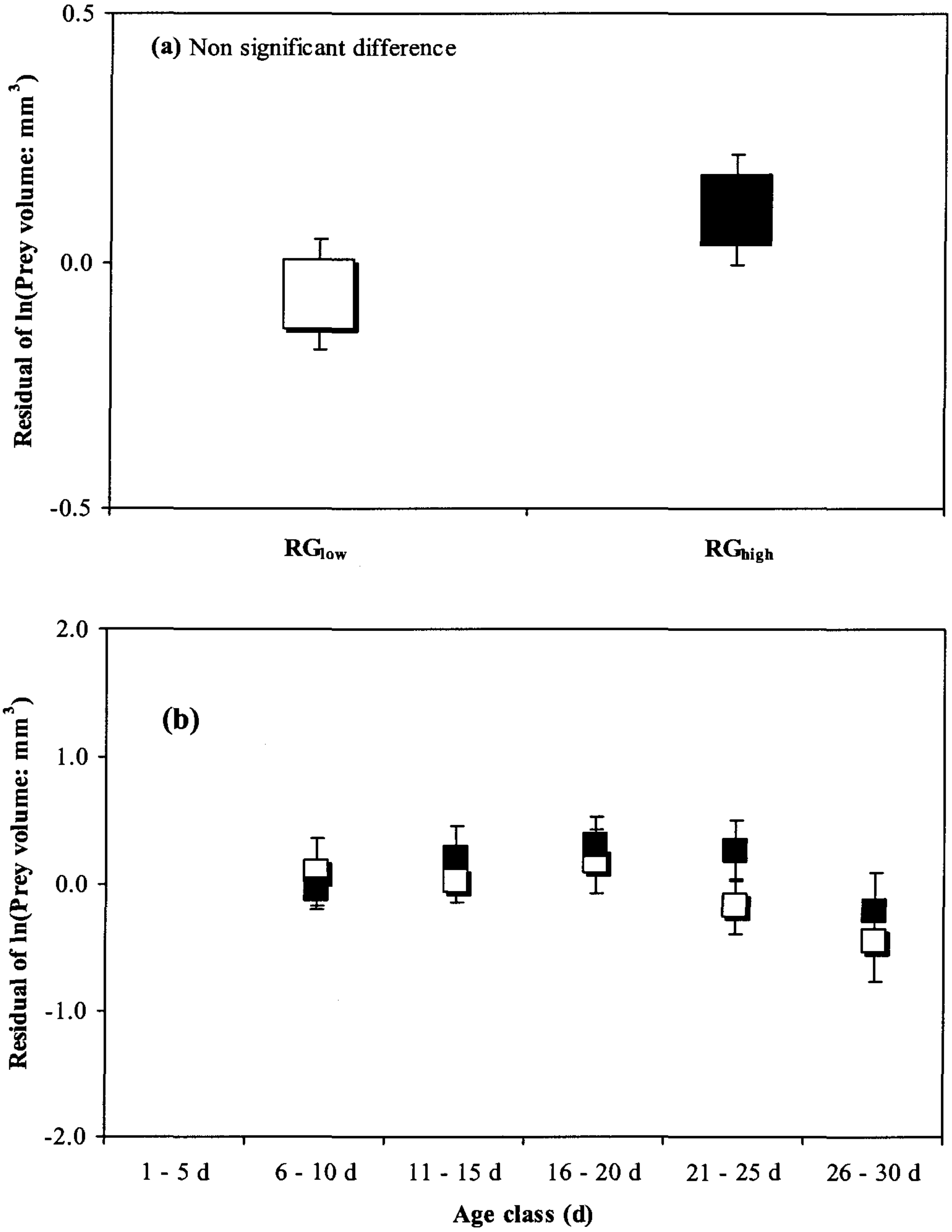

Figure 8. Mean residual prey volume (mm^3) in the guts of larval *Ulvaria subbifurcata* for RG$_{high}$ (black) and RG$_{low}$ (white) groups: (a) pooled across age-classes (result of one-way ANOVA reported in the panel), and (b) within age-classes. Arrows indicate significant differences between groups within an age-class. Error bars in both panels are 1 SE.

growth rates (Fig 7a). In contrast, recent growth history (*i.e.* over the five days prior to capture) had no discernible effect on larval gut fullness (Fig 8a).

When the larvae are divided by age the story becomes somewhat more complex. In every age-class individuals with high early growth had more food in their guts than did larvae of the same age but with poor early growth (Fig 7b). The differences between the groups become significantly different beginning at age 16d, continuing through to age 30d. In the length-at-age analyses, significant effects were evident in three of the six age-classes (Fig 6b), but as the three age-classes in question were not sequential it is difficult to interpret this result conclusively. On the other hand, there were no significant effects of recent growth rate either within age-class or when pooled across age-class (Fig 8b).

Although both length-at-age and early growth rate show growth-dependent effects on gut fullness, the pattern appears to be more consistent for the latter. These results confirm the idea that being large at a given age can have a positive effect on feeding success, but not always. Assuming that enhanced feeding success increases an individual's chance of survival, this result would seem to generally support the idea that "bigger-is-better". Perhaps more interesting, however, is the finding that (i) recent growth history did not affect feeding success, and (ii) high growth during the early larval stage appears to be a better predictor of future feeding success than length-at-age.

A number of studies have used high growth rate in the days immediately prior to capture as an indication of high overall condition. If this is generally true, then one might have expected that larvae with higher recent growth rates should also have fed more successfully than those with low recent growth rates. Suthers (1998) suggested that peripheral otolith growth and relative RNA content are the more appropriate condition index for larval fish. In his paper, he considered the possibility that larvae with faster peripheral otolith growth also have a higher condition and thus a higher survival possibility than larvae with slower peripheral otolith growth. In the present study, however, I found no statistically significant difference in the residual prey volume in any age-class, although the RG_{high} larvae generally ingested more prey than the RG_{low} larvae. Taken together these results suggest two possibilities: (i) that an individual's feeding ability is already established at (or shortly after) hatch, and (ii) that the early growth rate is a better indicator for individual ability (at least in terms of foraging success) than the more widely used proxies of length-at-age and recent growth state.

I considered these three proxy estimates for foraging ability because enhanced foraging success should have a positive effect on larval growth (assuming that larval fish are food limited). Besides reflecting an individual's foraging ability, growth rate should also reflect the nutritional condition of the larvae. Length-at-age and recent growth should better reflect an individual's recent nutritional condition than will early growth, since early growth is likely independent of the recent events experienced by an individual prior to capture (especially for older larvae). Nevertheless, the results showed that early growth rate is a better predictor of future feeding success than the other two estimates. Furthermore, there was no significant interaction between LAA_{short}- LAA_{long} groups and EG_{low}- EG_{high} groups in terms of the amount of prey ingested (Table 3). However, within the LAA_{short} and LAA_{long} groups, the EG_{high} larvae ingested significantly more prey than the EG_{low} larvae. In contrast, the LAA_{long} larvae did not ingest significantly more prey than LAA_{short} larvae within the EG_{low} and EG_{high} groups (Table 3). These results support that the idea that high growth during the early larval stage can affect an individual's future foraging ability.

Taken together, length-at-age and recent growth rate would seem to better reflect an individual's recent nutritional condition than its ability to ingest prey. However, given that the best predictor of feeding success was early growth rate, it would also appear that nutritional condition may not always be indicative of the an individual's foraging ability. In other words, an individual's very early growth rate may indicate its "potential fitness", while its length-at-age and recent growth rate may better reflect its nutritional condition at the time of capture. This result agrees with several previous studies that have shown that a large otolith (in diameter) during the first week after hatching is not necessarily a correlate of large body size, but may be an indicator of fast growth and enhanced survivorship (Mosegaard *et al.*, 1988; Mosegaard, 1990; Titus and Mosegaard, 1991).

Table 3. Results of two-way ANOVA on prey volumes in guts of larval *Ulvaria subbifurcata*. Factors used were length-at-age (LAA) and early growth (EG). The t values (and their associated P values) indicate results from Bonferroni adjusted t-tests.

Source of variation	df	F	P	t	P
LAA_{short}-LAA_{long}	1	4.601	0.033		
EG_{low}-EG_{high}	1	10.835	0.001		
LAA_{short}-LAA_{long} X EG_{low}-EG_{high}	1	0.0415	0.839		
EG_{low}-EG_{high} within LAA_{short}	90			2.358	0.020
EG_{low}-EG_{high} within LAA_{long}	69			2.312	0.022
LAA_{short}-LAA_{long} within EG_{low}	81			1.331	0.185
LAA_{short}-LAA_{long} within EG_{high}	78			1.716	0.088

Recently, Takasuka *et al.* (2004) tested the "bigger-is-better" and the "growth-selective predation" hypotheses by comparing the growth trajectories of larval Japanese anchovy (*Engraulis japonicus*) that had been consumed by predators against those of "survivors" (*i.e.* individuals that had not been consumed). Their results show that faster growing individuals were more likely to survive, even if the faster growers were smaller than slow growing larvae. This agrees with my results, insofar as length-at-age does not predict an individual's likelihood of survival. However, unlike my results, Takasuka et al (2004) found that, on average, the survivors had *lower* growth rates than did the original population at earlier stages (Takasuka *et al.*, 2004). They also examined the growth histories of larvae prior to and during metamorphosis and found that metamorphosing larvae had higher-growth rates than the non-metamorphosing larvae at earlier stages (Takasuka *et al.* 2004). This corresponds with my finding that larvae that achieve high early growth rates show better ability to ingest prey at later stages, possibly enabling such larvae to reach the juvenile stage faster.

Growth-related mortality hypotheses such as the bigger-is-better (Litvak and Leggett, 1992), the growth-mortality (Anderson, 1988), and the growth-selective predation hypothesis (Takasuka *et al.*, 2003) all contend that larval growth rates (or length-at-age) are indicative of an individual's future survival probability. All attribute growth variation between cohorts to variability in temperature and/or prey availability and growth variability within a cohort to differences in the prey availability encountered by individual larvae. On the other hand, studies that are primarily concerned with understanding the factors that regulate larval growth generally contend that environmental variability leads to growth rate variation, and usually interpret high growth rates as a precursor to strong recruitment. However, in spite of all of this research, a clear understanding of the fate of individual larval fish has remained elusive. In fact, the recent paper by Takasuka *et al.* (2004) represents the first time that researchers have been able to directly measure predation on larval fish in the field. This unexplained variability may, in part, be attributed to the assumption that the growth rate (or length-at-age) is indicative of an individual's ability to capture prey and possibly to avoid predators.

2.4.2 The relationship between individual feeding ability and growth

To understand the ontogenetic development of feeding ability of larval fish, the change in the size distribution of prey items consumed merits note. Like most teleost larvae, larval *Ulvaria* mainly ingest nauplii during the early larval period, before gradually switching their diet from nauplii to adult copepods as they grow (Fig. 5). This clearly demonstrates the ontogenetic progression of larval feeding ability, since copepod nauplii generally swim slower and have less effective escape response than do adult copepods (Titelman and Kiorboe, 2003). However, given the physical constraints that larvae have to overcome while foraging (*e.g.* low Reynolds number conditions, micro-scale turbulence, etc), it seems likely that any effect of individual variability in foraging ability (as reflected by differences in gut content) should be most evident among older larvae, given their relatively greater swimming ability. If so, this might explain why observed differences in prey volumes ingested by the EG_{high} and EG_{low} larvae did not become significantly different until age 16d.

On the other hand, these results also create something of a paradox. Given that early growth seems to be a good indicator of future feeding success, then it stands to reason that these same EG_{high} larvae (*i.e.* the EG_{high} group) should also grow larger and/or faster than the rest of their cohort, thereby ultimately becoming large at age. However, given the high degree of spatiotemporal patchiness of the larval prey field, the amount of prey ingested by an individual will be the result of both its foraging ability and a certain amount of luck (*e.g.* whether it encounters a high density prey patch). Therefore, under certain circumstances, it remains possible that weaker larvae will consume more prey than stronger larvae simply by luck (if, for instance, the weaker larva is feeding in a patch), and that this might even be reflected in their instantaneous growth rate (Hovenkamp, 1990; Ferron and Leggett, 1994). It may be that such short-term variations in feeding success (resulting from variability in the prey field encountered by individual larvae) might lead to the unexplained variability of growth rate for understanding of the fate of larval fishes.

In conclusion, results of this study suggest that larvae with the best feeding ability (the EG_{high} group) may not necessarily always be the largest larvae (*i.e.* due to luck), and thus large body length does not necessarily equate to the highest foraging ability. However, larvae with early high growth rate also continued to show good feeding ability at all ages, perhaps indicating a difference between length and ability at different ages. Similar finding were reported by Ringuette *et al.* (2002). Comparing several years of data on mackerel larvae (*Scomber scombrus*), they found that the larvae showed significantly higher gut fullness in 1982 than in any of 1985, 1987 or 1996, (and the 1982 cohort was the strongest), even though mackerel size at the end of each year was smallest in 1982.

To summarize, although individuals with high early growth are likely to be relatively larger at age, and individuals that are larger at age generally ingest more prey, the effect of length-at-age on feeding ability is slight compared to the effect of early growth rate. I conclude that early larval growth rate is a better proxy for foraging success and possibly for survival, assuming that the factors leading to enhanced foraging success (*i.e.* better swimming and prey detection) also contribute to avoiding and evading a predator.

One final area of concern is to determine which factors actually govern early larval growth. The results of this study show that the difference in prey volume between the early growth groups increased consistently with age (Fig. 7). This indicates that the an individual's feeding ability appears to be established shortly after hatch and is maintained for at least 30 days post hatch. This may suggest the existence of some sort of maternal effect on larval foraging ability. Recently, Berkeley *et al.* (2004) found that larvae produced by older female black rockfish (*Sebastes melanops*) grew faster and survived starvation longer than did larvae from younger females (and that the effect of maternal age was considerably stronger than the effect of maternal size). Other maternal effects on various phenotypic traits of fish eggs and larvae have also been documented, including increased size-at-hatch, increased yolk volume (or better yolk quality), and increased size at metamorphosis (Beacham and Murray, 1985; Bengston et al., 1987, Chambers et al., 1989,Chambers and Leggett, 1992). However, it remains to be seen whether such phenotypic maternal effects actually have a positive effect on larval survival. In contrast, the results of this study suggest the existence of a maternal effect on *foraging ability*, which might be expected to have a more direct effect on larval survival than traits that are strictly phenotypic. Taken together, the prey environment encountered by larval fish is likely important for larval survival but, within a cohort, maternal effects may play a role in determining individual ability and viability, and may therefore be more associated with larval survival. In the present study, although the relative importance of the effect of prey variability and maternal effects cannot be compared, the finding that early larval growth is the better predictor of larval feeding success could provide an important insight to understanding population fluctuations.

CHAPTER 3

Does enhanced feeding ability in larval fish increase individual survival probability or encounter rate with predators?

3.1 Introduction

Recruitment of marine fish is poorly correlated with the abundance of egg and larval stages, but often strongly correlated with the abundance of juveniles (Leggett and Deblois, 1994). The unpredictable and extremely high mortality rates during the larval stage have led to the idea that the growth and survival of larval fish are influenced not only by environmental variability but also by variability in individual *viability* (Rice *et al.*, 1993; Cowan and Shaw, 2002). For this reason, understanding the "characteristics of survivors" has recently become a major issue in fisheries oceanography (Fritz *et al.*, 1990; Letcher *et al.*, 1996). Starvation and predation have long been held to be the major sources of mortality among larval fish (Hjort 1914; Bailey and Houde, 1989; Leggett and Deblois 1994). Thus, interannual variability in survival among larval cohorts is believed to result from variability in the interactions among larval fish, their predators, and their prey (Pepin, 2004). However, studies examining interactions between larval fish and their prey are usually conducted independently of those considering larval fish and their predators (Hewitt *et al.*, 1985; Letcher *et al.*, 1996), despite the fact that such interactions co-occur in the field, and both predation and starvation are likely dependent on larval phenotype and/or an individual's ability for swimming and perception (Fritz *et al.*, 1990). The goal of this study is to identify the characteristics of potential survivors among larvae of the same age in terms of their predator-prey interactions.

During the larval period most fish undergo dramatic morphological and osteological changes (LeDrew and Green, 1975; Kendall *et al.*, 1984; Lee and Kim, 2000). These ontogenetic changes, together with fast gut evacuation rates during this period (Jordaan and Brown, 2003), require good nutritional conditions, and thus strong feeding activity is required throughout the larval period. Therefore, it has been proposed that among larvae of the same age, individuals that are best at swimming and perceiving prey should also increase their feeding success and, thus, their growth (Gallego and Heath, 1997; Fuiman and Cowan, 2003). For the same reason, many studies have employed larval growth rate or length-at-age as a proxy for an individual's survival probability. In contrast, however, I found (in Chapter 2) that an individual's growth rate during the first five days post-hatch was a better predictor of its future feeding success (when estimated as the volume of food in the gut) than either its length-at-age or recent growth rate (*e.g.* the five days prior to capture). To date, however, no study has been able to conclusively demonstrate whether individuals that feed more successfully also have higher survival probabilities, in part because the presumed positive effect on feeding success may be outweighed by the fact that increased searching activity also increases encounter rates with predators (Bailey and Houde, 1989; Cowan and Houde, 1992; Winemiller and Rose, 1993; Gallego and Heath, 1997).

The rate at which an individual encounters predators and prey is a positive function of the volume of water it searches (Blaxter, 1986; Cowan and Houde, 1992). The water volume searched is itself a function of (i) how much food the larva needs to consume per day day, (ii) the prey density, (iii) the speed at which the larva swims, and (iv) the ability of the larva to capture any prey that it encounters (Gallego and Heath, 1997). Therefore, given that (i) most of the swimming activity of larval fish is associated with foraging, and that (ii) most larval fish spend much of their day engaged in foraging (Rosland and Giske, 1994; Pepin and Penney, 2000), a large portion of the larval energy budget is associated with foraging. Therefore, understanding the role of individual variability in foraging ability may help to understand the characteristics of survivors, since the less time an individual spends foraging, the less energy it expends and the fewer predators it will encounter.

The objective of the present study is to explore further the characteristics of potential survivors, among larvae of the same age, as reflected by variability in their individual feeding patterns. To accomplish this I first examine ontogenetic development in feeding patterns by examining shifts in the size distribution of larval gut contents with age. I then compare the individual feeding patterns among larvae within the same age-class divided on the basis of (i) length-at-age and (ii) growth rate for the first five days post-hatch in order to define the potential survivors at age, because the measurements have achieved relatively wide acceptance as a proxy for a larval survival probability, or at least for a larval feeding ability (Miller *et al.*, 1988; Mosegaard *et al.*, 1988; Mosegaard, 1990; Sogard, 1997). I discuss the optimal foraging strategy in terms of whether individual larvae that feed more successfully also could have higher survival probabilities in prey-predator interactions.

3.2 Materials and methods

3.2.1 Field methods

Larval fish were collected from 21-29 July 2000 from Trinity Bay (48°N, 53.5°W), Newfoundland, using a 4 m^2 tucker trawl with sections of 1000, 570, and 333 μm mesh size. An oversized cod-end (20 cm diameter, 30 cm length) was used to minimize trauma sustained by the larvae during capture (Dower *et al.*, 1998; 2002). The net was towed obliquely at a speed of 1 m/s between the surface and 40m depth, as this layer typically contains more than 95% of the ichthyoplankton in coastal Newfoundland (Pepin *et al.*, 1995). I chose to focus on larvae of the radiated shanny, *Ulvaria subbifurcata*, because: (i) they are numerically dominant in the summer ichthyoplankton community of coastal Newfoundland, (ii) they are robust to handling, and (iii) the larvae begin exogenous feeding almost immediately after hatching (Dower *et al.*, 1998; 2002; Pepin and Penney, 2000). Individual *U. subbifurcata* (*Ulvaria*, hereafter) larvae were sorted from the sample and immediately transferred into 95% ethanol in individual 1.5 ml microcentrifuge tube for later analysis.

3.2.2 Laboratory methods

A total of 191 *Ulvaria* larvae were videotaped and their total lengths measured to the nearest 0.1 mm using an optical imaging system (Scion Image®, Scion corp.). To obtain prey size data, larval guts were excised and the individual prey items in each gut were videotaped and measured using a dissecting microscope equipped with an ocular micrometer. The prosome length of each individual prey item was measured to the nearest 0.01 mm. Prey items were categorized as either nauplii, copepodites, adult copepoda, or others.

Sagittal otoliths were extracted from the same 191 *Ulvaria* larvae. Otoliths were embedded in epoxy resin, ground to near the sagittal plane with a series of graded silicon carbide papers (1000 and 1200 grits), and polished with alumina powder of 0.3 μm diameter (Lee and Kim, 2000). The hatch mark in *Ulvaria* otoliths was previously defined, and the daily periodicity of increment formation validated, by Fisher (2000). All otoliths were measured under a Leica DMLS compound microscope (1000X) connected to a Nikon Coolpix® 995 digital camera. The width of each otolith increment was measured by marking the outer edge of the increment along the longest axis of the otolith. Because of the potential for measurement error (Pepin *et al.*, 2001), all otoliths were read three times, and the width of each increment was measured twice. If the age estimated on the second and third readings differed from the first or second, the specimen was excluded from further analysis. If the increment width of the second measurement differed by more than 5% from the first measurement, the second measurement was considered incorrect. If the number of incorrect measurements was more than 10% of the total number of increments in a given otolith, the specimen in question was excluded from further analysis.

3.2.3 Data Analyses

Comparisons between age-classes: In order to understand the foraging strategy of potential survivors at a given age, I first examined ontogenetic shifts in diet. Since capture success by larval fish is known to be a strong function of both prey size and the development stage of the larva (Folkvold and Hunter, 1986; Blaxter and Fuiman, 1990; Juanes, 1994; Munk, 1992; 1997; Brodeur, 1998), I looked for ontogenetic shifts in feeding by comparing both the length-frequency distributions of prey and the mean prey sizes ingested by *Ulvaria* larvae of different ages (total age range of 1-30 days old).

I initially grouped the 191 *Ulvaria* larvae into six 5-day age classes (1-5, 5-10, 11-15, 16-20, 21-25 and 26-30 days). To determine the ages at which larvae underwent significant shifts in diet, differences in prey size between adjoining age-classes were tested using a multiple comparison procedure following a one-way ANOVA. In this analysis, as expected, there was a significant difference in the mean prey size ingested by the different age classes (ANOVA, F=178.78, df=5, P<0.001). To determine which age classes differed I used Bonferroni adjusted t-tests. On the basis of these results, the *Ulvaria* larval period was divided into three stages (early, middle and late) for all subsequent analyses.

Comparisons between growth groups within age-classes: To test for differences in feeding patterns within a given age-class, the larvae were first separated on the basis of length-at-age (and grouped as either LAA_{long} or LAA_{short}) using residuals from a linear regression of total length (TL) on age (Fig. 9a). This procedure effectively eliminates any age-dependent bias which might otherwise occur due to differences in the feeding habits between young and old larvae.

To test the effect of early growth rate the larvae within a given-age class were separated into two groups: a high early growth group (EG_{high}) and a low early growth group (EG_{low}) on the basis of residuals from a regression of otolith growth during the first five days post-hatch (OG) versus age (Fig. 9b). This procedure effectively eliminated any time-dependent effects (*e.g.* different temperature histories) that might have occurred as a function of different birthdates between comparative groups. Note that only those larvae

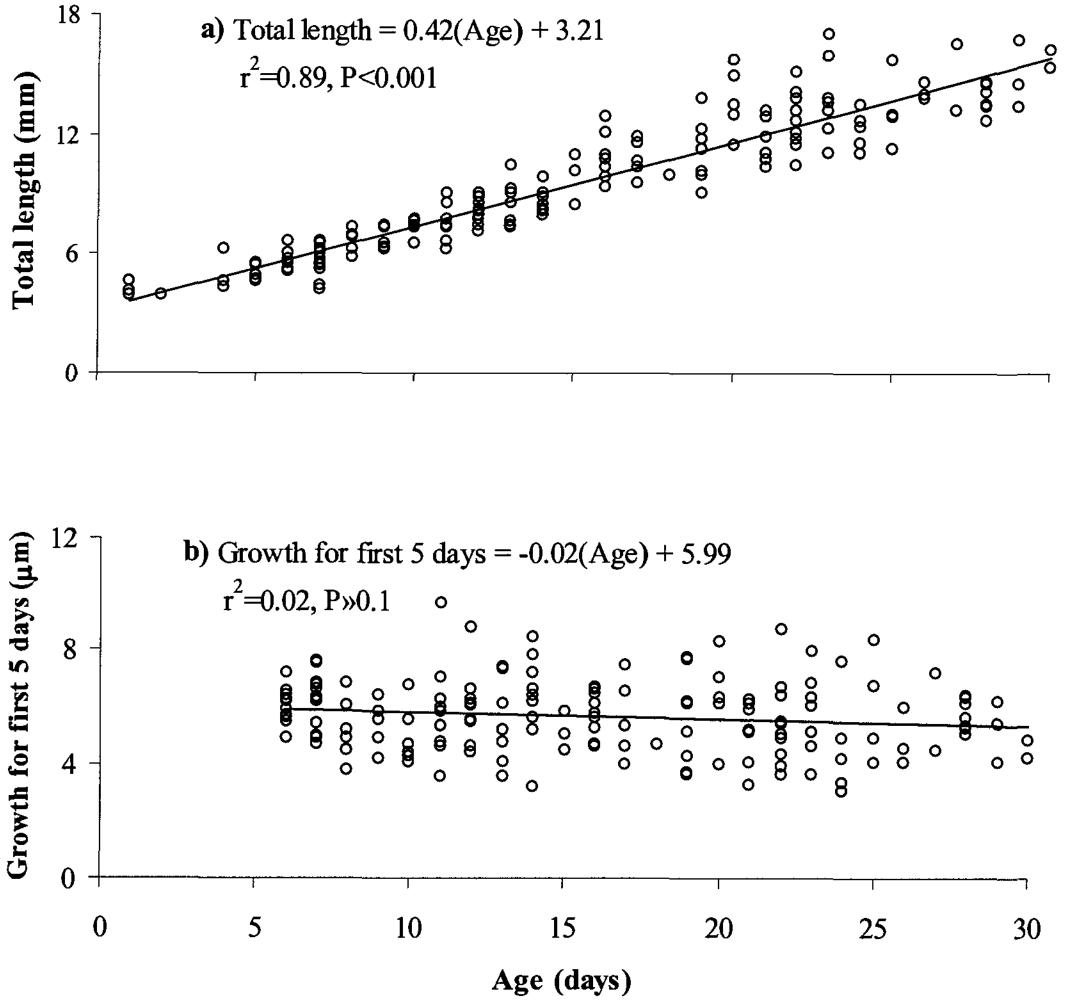

Figure 9. Linear regressions of (a) total length (mm), and (b) otolith growth for the first five days (µm), versus larval age (days). Residuals from these regressions were used to group the larvae on the basis of LAA, EG (see text for details).

more than five days old were considered in this analysis.

To determine whether there were differences in feeding patterns between the growth groups (*i.e.* LAA_{long} vs. LAA_{short} and EG_{high} vs. EG_{low}), two-sample Kolomogorov-Smirnov tests were used to examine the prey length-frequency distributions within each age-class. In order to compare the actual shapes of the two distributions (*i.e.* with no regard for the mean prey size), the data from each distribution were also "centered" around zero by subtracting the mean from each observation. Differences in both the size and the number of prey ingested were also tested using a two-way ANOVA (with length-at-age and early growth rate as the two factors). Within each age-class, differences in the size and number of prey between growth groups were tested using Bonferroni adjusted t-tests.

3.3 Results

3.3.1 Ontogenetic shifts in the diet of *Ulvaria* larvae

The average prey size consumed by the *Ulvaria* larvae increased with larval age (Fig. 10). The maximum prey size consumed also increased with larval age. However, the smallest prey lengths consumed changed little over the entire age range considered (*i.e.* 1-30 days). In other words, despite an increase in the main prey size consumed throughout their ontogeny, even the oldest larvae continued to ingest small prey as well. Also, within each age-class, the prey size distributions were also not affected by age-dependent variation, with most individuals consuming a range of prey sizes. Comparing age-classes, (Fig. 10, Table 4), although there were significant differences in the size-frequency distribution of prey ingested by 1-5 and 6-10 day old larvae (K-S test, $p<0.01$), there was no significant difference in the mean prey size ingested ($df = 459$, $p=0.600$), and both age groups mainly ingested copepod nauplii (252±78 μm, mean length±SD).

Between the ages of 11-20 days the *Ulvaria* larvae began to consume a broader range of prey sizes (mainly between 250-500 μm) and their main prey switched from copepod

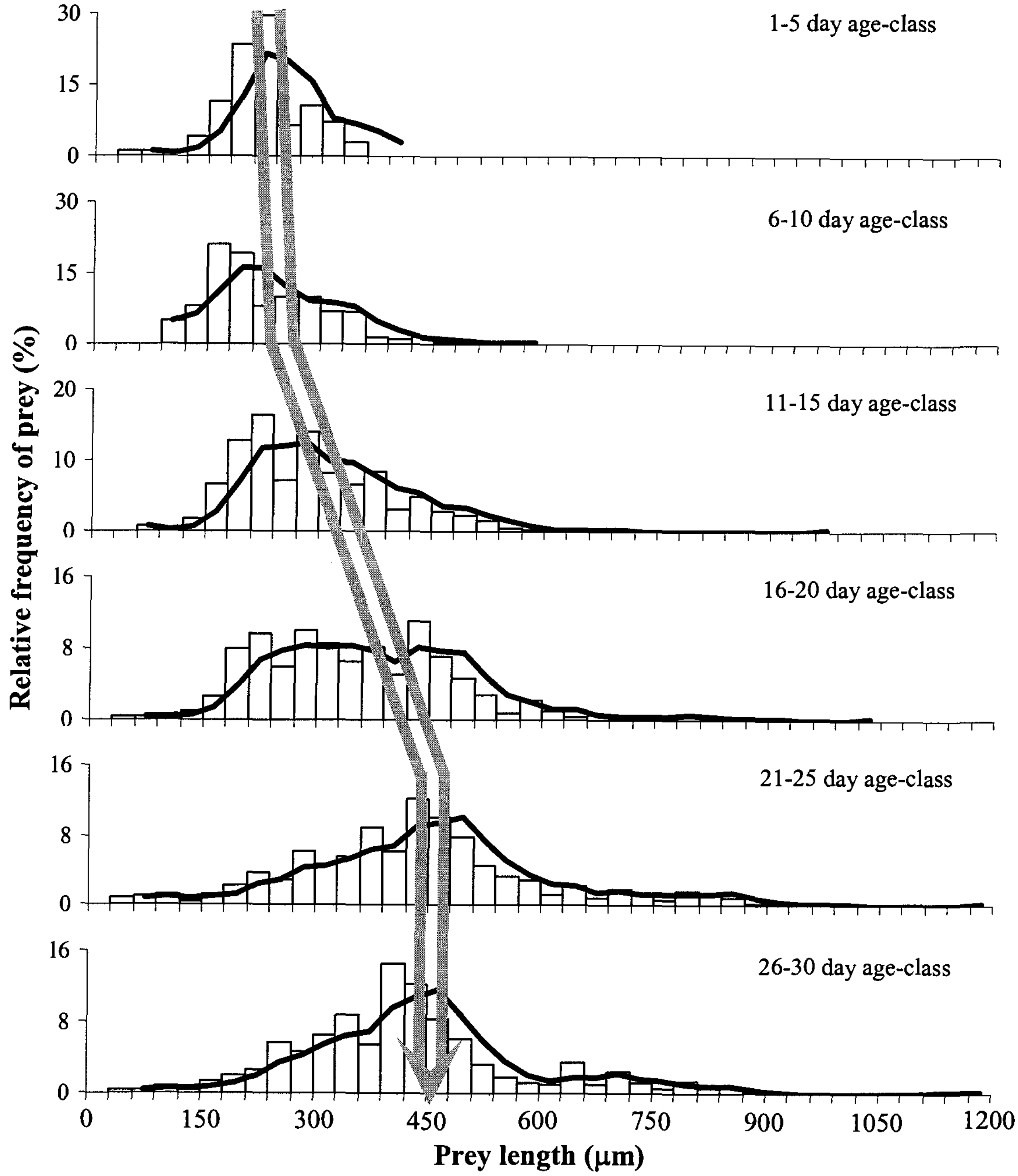

Figure 10. Relative size-frequency distributions of prey in the guts of *Ulvaria* larvae within successive age-classes. The histogram bars represent relative frequencies of prey abundance within a size-interval of 30 μm. Curves were fit using a three-point moving average curve. The grey arrow tracks the change in the mean prey sizes.

Table 4. Results of two-sample Kolomogorov-Smirnov tests and t-tests between adjacent age-classes for prey size distribution and mean prey size, respectively.

Comparison	No. of fish	No. of prey	K-S test		t-test	
			Z	P	t	P
1-5d class vs. 6-10d class	61	461	1.752	0.004	2.055	0.600
6-10d class vs. 11-15d class	85	971	2.338	<0.001	3.999	<0.001
11-15d class vs. 16-20d class	70	1235	3.860	<0.001	7.365	<0.001
16-20d class vs. 21-25d class	61	1397	4.325	<0.001	10.465	<0.001
21-25d class vs. 26-30d class	50	1257	1.116	0.165	1.507	1.000

nauplii to copepodites and adult copepods (Fig. 10). There were significant differences in both the size-frequency distribution and the mean prey size ingested by 11-15 and 16-20 day old larvae (Table 4). Maximum prey length also increased rapidly during this period. Both the size-structure and the mean size of the ingested prey were not significantly different between the 21-25 and 26-30 day age-classes (Fig. 10, Table 4). During this period (age 21-30 days), the *Ulvaria* larvae continued to ingest a broad range of prey sizes, but consumed proportionally more large prey (mean size>500 μm) than did the younger age-classes, corresponding mainly to copepodites and adult copepods.

On the basis of these results, the feeding ontogeny of *Ulvaria* larvae can be divided into 3 stages: an early stage (1-10 days) during which they feed mainly on copepod nauplii, a middle stage (11-20 days) during which they ingest a wide range of prey sizes, and a late stage (21-30 days) during which feeding activity seems to focus primarily on larger prey.

3.3.2 Characteristics of the larval growth groups

When individuals within each age-class were grouped by the two potential proxies for individual survival (*i.e.* length-at-age and early growth rate), the LAA_{long} larvae were naturally larger than the LAA_{short} larvae at all age-classes ($p<0.001$). The EG_{high} larvae were generally larger than EG_{low} larvae ($p=0.007$); however, at age 6-10 days the EG_{low} larvae were larger than the EG_{high} larvae (Table 5; Table 6 a).

Overall, the *Ulvaria* larvae that grew faster during their first five days post-hatch were also likely to be large-at-age later in life. However, within every age-class, differences in length were greater between the LAA_{long} and LAA_{short} groups than between the EG_{high} and EG_{low} groups (Table 6 a). Likewise, within a given age-class differences in otolith growth during the five days post-hatch were greater between EG_{high} and EG_{low} groups than between the LAA_{long} and LAA_{short} groups (Table 6b). In contrast, there were no significant differences in individual ages on the basis of either length-at-age or early growth within age-classes (t-tests, $p=0.91$ and 0.65 for the LAA and EG groupings, respectively).

3.3.3 Comparison of gut contents

With respect to length-at-age, the prey size distributions of the LAA_{long} and LAA_{short} groups only differed among the 11-20 day age-class (Table 7a, Fig. 11). When examined only for the difference in the shapes of the distributions (*i.e.* ignoring differences in mean prey size), there were no significant differences within all age classes. In contrast, the prey size distributions of the EG_{high} and EG_{low} groups were significantly different within each age class (Table 7a, Fig. 11), and the significance values for centered prey length distributions also indicated that the shapes of the two distributions are significantly different within each age classes.

Pooling across age-classes, it appears that individuals that were large-at-age ingested significantly more prey items than did smaller larvae of the same age (two-way ANOVA,

Table 5. Average length of *Ulvaria* larvae in the early, middle and late larval periods when grouped by (a) length-at-age and (b) growth rate over the first 5 days post-hatch. Note that (b) only includes larvae that were older than 5 days at the time of capture.

(a) Grouped by the length-at-age n = 181

Age	LAA_{long}		LAA_{short}		df	t	P
	n	TL ± SE (mm)	n	TL ± SE (mm)			
1-10d	31	6.21 ± 0.19	30	5.42 ± 0.14	59	3.296	0.002
11-20d	31	11.02 ± 0.34	39	8.34 ± 0.19	68	7.295	<0.001
21-30d	20	14.36 ± 0.33	30	12.61 ± 0.25	48	4.342	<0.001

(b) Grouped by the growth rate for the first five days post-hatch n = 163

Age	EG_{high}		EG_{low}		df	t	P
	n	TL ± SE (mm)	n	TL ± SE (mm)			
6-10d	22	6.10 ± 0.17	21	6.35 ± 0.20	41	-0.948	0.348
11-20d	37	10.00 ± 0.38	33	8.99 ± 0.26	68	2.131	0.037
21-30d	21	14.10 ± 0.32	29	12.74 ± 0.28	48	3.176	0.003

Table 6. Results of ANOVA comparisons between growth groups and results of Bonferroni t-test comparisons between growth groups within each age class for length of larval fish.

(a) Length of larval fish

Source of Variation	df	F	P	t	P
LAA_{long} - LAA_{short}	1	75.901	<0.001		
LAA_{long} - LAA_{short} within the 1-10 days old age class	59			2.342	0.020
LAA_{long} - LAA_{short} within the 11-20 days old age class	68			8.462	<0.001
LAA_{long} - LAA_{short} within the 21-30 days old age class	48			4.594	<0.001
EG_{high} - EG_{low}	1	7.535	0.007		
EG_{high} - Eg_{low} within the 6-10 days old age class	41			0.508	0.612
EG_{high} - Eg_{low} within the 11-20 days old age class	68			2.628	0.009
EG_{high} - Eg_{low} within the 21-30 days old age class	48			2.964	0.004

(b) Growth for the first five days post-hatch

Source of Variation	df	F	P	t	P
LAA_{long} - LAA_{short}	1	17.464	<0.001		
LAA_{long} - LAA_{short} within the 1-10 days old age class	59			0.204	0.839
LAA_{long} - LAA_{short} within the 11-20 days old age class	68			3.383	<0.001
LAA_{long} - LAA_{short} within the 21-30 days old age class	48			3.978	<0.001
EG_{high} - EG_{low}	1	282.039	<0.001		
EG_{high} - Eg_{low} within the 6-10 days old age class	41			7.440	<0.001
EG_{high} - Eg_{low} within the 11-20 days old age class	68			12.118	<0.001
EG_{high} - Eg_{low} within the 21-30 days old age class	48			10.213	<0.001

Table 7. (a) Results of two-sample Kolmogorov-Smirnov tests comparing the length-frequency distributions of prey between growth groups (i.e. LAA_{long} vs. LAA_{short} or EG_{high} vs EG_{low}) within each age-class. P and Ctr P indicate the significance values with the tests of length-frequency distribution and centered length-frequency distribution. The centered length-frequency distribution was corrected by eliminating the difference in the mean length of prey between the two groups. (b), (c) Results of ANOVA comparisons between growth groups and results of Bonferroni t-test comparisons between growth groups within each age-class for (b) number of prey and (c) prey size in stomachs of *Ulvaria* larvae.

(a) Length-frequency distribution of prey consumed

Source of Variation	Age class	No. of prey*	P	Ctr P
LAA_{long} - LAA_{short}	1-10 days old	461	0.451	1
	11-20 days old	1235	<0.001	1
	21-30 days old	1257	0.977	1
EG_{high} - EG_{low}	6-10 days old	367	<0.001	0.003
	11-20 days old	1235	<0.001	<0.001
	21-30 days old	1257	0.016	0.040

* No. of prey: Number of prey examined

(b) Number of prey consumed

Source of Variation	df	F	P	t	P
LAA_{long} - LAA_{short}	1	6.618	0.011		
LAA_{long} - LAA_{short} within the 1-10 days old age class	59			0.353	0.725
LAA_{long} - LAA_{short} within the 11-20 days old age class	68			1.127	0.261
LAA_{long} - LAA_{short} within the 21-30 days old age class	48			2.800	0.006
EG_{high} - EG_{low}	1	2.441	0.120		
EG_{high} - Eg_{low} within the 6-10 days old age class	41			0.672	0.503
EG_{high} - Eg_{low} within the 11-20 days old age class	68			0.087	0.931
EG_{high} - Eg_{low} within the 21-30 days old age class	48			3.592	<0.001

Table 7 (cont.)

(c) Average size (μm) of prey consumed

Source of Variation	df	F	P	t	P
LAA_{long} - LAA_{short}	1	2.298	0.130		
LAA_{long} - LAA_{short} within the 1-10 days old age class	459			0.352	0.725
LAA_{long} - LAA_{short} within the 11-20 days old age class	1233			3.153	0.002
LAA_{long} - LAA_{short} within the 21-30 days old age class	1255			0.725	0.469
EG_{high} - EG_{low}	1	25.983	<0.001		
EG_{high} - EG_{low} within the 6-10 days old age class	365			2.596	0.009
EG_{high} - EG_{low} within the 11-20 days old age class	1233			3.493	<0.001
EG_{high} - EG_{low} within the 21-30 days old age class	1255			3.604	<0.001

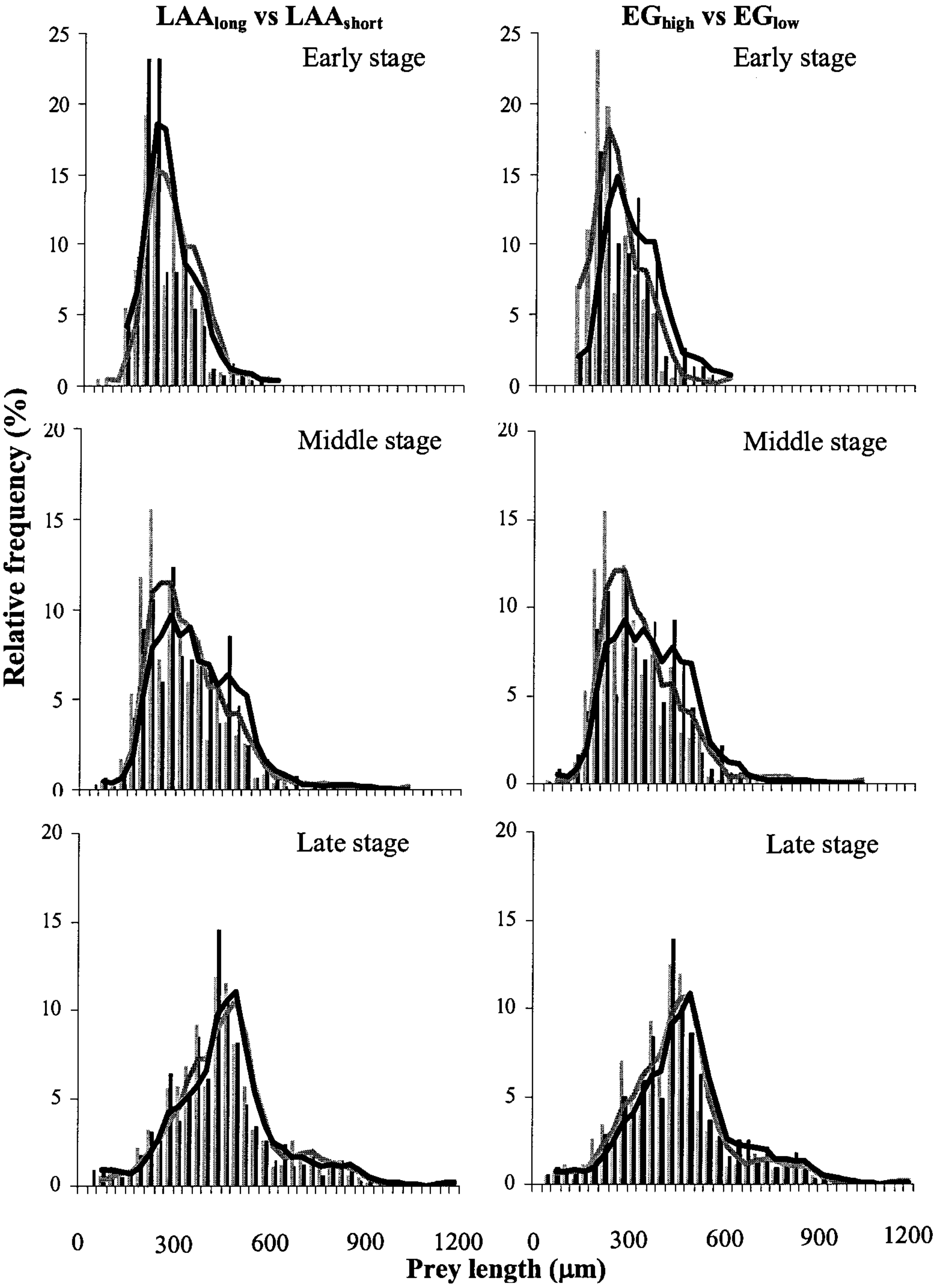

Figure 11. Relative size-frequency distributions of preys in the guts of *Ulvaria* larvae during the early, middle and late larval stages, divided on the basis of length-at-age (left column) and early growth rate (right column). The histogram bars represent relative frequencies of prey abundance within a size-interval of 30 µm. Curves were fit using a three-point moving average curve. Grey for LAA_{short} or EG_{low} and Black for LAA_{long} or EG_{high}.

P=0.011). When examined by age-class, however, significant differences exist only within the 21-30 day age-class (Table 7b). In contrast, pooling across age-classes reveals no significant difference in the numbers of prey ingested by individuals with high vs. low early growth rates (although significant difference did occur within the 21-30 days age-class). In fact, the trends in Table 7b appear to suggest that individuals with high early growth ingest *fewer* prey than those with low early growth during early and middle stages. In terms of prey size, individuals with high early growth rates ingested significantly larger prey than did those with low early growth, both within and across age-classes (Table 7c). In contrast, larvae that were large-at-age ingested the same size of prey as did smaller larvae of the same age (with the exception of the 11-20 day age-class).

To summarize, individual *Ulvaria* larvae that displayed high early growth rates generally ingested larger (but not necessarily more) prey items than did individuals of the same age with low early growth rates (Fig. 11). On the other hand, individuals that were larger-at-age ingested more (but not necessarily larger) prey items than did smaller individuals of the same age (Fig. 11).

3.4 Discussion

3.4.1 Mechanisms regulating the prey size distribution

The feeding patterns of potential survivors among larval fish of the same age can be explored by identifying the factors generating individual variability in feeding patterns, and by examining how feeding patterns change with age. Therefore, a first step is to understand the mechanisms underlying changes in gut contents *between* age-classes (*i.e.* as a function of age). As *Ulvaria* larvae grow they consume larger prey; switching from nauplii to copepodites at around age 10 days and, finally, to predominantly adult copepods at around age 21 days. Since the same pattern is seen in most species of larval fish (Munk, 1992; 1997; Juanes, 1994; Pepin and Penney, 1997; Brodeur, 1998), even though smaller prey usually remain more abundant (and are easier to catch), the switch to larger prey is most likely an optimal foraging strategy (Schoener, 1987; Mayer and Wahl, 1997). However, it is also true that larger prey are generally harder to capture (Browman and O'Brien, 1992; Munk, 1992), and so the switch to larger prey seen in older larvae must also indicate an increase in their foraging ability (Folkvold and Hunter, 1986; Blaxter and Fuiman, 1990; Reimchen, 1991). Consequently, individual variability in foraging ability may be an important factor in generating the variation in feeding patterns observed among larval fish of the same age.

It is generally held that feeding ability is associated with the ability to swim and to detect and capture prey (Gallego and Heath, 1997; Fuiman and Cowan, 2003). In practice, however, quantifying differences in larval swimming performance and perceptive abilities is logistically challenging (especially in field studies). Thus, enhanced feeding ability is generally identified on the basis of proxies for swimming and perceptive abilities such as differences in length-at-age, growth rates, or gape sizes. However, my results show that although the average prey size consumed by *Ulvaria* larvae increases with larval size, the increase is not linear with respect to larval growth. It would seem that there is a difference between the physical development of the larvae and their ability to ingest prey. This result is consistent with those of Pepin and Penney (1997), who showed that mean prey size increased with maxilla length in 10 species of larval fish (including *Ulvaria subbifurcata*), though not constantly, and suggested that larvae increase their mean prey size more slowly than their physical capacity to ingest prey. Thus, an individual's ability to ingest prey is better reflected by the actual size distribution of its gut contents rather than its actual physical capacity (*e.g.* total length) *per se*.

In my results, the pattern of increasing prey size with larval ontogeny is likely associated with not only an increased foraging ability but also a change in prey preference (Miller *et al.*, 1990; Munk, 1997). In other words, although larvae may attempt to ingest the largest prey possible at each developmental stage, if they are unable to do so then they can still ingest smaller (presumably easier to catch) prey. The consequence, however, is that they will then need to consume more prey, thereby spending more time (and energy) foraging while simultaneously increasing the risk of encountering predators. Thus, differences in foraging ability among larval fish of the same age should be reflected in the size distribution of their gut contents. Munk (1992) observed the foraging behavior of four size-classes of larval herring *Clupea harengus* that were fed six sizes of prey items. He found that although the attack rates of the larvae in each size group generally increased with increasing prey size offered, their capture success generally decreased with increasing prey size. In summary then, within a particular prey environment the size distribution of larval gut contents is a combination of preference for particular prey sizes, moderated by a negative size-bias in capture success. Regardless, the optimal foraging strategy would be to ingest fewer large prey (rather than many small prey).

3.4.2. The feeding characteristics of potential survivors

In this study, *Ulvaria* larvae that were large-at-age (LAA_{long}) ingested significantly more (but not significantly larger) prey items than did smaller larvae of the same age. On the other hand, *Ulvaria* larvae that displayed high early growth rates (EG_{high}) usually ingested significantly fewer (but significantly larger) prey items than did their EG_{low} counterparts. Consequently, in terms of food *volume*, the LAA_{long} and EG_{high} larvae ingested more prey than did their LAA_{short} and EG_{low} counterparts, respectively. However, the extent to which the LAA_{long} larvae benefit from their increased prey consumption remains unclear, since their increased foraging activity should also increase their encounter rates with predators (Heath and Gallego, 1997). In contrast, the EG_{high} larvae would seem to derive a three part benefit. They not only ingest (i) more food than their EG_{low} counterparts, but they probably accomplish the task in less time (by ingesting larger prey items), which (ii) reduces the energy they spend on foraging, while (iii) simultaneously lowering their risk of predation.

One outstanding question is whether individuals that feed most successfully also have higher individual survival probabilities. A similar question arises in the controversy of whether bigger is better, since larvae that are large-at-age may have better foraging abilities, but should also be more visually conspicuous to visual predators. However, our understanding of the processes governing predator-prey interactions in planktonic ecosystems remains limited by the challenge of reproducing realistic conditions in a laboratory setting, not to mention the challenge of extending such observations to a field setting. Likewise, although modeling efforts (particularly individual-based modeling) have made significant advances in the past decade (Grimm, 1999), such models should ideally be based on knowledge acquired from field research (Heath, 1992; Paradis and Pepin, 2001) and thus remain rather limited in their ability to realistically represent the encounter process. For example, the Gerritsen and Strickler (1977) encounter rate formula has been widely employed in studies modeling the vulnerability of larval fish to predation (Bailey and Batty, 1983; Cowan and Houde, 1992; Cowan *et al.*, 1996; Letcher *et al.*, 1996, Paradis *et al.*, 1999; Chick and Van Den Avyle, 2000; Paradis and Pepin, 2001). However, Gerritsen and Strickler (1977) really only considered the processes occurring *after* a larva encounters a predator. Therefore, the model of Gerritsen and Strickler (1977) may actually represent the detection rate of predators rather than encounter rate between prey and predators, whereas the actual encounter rate will vary partly as a function of the searched water volume which is itself related to individual variability in larval searching and feeding activity (Blaxter, 1986; Gallego and Heath, 1997).

The results of this study may help to resolve some of the controversy related to the above questions. If we accept that (i) the preference for larger prey is an optimal foraging strategy (Schoener, 1987; Mayer and Wahl, 1997), and that (ii) larval capture success declines with increasing prey size (Browman and O'Brien, 1992; Munk, 1992) then an individual that ingests relatively many small prey could be interpreted as a relatively "poor forager". Munk and Kiorboe (1985) showed that larval swimming activity increases by ~100% at low prey densities (*i.e.* relative to high prey densities), and that the water volume searched by larval fish increases significantly when prey density declined. As a consequence, poor foragers (*i.e.* individuals less capable of capturing large prey) will spend proportionally more time and energy on foraging than more competent foragers (*i.e.* those capable of capturing large prey), thereby also increasing the probability that the poor foragers will encounter predators.

In summary, I conclude that one characteristic of potential survivors should be the ability to ingest fewer large prey rather than many small prey. This characteristic was more evident in comparison between larvae grouped on the basis of their early growth rates (EG_{high} and EG_{low}) than when grouped on the basis of their length-at-age (LAA_{long} and LAA_{short}), even though the latter is one of the most popular proxies for individual survival probabilities currently in use by fisheries oceanographers. Thus, my results suggest that the growth rate for the first few days post-hatch is a better predictor for an individual's feeding ability and its survival probability, than is length-at-age. Further, considering that larval fish spend a large proportion of their time engaged in foraging (Rosland and Giske, 1994; Pepin and Penney, 2000), even small differences in individual foraging ability (which seem to be established at early larval development) could result in large differences in survival to metamorphosis from larvae to juvenile stage due to the cumulative effect of better feeding while also minimizing the risk of predation.

CHAPTER 4

Conclusions and Synthesis

4.1 Proxies for survival probability and the characteristics of survivors

The analyses undertaken in this thesis could only have been accomplished by combining otolith microstructure analysis with gut analysis on the same set of individuals. To my knowledge, however, no study has previously combined these approaches, even though it offers a powerful means of exploring links between larval feeding, growth and survival.

Contrary to expectations, the results in Chapter 2 illustrate that an individual's growth rate during the first 5 days post-hatch is a better predictor of its future feeding success (and therefore ability) than are length-at-age or recent larval growth. Although both length-at-age and early growth rate show significant growth-dependent effects on gut fullness when pooled across age-classes, only early growth rate showed a consistent trend in its effect on gut fullness within age classes. Therefore, the consistent trend in the high early growing larvae (i.e. even among larvae of up to 30 days of age) may indicate the persistence of an individual's feeding ability from very early in the larval stage. This study also indicates that focusing strictly on mean values (and ignoring the importance of individual variability) can lead to false conclusions regarding the "bigger-is-better" hypothesis (Pepin, 2004).

Chapter 3 demonstrates that the size distribution of larval gut contents better reflects the feeding ability of an individual larval fish than does its physical capacity *per se*. The results of this study illustrate that one characteristic of potential survivors might be the ingestion of larger prey (which is associated with individual foraging ability) and that this characteristic is more prevalent among individuals with high early growth than among individuals that are large at age. Considering larval fish as predators, the results of this study are consistent with the general predictions of optimal foraging theory, which predicts that, all else being equal, a predator that selects larger prey should maximize its fitness (Stephens and Krebs, 1986). Similar results have also been seen in other studies (Pazzia, 2001; Sherwood *et al.*, 2002; Henderson *et al.*, 2004; Johansson *et al.*, 2004). For instance, Henderson *et al.* (2004) compared the growth efficiencies, ingestion rates, and activity levels of walleye, *Sander vitreus*, living in lakes with and without lake herring. The main prey species in lakes without herring was yellow perch, which are much smaller than herring. They reported that walleye living in lakes with herring had higher growth efficiencies, lower ingestion rates and lower activity rates than in lakes without herring.

In addition to this positive effect on feeding success, high early growth may further enhance an individual's probability of survival by reducing its encounter rate with predators (*i.e.* by reducing the time spent foraging). Considering larval fish as prey, my results also support predictions from optimal foraging theory insofar that the potential survivors (as estimated by their feeding success) were not the largest larval fish at age but the high early growers. Given their limited swimming ability, larval fish are generally no match for larger visual predators (*e.g.* larger fish), and so their survival may depend more upon not being detected by their predators, rather than on actively evading predators once detected. Therefore, if the high early growers (which are not necessarily the largest at age) can reduce their foraging activity, their survival probability may be higher than those larvae that are largest at age (but which are less capable foragers).

Unlike other recent studies on this subject (Meekan *et al.*, 2003; Takasuka *et al.*, 2004; reviewed in Pepin, 2004 and Underwood *et al.*, 2004) the present study predicts larval survival through understanding one of the processes that directly regulates larval survival (*i.e.* the effect of foraging ability on feeding success and possibly exposure to predators) rather than simply inferring the process from the pattern it produces. That is, the approach used in this study was to explore how foraging ability might affect survival rather than to simply estimate or compare growth rates between larval groups (*i.e.* as an indication of their relative survival probabilities).

Although growth rate differences between groups of larvae can certainly be influenced by other factors (*e.g.* differences in temperature or prey availability) simply comparing gross differences between groups may hinder us from understanding the underlying mechanism because of variability in the pattern observed (Hilborn and Ludwig, 1993). For instance, temperature is widely recognized as the major factor controlling assimilation, metabolism, transformation of fish (Jobling, 1994). Following predictions from the "growth-mortality" hypothesis, numerous studies therefore have compared the growth rates of larval fish collected from different water temperatures and proposed, in most cases, a positive effect of temperature on both somatic and population growth rates (Nakken and Raknes, 1987; Jorgensen, 1992; Brander, 1994; Myers *et al.*, 1997; Otterlei *et al.*, 1999). In some cases, observations of high growth and survival rates of larval fish are explained by high temperature alone (Meekan *et al.*, 2003), with no mention of the role of prey availability, in spite of the fact that metabolic rates (and therefore energetic demands) *increase* with temperature (Jobling, 1988; Houde and Zastrow, 1993).

However, many other studies of temperature on fish recruitment (or survival rate) also show that increased temperature has a *negative* effect on fish survival and recruitment (Otterlei *et al.*, 1999; Myers *et al.*, 2001; Beaugrand *et al.*, 2003; Ravier and Fromentin, 2004). These studies attributed the underlying process to higher metabolism and energetic costs (Otterlei *et al.*, 1999; Beaugrand *et al.*, 2003), competition (Myers *et al.*, 2001) or changes in habitats or migration patterns (Rivier and Fromentin, 2004) in response to increased temperature, each of which could also have resulted from food-limitation rather than temperature effects *per se*. For instance, in the present study, copepod nauplii constituted a significant portion of the larval *Ulvaria* diet. Considering that high temperature also leads to rapid growth of nauplii (Huntley and Lopez, 1992), high temperatures could negatively affect the feeding environment for very young *Ulvaria* larvae by decreasing the time over which nauplii are available. Under such circumstances, although temperature would appear to have a negative relationship with larval survival, reduced prey availability would actually have the more direct effect. Such possibility merits examining the effect of temperature on the growth rates of both larval fish and their prey.

4.2 Directions for future research

4.2.1 Shortcomings in traditional methods linking prey availability to larval survival

Historically, marine mesozooplankton collections have extensively been made using >333 μm mesh plankton nets (Currie, 1963; Clarke, 1964; Clutter, 1965; Davies and Barham, 1969; Hempel and Weikert, 1972; Baker *et al.*, 1973; Hopkins *et al.*, 1973; Posgay and Marak, 1980; Wiebe *et al.*, 1985; Nester, 1987; Burd and Thompson, 1993; Motoda, 1994; McGowan *et al.*, 1998; Wiebe and Benfield, 2003; Buckley *et al.*, 2004). There are several reasons for this, including the fact that finer mesh nets have a tendency to quickly become clogged (especially when towed through highly productive waters) plus the fact that zooplankton ecologists have traditionally focused on mesozooplankton (usually defined as 0.2-20 mm in length) as opposed to microzooplankton (Sameoto *et al.*, 2000). However, as shown in Chapter 3, a large proportion of the prey consumed by larval fish are <333 μm and are better described as microzooplankton. For instance, almost 50% of all the prey ingested by the *Ulvaria* larvae in this study were <333 μm in length. The differences are even more striking when we examine the larvae by age: 84%, 57%, and 22% of the prey ingested by larval fish in, respectively, the 1-10, 11-20, and 21-30 day age ranges were less than the traditional mesh size of 333μm (Fig. 12). Similar results have been seen in other studies. For example, examining the feeding habits of Atlantic cod and haddock larvae, Kane (1984) found that although the range of prey lengths consumed was 70-480 μm, the greatest demand was for prey between 100-190 μm in length. Similar results were also reported by Pepin and Penney (1997) for 10 species of larval fish from coastal Newfoundland.

These data confirm that zooplankton samples collected with 333 μm mesh nets do not accurately estimate the actual prey availability for larval fish, especially for very young larval fish (which are also the most vulnerable to starvation). In fact, given that

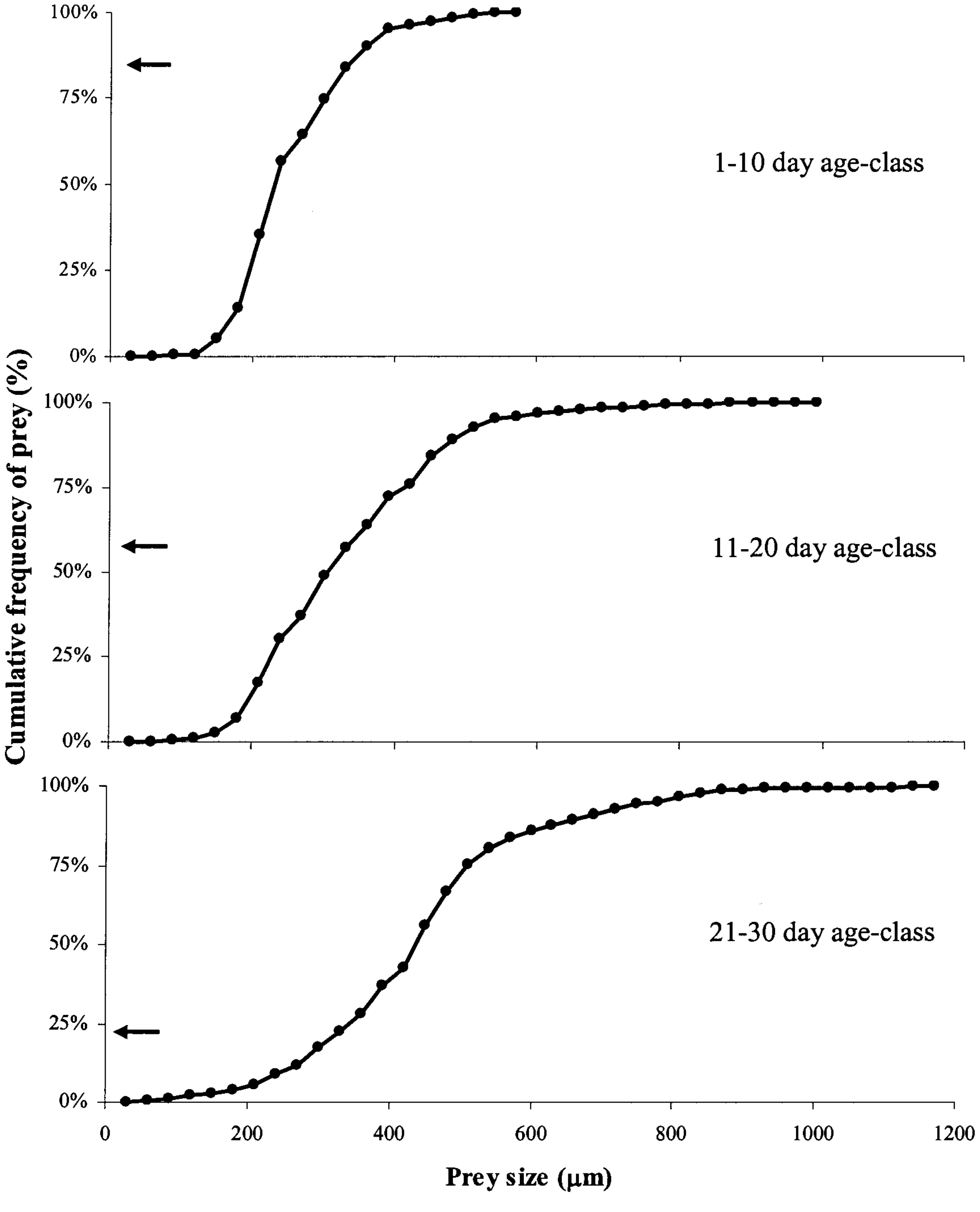

Figure 12. Cumulative size-frequency distributions of prey ingested by *Ulvaria* larvae during the early (1-10 day, n = 61), middle (11-20 day, n = 70) and late (21-30 day, n = 50) larval periods. Size interval of 30 μm was used for the dots. Arrows indicate the relative frequency of prey smaller than 333 μm in length.

length:width ratios for most copepods are typically about 3:1, a 333 μm net is really only effective at capturing organisms with a width greater than 333 μm. On average, we might therefore predict that such organisms have a typical length of almost 1mm. In the current study, fewer than 1% of all the prey consumed by even the oldest *Ulvaria* larvae were >1 mm in length. Recognizing that traditional plankton nets really only census adult copepods accurately, some authors have proposed that the abundance of copepod nauplii should at least be proportional to the abundance of adult copepods (Kane, 1984; Anderson, 1994; Runge *et al.*, 1999). However, Ohman and Hirche (2001) have recently shown evidence for nonlinear density-dependent mortality rates of marine zooplankton. In their study, they found that the birth rates of *Calanus finmarchicus* were independent of the abundance of adult female *C. finmarchicus*.

Although some researchers have used 80 μm (or finer) mesh nets to collect zooplankton for estimating prey availability for larval fish, most still compared the *total abundance* (or total biomass) of zooplankton to larval fish abundance or recruitment (Crecco and Savoy, 1984; Buckley and Lough, 1987; Aksnes and Magnesen, 1988; Meekan *et al.*, 2003). However, this study clearly shows that larval fish change both the mean and the range of the prey sizes that they consume as they get older. Thus, not even all of the zooplankton from a 70 μm mesh net are equally available to all larvae (Fig. 13). Therefore, future studies attempting to link prey availability to larval growth and survival should consider that prey availability for larval fish changes with age, even within the same prey environment at the same time. Given the finding that early larval growth rates appear to be important for future survival, studies of prey availability to very young larvae may provide significant insights into understanding individual variability in growth and survival of larval fish in general.

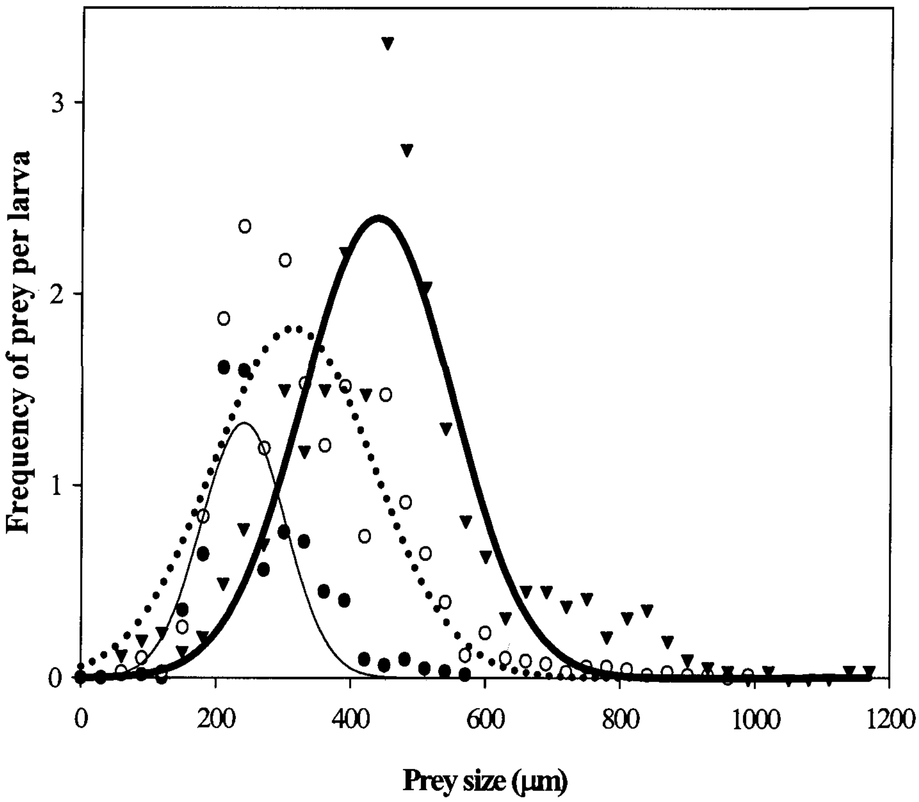

Figure 13. Prey size distribution ingested by 1-10 day (n = 61, thin line and solid circles), 11-20 day (n = 70, dotted line and open circles), and 21-30 day old (n = 50, thick line and triangles) *Ulvaria* larvae. Each symbol represents the number of prey within a 30 µm size increment. All lines were fit using a Gaussian function with 3 parameters. Thin line: $r^2=0.76$, $p \ll 0.001$; Dotted line: $r^2=0.80$, $p \ll 0.001$; Thick line: $r^2=0.85$, $p \ll 0.001$.

4.2.2 The relative importance of the prey environment and maternal effects on the early growth of larval fish

The exact nature of the effect that confers high early growth rates in the *Ulvaria* larvae in this study remains unclear. Two possibilities are simple chance (*i.e.* some larvae are simply stronger than others) or some sort of maternal effect. Recently, Berkeley *et al.*

(2004) reported that progeny from older female of black rockfish (*Sebastes melanops*) display higher survival rates than do those from younger females. A similar result was also seen by Trippel (1998) for Atlantic cod. Buckley *et al.* (2004) noticed, however, that management programs for maintaining fish populations do not generally consider the importance of the 'old-growth age structure' (*i.e.* some sort of maternal effect). If maternal effects on larval survival turn out to be a widespread phenomenon, one practical consequence is that protecting the older females within exploited fish populations may be critical to the long-term stability of stocks. This would require a fundamental change in fisheries management, however, since current fishing practices specifically target the oldest, largest, fish. The results from this and similar studies, which suggest that maternal effects may affect early larval growth and survival, certainly merit further inquiry.

Understanding the relative importance of variations in prey environment vs. maternal effects on early larval growth could be essential to better understand the mechanisms regulating interannual variability of larval survival. A number of possible experiments come to mind. First, comparing the growth rates of siblings (*i.e.* groups of larvae derived from the same mother) reared under different prey densities could help delimit the scope of variation in prey availability on larval growth. Second, comparing the relative growth rates of larvae from different mothers, but reared under the same prey densities, would help to quantify the potential for maternal effects on larval growth. Comparing the results of these two sets of experiments would help to understand the relative importance of prey availability vs. maternal effects on the early growth of larval fish, and to what extent (if at all) the two effects might interact.

Advances in isotope analysis also merit noting. Carbon:nitrogen isotope ratios in organisms can be influenced by metabolic process, somatic growth, and changes in diet (Schell *et al.*, 1998; Hobson, 1999). Recent evidence indicates that trophic enrichment of isotopes such as C^{13} and N^{15} can be further influenced by the elemental composition of prey (Pearson *et al.*, 2003; Post, 2003). The current study is novel in that it combines the analysis of gut contents with measures of otolith microstructure from the same individuals. However, the addition of stable isotope analyses could provide an even more powerful means for exploring differences in feeding habit among larval fish. Likewise, the addition of fatty acid analyses (*e.g.* Lochmann *et al.*, 1995) would enable us to begin to examine the role of prey quality (in addition to prey quantity) on larval growth. Such analyses should also be done on the same individuals, to provide further insight into the processes governing feeding ability, and the relationship between larval survival and prey availability.

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