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Original Article

Individual growth history of larval Atlantic mackerel is reflected in daily condition indices

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We tested the hypothesis that faster-growing Atlantic mackerel (*Scomber scombrus*) larvae generally achieve better feeding success than their slower-growing counterparts. Feeding success and growth were derived from the analysis of gut content and otolith microstructure of larvae from four cohorts (1997–2000) from the southern Gulf of St Lawrence. We observed a high degree of serial correlation in otolith growth (OG) from hatching, suggesting that events occurring early in life have long-standing effects on future growth potential. The diet of fast-growing individuals was dominated by large prey, such as cladocerans and fish larvae (including conspecifics), while slow-growing larvae foraged primarily on smaller copepod naupliar stages. Both feeding success (stomach content) and an index of condition (body depth) were positively correlated with OG, and these relationships explained approximately three times more variance in mackerel than in larval radiated shanny (*Ulvaria subbifurcata*) of similar size. Relationships linking age-dependent scores of body depth to feeding success and growth were ~3.5–4 times stronger than those based on length-dependent indices, suggesting that differences in energy allocation during early ontogeny may play a significant role in determining an individual's capacity to cope with variations in feeding conditions.

Keywords: feeding, growth, larval fish, otolith microstructure, *Scomber scombrus*, stomach content.

Introduction

The availability of adequate prey during the early larval stage is considered one of the main sources of year-class fluctuations in marine fish populations (Hjort, 1914; Cushing, 1990; Houde, 2008). It is widely accepted that poor feeding success leads to increased larval mortality through suboptimal growth (Anderson, 1988), as slow-growing individuals generally suffer higher vulnerability to predation (e.g. Miller *et al.*, 1988; Takasuka *et al.*, 2003) for an extended period (e.g. Chambers and Leggett, 1987). However, despite being a key assumption of the growth-survival paradigm, the link between feeding success and growth at the individual level remains poorly characterized in the field (Dower *et al.*, 2009). The main problem when linking feeding and growth in larvae captured at sea is that both vital rates are not sampled on the same temporal scale. Feeding success is estimated from stomach content, representing at most the last few hours of foraging before capture (e.g. Llopiz and Cowen, 2008), while growth derived from otolith microstructure integrates events experienced during the days before capture (e.g. Pepin *et al.*, 2001).

Despite the temporal resolution mismatch between stomach content and otolith microstructure, a positive relationship linking feeding success to growth is to be expected. The strong serial correlation usually found in larval daily growth trajectories (Pepin *et al.*, 2001; Dower *et al.*, 2009) implies that events

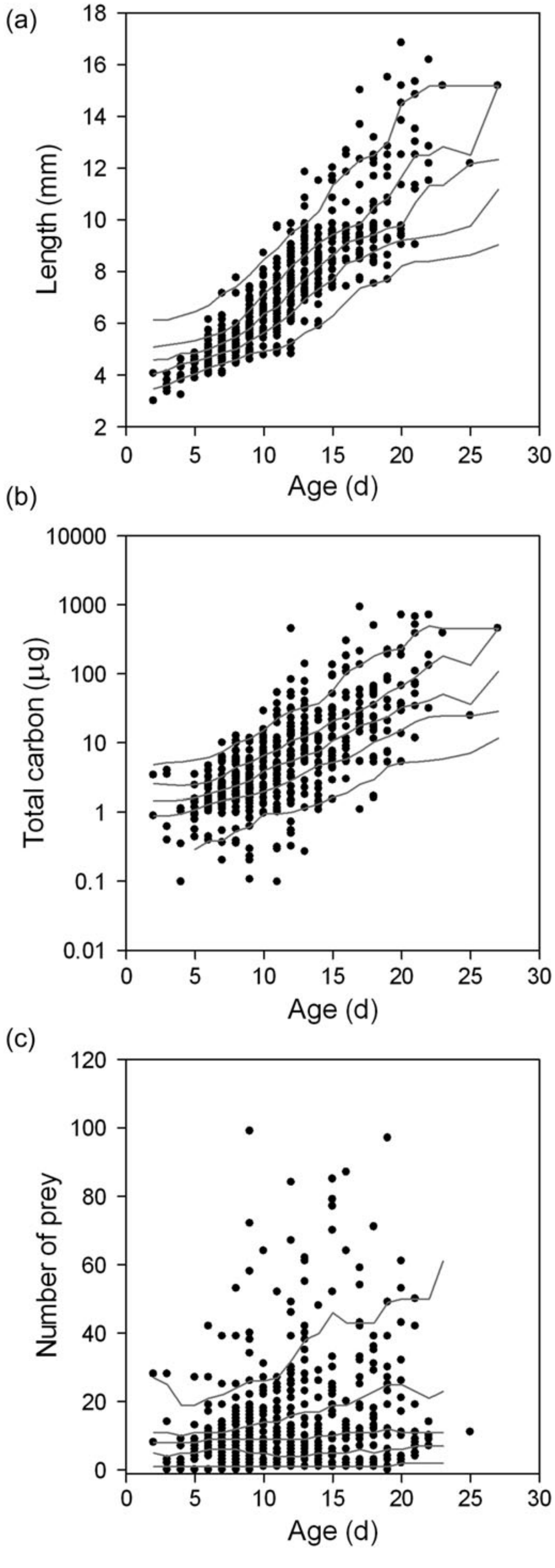

Figure 1. (a) Length (bandwidth = 0.75 d), (b) total carbon of prey per stomach (bandwidth = 1.45 d), and (c) number of prey per stomach (bandwidth = 1.95 d) in relation to otoliths estimated age of Atlantic mackerel larvae. Solid lines indicate the 10th, 30th, 50th, 70th, and 90th percentiles of the distribution of observations based on non-parametric local density estimation.

experienced early in life may drive future survival potential. Hence, the Markov chain of successful feeding events resulting in a fast growth trajectory would strongly depend on initial feeding success and the capacity of individuals to overcome the influence of environmental variability and stochasticity. Fast-growing individuals could in turn achieve large size-at-age, high swimming performance, and ultimately high feeding success through a positive feedback loop. Atlantic mackerel (*Scomber scombrus*) is an ideal candidate species for testing retroactive mechanisms linking feeding success to growth: the larval stage is characterized by fast yet variable growth, and intra-cohort cannibalism implies that the fastest-growing individuals rapidly acquire the ability to prey on their smaller siblings (Robert *et al.*, 2008). The latter characteristic likely explains the strong selection for fast growth usually occurring throughout the larval stage (Robert *et al.*, 2007).

A previous study by Robert *et al.* (2009) revealed relationships linking feeding success and growth performance to preferred prey availability in first-feeding Atlantic mackerel larvae. Both feeding success and growth increased exponentially at a decreasing rate until reaching satiation at a density of $\sim 1\ \mu g\ C\ l^{-1}$ of their preferred *Pseudocalanus* sp. nauplii prey. The similarity of both relationships provided direct evidence for food limitation during the first-feeding stage and indirect evidence for the assumed link between larval growth and feeding success. In the present study, we provide a direct test to the expected relationship linking growth performance with feeding success. Non-parametric local density estimators (Pepin *et al.*, 1999; Dower *et al.*, 2009) are used to assess correlation among individual age-dependent percentile scores of larval states (body length, depth at anus, stomach content, growth). Furthermore, we contrast early life strategy of Atlantic mackerel to that of radiated shanny (*Ulvaria subbifurcata*) described by Dower *et al.* (2009).

Material and methods

Field methods

Mackerel larvae (standard length 3–18 mm) were sampled from July to mid-August in four consecutive years (1997–2000) during weekly one-day (16:00–24:00 h) surveys offshore of the Magdalen Islands, southern Gulf of St Lawrence (Robert *et al.*, 2009). Sampling methods for mackerel larvae and zooplankton are detailed in Robert *et al.* (2007, 2008). Briefly, the sampler consisted of a rectangular metal frame carrying four plankton nets deployed in a double-oblique tow pattern (~20 min duration at a ship speed of $\sim 1.3\ m\ s^{-1}$): two 750-μm mesh nets captured fish larvae, while two 64-μm mesh cylindrical nets sampled mesozooplankton. Temperature and depth profiles were obtained from a Vemco Minilog® probe set on the frame. Mackerel larvae were preserved in 95% ethanol for further otolith analyses, while mesozooplankton collected in the 64-μm mesh nets was fixed in a 4% formalin seawater solution. The standard lengths of preserved larvae were measured in the laboratory under the dissecting microscope and converted into fresh standard length using the regression equation provided by Migoya (1989). Stratified subsamples of mackerel larvae were then used for the assessment of growth and feeding success by randomly selecting individuals from predetermined length classes in each year. Over the 4 years of sampling, both feeding and growth patterns were evaluated in 516 larvae.

The analysis of larval stomach content is detailed in Robert *et al.* (2008). In summary, the digestive tract of each mackerel larva was dissected under a stereoscopic microscope and each prey item was measured and identified to the lowest taxonomic level possible. Carbon content of each prey item was estimated using specific length-weight relationships (Robert *et al.*, 2008). For larval fish prey, tissue degradation due to rapid digestion often prevented the precise measurement of standard length. Because most identifiable larval fish prey were newly hatched Atlantic mackerel (Robert *et al.*, 2008), we adopted a conservative approach and considered the mean hatching size of mackerel (3.5 mm) to attribute a carbon value (5.168 μg C) to these digested prey.

Larval age and somatic growth trajectory were estimated from the number and width of otolith daily growth increments (Robert *et al.*, 2007). Sagittal otoliths were mounted on slides using Crystalbound® thermoplastic cement, and polished with 3M® 30 and 3 μm metallurgical lapping films when needed. Otolith microstructure was assessed using an optical microscope (×1000) connected to an Image-Pro Plus® image analysing system with a digital camera.

Data analysis

We used non-parametric local density estimators (Davison and Hinkley, 1997) to describe the change in variability in larval state (i.e. length, growth, feeding) with age. Details of the approach are outlined by Pepin *et al.* (1999). Briefly, the method provides a locally weighted estimate of the cumulative probability distribution (CDF) of observations as a function of a covariate x (such as length or age) and surrounding observations using kernel smoothing. In our analysis, the weighting function is $w(d) = e^{-d}$, where $d = |x_i - x|/b$, and b is a bandwidth parameter which describes how far "local" extends. We determined the value of b by cross–validation: we deleted each observation in turn, used the rest of the data to predict the deleted observation, computed the sum of squared differences of the residuals for all observations, then chose the value of b that minimized this sum. This was possible because of the large number of observations in our dataset, which produced a relatively smooth change in the CDF of variables in relation to age using cross-validation (i.e. the CDF was not over fit, which can happen when data are scarce or widely separated, as was encountered by Dower *et al.* (2009) who had to specify a bandwidth of 2.5 d). Relative to most generalized linear models, this approach has the advantage of making no assumptions about the underlying age- or length-dependence of the variance structure. Hence, the states [i.e. gut content, body length, body depth, and otolith growth (OG)] of each individual can be described in terms of age- or length-dependent percentile scores, providing relative indices of larval "performance" standardized over a uniform distribution ranging from 0 to 1.

Results

Length increased monotonically with age with some indication of an accelerating rate of increase in older larvae (Figure 1a). The scatter (i.e. the difference between the 10th and 90th percentiles

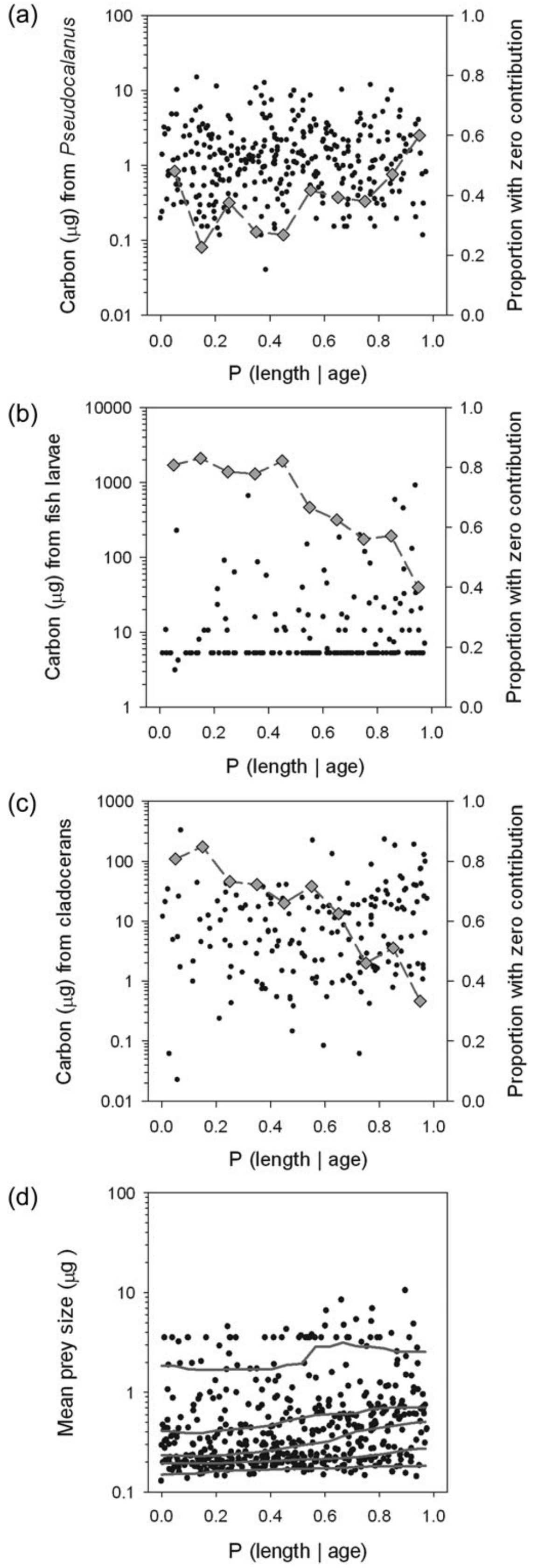

Figure 2. Carbon content of (a) *Pseudocalanus* sp., (b) fish larvae, (c) cladoceran prey in the larval diet, and (d) average prey size of individual larvae in relation to the percentile score of length-at-age of Atlantic mackerel larvae (black circles). In (a)–(c), the proportion of stomachs with zero contribution of each prey type for each 10th percentile score interval of length-at-age is represented by the grey diamonds and dashed line referenced to the right axis. In (d), solid lines indicate the 10th, 30th, 50th, 70th, and 90th percentiles of the distribution of observations based on non-parametric local density estimation.

of the distribution) increased significantly from 1.34 mm in 2-d-old larvae to ∼6 mm in 20-d-old larvae. Percentile scores of length-at-age [P(length|age)] were very weakly and negatively correlated with water temperature at capture ($r = -0.28$, $p < 0.001$).

Only 21 of the 516 mackerel larvae (4.1%) had empty stomachs. Total stomach carbon content followed a non-linear relationship with age (Figure 1b). The logarithm of scatter was relatively constant with age. Deviations of percentile scores from the median did not show evidence of a strong diurnal pattern in feeding success. Percentile scores of total stomach carbon content at age [P(carbon|age)] were weakly and negatively correlated with water temperature at capture ($r = -0.16$, $p < 0.001$). The maximum number of prey per stomach also increased with age (Figure 1c). While the median increased only slightly from 8 prey in 2-d-old larvae to 11 prey in 20-d-old larvae, the 90th percentile increased from ∼20 to ∼50 prey over the same age interval (Figure 1c).

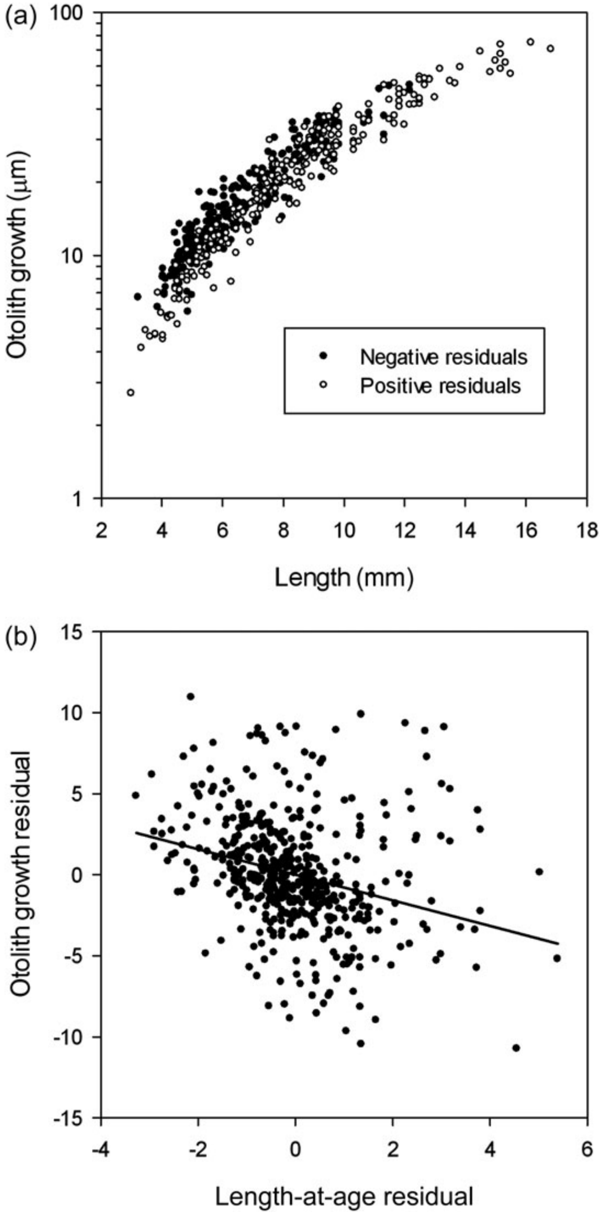

Figure 3. (a) OG in relation to standard length. Closed symbols represent individuals with negative residuals from the linear length-at-age relationship (smaller at age); open symbols represent individuals with positive residual from the length-at-age relationship (larger at age). (b) Residuals from the otolith–length relationship plotted against the residuals of the length-at-age relationship.

The calanoid copepods *Pseudocalanus* sp. and *Temora* sp., cladocerans, and fish larvae were found in 62, 35, 34, and 30% of stomachs, respectively. Together, these four prey categories accounted for an average proportion of 0.68 of prey found in mackerel stomachs (median = 0.77, s.d. = 0.29; interquartile range: 0.5–0.91). The contribution of *Pseudocalanus* sp. to the total carbon was largely independent of the percentile score of length-at-age, although the relative frequency of individuals found without this prey item increased slightly in larger-at-age individuals (Figure 2a). In contrast, mackerel larvae that were small-at-age tended to have lower relative and absolute contributions of carbon from larval fish prey relative to individuals that were large-at-age (Figure 2b). Cladocerans were also more likely to be found in the stomachs of larger individuals at a given age, although no trend was observed between cladoceran carbon content and the percentile score of length-at-age when this prey taxon was found in the stomach (Figure 2c). The changes are reflected in the near doubling of the median average prey size of individuals that were large-at-age relative to the smallest individuals at age (Figure 2d).

Before growth analyses, we assessed the strength of the link between OG (distance from hatch mark to the edge) and standard length, as well as the potential decoupling between these two growth metrics with changes in environmental conditions (e.g. Folkvord *et al.*, 2000). To address this issue, the linear relationship of length-at-age was first estimated (L–A; $L = 1.67 + 0.49\,A$, $r = 0.87$, $p < 0.001$; Figure 1a). OG was then modelled in relation to standard length using non-linear least squares because of increasing variability in the former with increasing length (OG–L; $\mathrm{OG} = -1.9 + 0.98\,L^{1.55}$, $r = 0.96$, $p < 0.001$; Figure 3a). In the eventuality of decoupling between OG and standard length, the distribution of residuals of the OG–L relationship should differ between individuals with high and low growth rates (residuals from L–A). The residuals from the L–A relationship were not

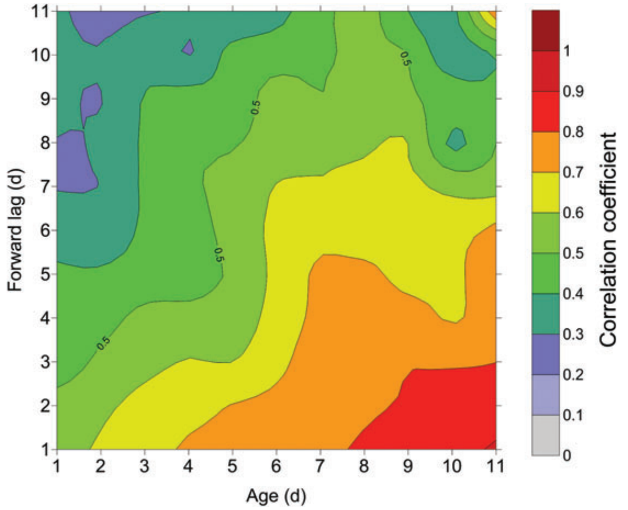

Figure 4. Age-dependent serial correlation coefficient (r, value represented by the colour scale) of otoliths increment widths of Atlantic mackerel larvae. Forward lag is the number of daily increments after a given otolith increment.

independent of those from the OG–L relationship ($r = -0.28$, $p < 0.001$, $n = 516$; Figure 3b), indicating a small degree of decoupling between otolith and somatic growth in Atlantic mackerel. Slow-growing individuals were characterized by greater cumulative OG at length relative to younger individuals at the same length, though based on a relatively weak trend that accounts for less than 8% of the variance in residuals of the OG–L relationship.

We found strong serial correlation in growth of Atlantic mackerel, which tended to increase with age (Figure 4). The *e*-folding scale (time-scale for r to decrease to the value of $1/e = 0.368$) was about 5 d in the youngest larvae and increased to 10 d or more when the larva reached ~1 week of age.

The percentile score of total carbon ingested by mackerel larvae [P(carbon|age)] was strongly correlated with length-at-age [P(length|age); $r = 0.48$, $p < 0.001$], whereas the relationship with the number of prey per stomach [P(number|age)] was much weaker ($r = 0.15$, $p < 0.001$; Figure 5). Overall, larger individuals at a given age were more likely to have a larger prey mass in their stomach; however, greater ingestion rate was achieved by feeding on larger organisms rather than on a greater number of smaller prey (Figure 2).

Except the youngest larval age class (1–5 d), the percentile score of total prey carbon at age was always positively correlated with increment width (Figure 6). The percentile score of the number of prey in the stomach at age was nearly uncorrelated with increment width, except the oldest larval age class (16–20 d) from the age of 10 d on (Figure 6b).

Body depth at anus, often used as an index of condition in larval fish, followed an allometric relationship with SL according to a power of 1.44, which was significantly greater than direct proportionality ($t = 60.3$, $p < 0.001$; Figure 7a). The age-dependent percentile score of body depth [P(body depth|age)] was strongly correlated with OG [P(OG|age); $r = 0.74$, $p < 0.001$] (Figure 7b). A weaker relationship between the age-dependent

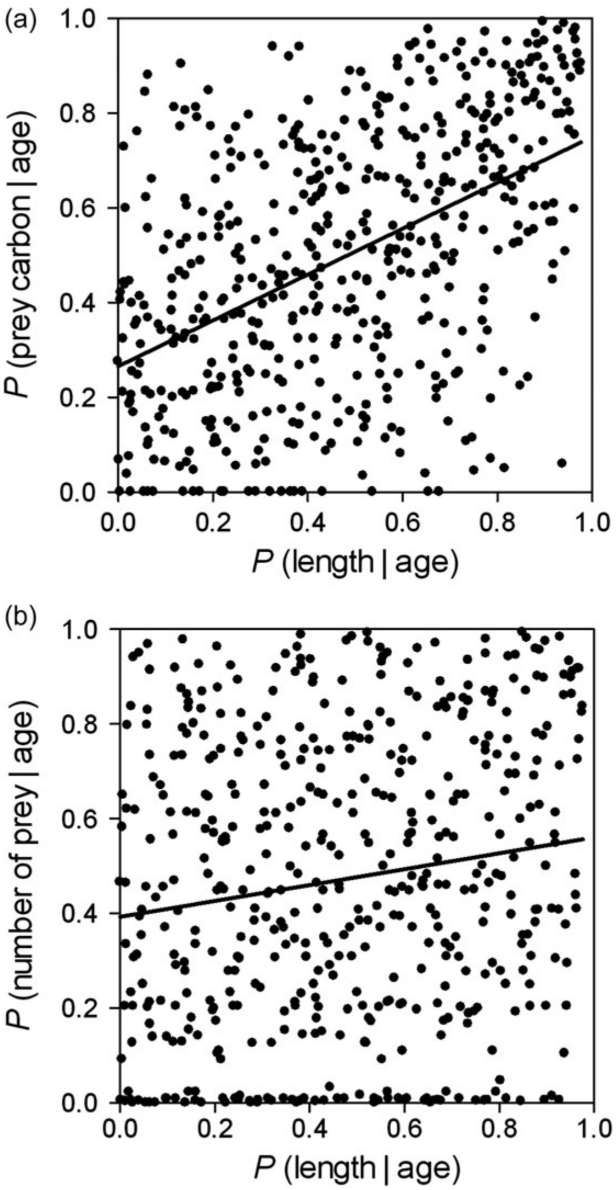

Figure 5. Percentile score of (top panel) total prey carbon and (bottom panel) number of prey in relation to percentile score of length-at-age.

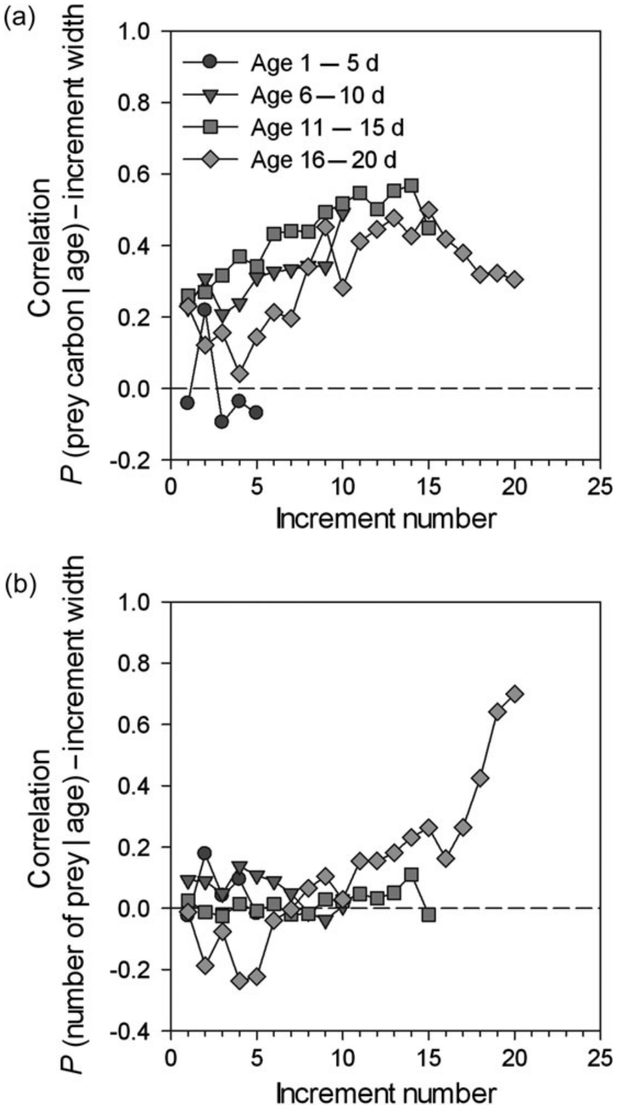

Figure 6. Age-specific correlation of otolith increment width with (a) percentile score of total prey carbon and (b) number of prey per stomach.

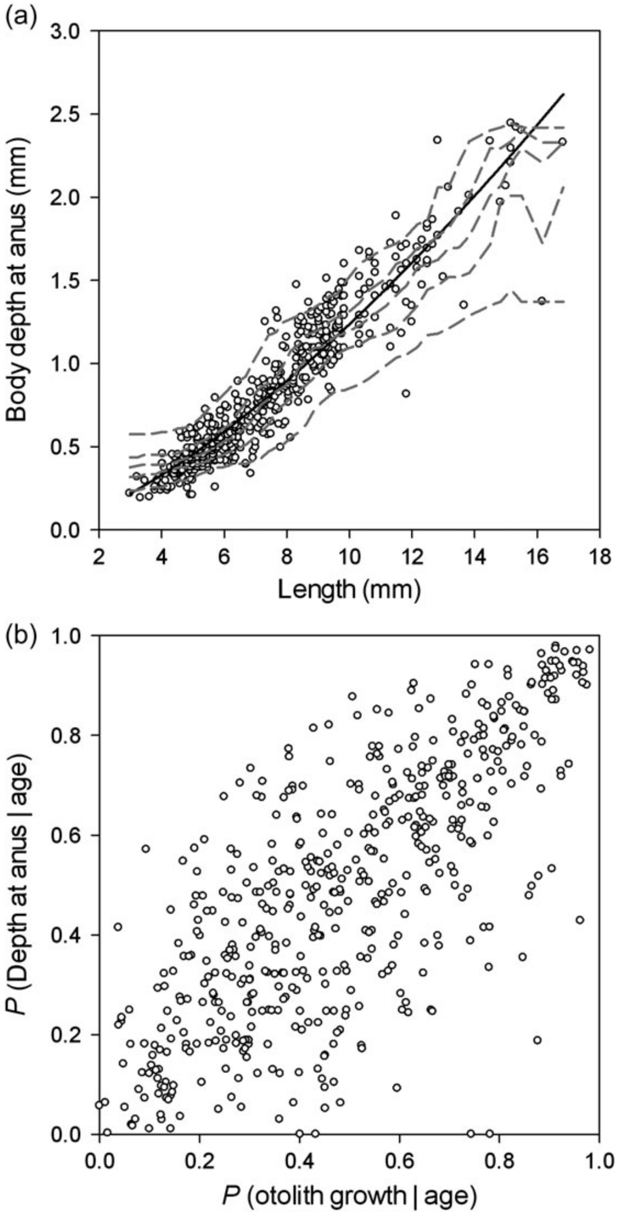

Figure 7. (a) Body depth at anus in relation to the standard length of mackerel larvae. The solid line represent least squares fit to the allometric relationship $Y = 0.045\ X^{1.44}$ [$r = 0.94$, $p < 0.001$; s.e.(multiplier) = 0.0024, s.e.(exponent) = 0.024)]. The short dashed lines represent the 10th, 30th, 50th, 70th, and 90th percentiles of the distribution of observations based on a bandwidth of 0.9 mm. (b) Percentile score of body depth at anus in relation to the percentile score of increment width.

percentile score of body depth and total prey carbon ($r = 0.51$, $p < 0.001$) (not shown) was found, similar to that between prey carbon and length-at-age (Figure 5a). The length-dependent percentile score of body depth at anus [P(body depth|length)], a common index of condition that does not require ageing (Ferron and Leggett, 1994), was correlated with both OG at age ($r = 0.37$, $p < 0.001$) and total prey carbon at age ($r = 0.27$, $p < 0.001$), but not to length-at-age [P(length|age); $r = -0.011$, $p > 0.2$].

Discussion

Although random events are likely to play some role in an individual's growth history, it is inevitable that fish larvae achieving good growth rely on some considerable degree of effective foraging rather than exclusively on good luck. A large body of literature supports the growth-survival paradigm that fast-growing individuals generally survive in a larger proportion relative to their slower-growing counterparts (e.g. Meekan and Fortier, 1996; Robert *et al.*, 2007; Takasuka *et al.*, 2007). A key assumption of the paradigm is that fast growth of these survivors is generally achieved through superior feeding (Anderson, 1988; Cushing, 1990). Variability in individual feeding success is mainly determined by the combination of individual differences in ability to capture prey and spatio-temporal variability in adequate prey availability. Our results clearly demonstrate that individuals achieving higher growth rate at a given age were generally those that foraged the most efficiently. Growth achieved on a given day was significantly correlated with indices of both short-term (stomach content) and long-term (depth at anus) feeding success. These findings are similar to those for radiated shanny (Dower *et al.*, 2009), but the relationship between carbon stomach content and length-at-age explained approximately three times more variance in mackerel than in shanny. The percentile score of total prey carbon at age was always positively correlated with increment width past the first-feeding stage (Figure 6a). Moreover, the correlation coefficient increased with age, suggesting that an individual's past growth history becomes increasingly reflected in its ability to capture prey. The absence of correlation between the percentile score of the number of prey and increment width (Figure 6b) before the age of 16 d indicates that this retroaction loop is achieved by increasing prey size rather than prey number (Figure 2; Robert *et al.*, 2008). In combination with the strong autocorrelation in OG (Figure 4), these results indicate that feeding success achieved by Atlantic mackerel at the onset of exogenous feeding can have long-lasting consequences to growth patterns, which may in turn determine the survival probability of an individual.

Feeding success is the outcome of the probabilities of encounter, attack, and capture, which is affected by both the environment (e.g. physical structure and dynamics, prey type) and individual ability related to morphological features and behaviour (Hunter, 1980; Buskey *et al.*, 1993). Larvae of both Atlantic mackerel and radiated shanny emerge during early summer, when prey are generally abundant and the water column is stratified. Morphologically, mackerel larvae have a larger mouth than radiated shanny of the same length (Ware and Lambert, 1985; Pepin and Penney, 1997), thereby providing them with opportunities to feed on larger prey and which they take the advantage of by feeding on fish larvae at an early stage of their ontogeny (Ware and Lambert, 1985; Fortier and Villeneuve, 1996; Robert *et al.*, 2008), whereas shanny feed almost exclusively on nauplii and copepodites of calanoid copepods (Dower *et al.*, 2009; Young *et al.*, 2010). These contrasting patterns of prey preference also suggest that mackerel may be considered an aggressive predator capable of pursuing and catching highly active prey. Dower *et al.* (2009) proposed that the feeding abilities of radiated shanny were probably limited, citing evidence from a decoupling of feeding patterns and reconstructed growth histories when shanny larvae were undergoing transitions from feeding on nauplii to copepodites. The results of the morphological and behavioural differences between larvae of Atlantic mackerel and radiated shanny are apparent in the greater degree of autocorrelation of individual growth rates in the former relative to the latter (Figure 4; Dower *et al*., 2009). Effective predators are more likely to be able to maintain optimal growth rates relative to predators that are less efficient. Although we do not have information on the maximum feeding rates of Atlantic mackerel larvae, we know that under most circumstances radiated shanny do not achieve maximal feeding rates, with the majority of individuals achieving less than 50% of their maximum daily weight-specific consumption rate (Young *et al*., 2010). This would, in turn, affect their ability to maintain their growth rates and thereby lead to weaker autocorrelation as a result of day-to-day variations in feeding success relative to species that are more effective at achieving higher relative feeding rates, as may be the case for Atlantic mackerel. When the data from Young *et al*. (2010) are contrasted with this study, two features become apparent (Figure 8). First, there is less scatter (i.e. variance) in the data for Atlantic mackerel relative to radiated shanny; second, the amount of material found in stomachs of radiated shanny begins to level off at a length of ~7 mm, a size at which Atlantic mackerel increase the diversity of their prey and feed more extensively on cladocerans and fish larvae (Robert *et al*., 2008). Obligated fast growth resulting from intracohort cannibalism is likely the main factor explaining the high food intake observed throughout the larval and early juvenile stages of Atlantic mackerel. Extending similar analyses to other species would provide insight into interspecific differences in feeding ability if patterns of autocorrelation are shown to exhibit corresponding changes with immediate measures of state (e.g. stomach content).

Previous studies have demonstrated considerable evidence of decoupling between otolith and somatic growth in larval fish exposed to suboptimal feeding conditions (Secor and Dean, 1989, 1992; Campana, 1990; Folkvord *et al*., 2000). Under most circumstances, slow-growing individuals under poor feeding conditions have larger otoliths at length than do individuals with faster growth rates. Dower *et al*. (2009) were unable to find statistical significant evidence for this in radiated shanny, which seldom feeds at maximal rates (Young *et al*., 2010). Contrastingly, we found uncoupling in Atlantic mackerel, which have fuller stomachs than shanny at a given length, particularly in large individuals. In all instances, the contrast in the residuals from the OG−L relationship of fast- vs. slow-growing individuals, defined as their position relative to a length-at-age relationship, is generally small relative to the overall OG−L function but does indicate that some level of error would be incurred by using otolith size alone as an index of condition. Departures from a direct functional response in both otolith and somatic growth may be of little importance when contrasting age-dependent growth histories to assess the significance of selective mortality (Meekan and Fortier, 1996; Baumann *et al*., 2003) but the issue may be of particular consequence in attempting to reconstruct body size over time (Campana, 1990; Francis, 1990; Secor and Dean, 1992) as well as in the development of inferences between OG and feeding conditions. Such decoupling could result from a slower response in OG relative to somatic growth due to the deterioration in feeding conditions (Folkvord *et al*., 2000) or from a minimum level of OG occurring independent of a larva's metabolic state (Secor and Dean, 1989, 1992). As a result, OG would be considered to have stronger serial correlation and thereby provide a reflection of the "average" conditions encountered by each larva, relative to somatic growth. The degree of decoupling will be the result of the sensitivity of growth rates to changes in ingestion rates as well as the magnitude of variations in feeding success among individuals. Given that we found less variation in stomach contents in Atlantic mackerel relative to radiated shanny but that we found greater evidence for decoupling between otolith and somatic growth rates, we can infer that differences in the sensitivity of these two physiological processes appear to be greater in mackerel. One must be cautious about this interpretation, however, because this may also depend on the extent to which individuals achieve maximal feeding rates, which we know for radiated shanny (Bochdansky *et al*., 2008) but not for mackerel, and possibly as a result of differences in the functional relationship of otolith and somatic growth rates with ingestion rates, as suggested by Folkvord *et al*. (2000). If we assume that ingestion follows a Holling type II response relative to prey availability, the greatest rate of change in feeding rates occurs at low prey concentrations rather than at concentrations at which larvae can achieve maximal feeding rates. Thus, larvae in suboptimal feeding conditions would be more likely to exhibit variations in feeding success, and thereby greater decoupling between somatic and OG, than would individuals feeding near maximal ingestion rates. We have reason to believe, however, that the occurrence of suboptimal feeding conditions in our study is unlikely to influence our interpretation about the greater sensitivity of mackerel. Growth rates measured in this study are at the upper range of those measured by Ware and Lambert (1985) at average temperatures ~15°C, and greater than those measured under laboratory conditions by Mendiola *et al*. (2007). This suggests that mackerel larvae from our study were feeding close to their maximal ingestion rates, whereas most of shanny larvae examined by Dower *et al*. (2009) were feeding well below 50% of their maxima (Young *et al*., 2010). Although previous studies have inferred that decoupling

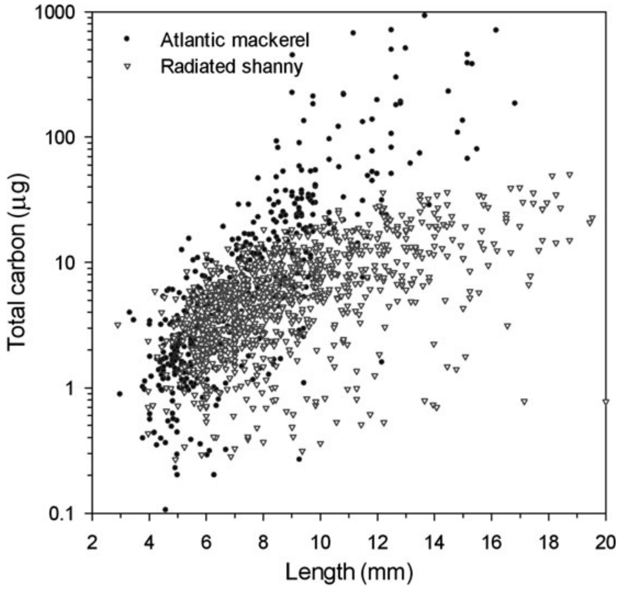

Figure 8. Comparison of total prey carbon per stomach in relation to length for Atlantic mackerel and radiated shanny. Data for radiated shanny are from Young *et al*. (2010) and represent the combined information from several years of sampling using protocols similar to those used in this study.

between otolith and somatic growth is the result of poor or rapid changes in feeding conditions, the contrast we note between radiated shanny, feeding at suboptimal rates, and Atlantic mackerel, likely feeding near their maximum rate, may indicate that taxonomic differences may also affect the link between these two indices of development.

Beyond approaches based on the analysis of otolith microstructure, the state or condition of larval fish has been evaluated using a variety of morphological, biochemical (e.g. nucleic acid ratios), and histochemical (e.g. liver, pancreatic or intestinal enzymes) indices (Ferron and Leggett, 1994; Gisbert *et al.*, 2008). The value of each index in detecting subtle changes in the state of larvae depends on how much of an individual's past is represented by changes in the metric(s). Although only otolith can provide an individual's daily growth history, multivariate approaches based on morphometric measurements have often proven useful in interpreting the state of an individual, e.g. with elements related to body depth and/or girth frequently demonstrating a high degree of sensitivity to changes in feeding conditions (e.g. Lochmann and Ludwig, 2003; Morton, 2012). Our comparison of the percentile scores of anal body depth revealed moderate to strong relationships with age-dependent scores for growth rates and stomach contents, confirming the value of this simple morphometric index as a measure of an individual's condition. More importantly, these relationships were ~3.5–4 times stronger than those based on length-dependent scores. This sharp contrast in the correspondence between the different metrics of state based on age- vs. size-dependent perspectives suggests that the history of individual larvae may play a significant role in determining the state of the animal at the time of capture. Developmental norms and ontogenetic events may largely follow weight- or length-dependent relationships (Ferron and Leggett, 1994) but variability around these norms can result in differential feeding abilities (Portt and Balon, 1984). Many processes in aquatic systems are well represented using size-dependent relationships, which has been exploited in attempts at generalizations (Houde, 1989; Pepin, 1991) as well as in modelling (e.g. Hufnagl and Peck, 2011), but these approaches have essentially overlooked how differences in the ontogenetic development of each individual might have varied and affected their capacity to cope with variations in feeding conditions. Studies of ontogenic events are generally qualitative (e.g. Baglole *et al.*, 1997; He *et al.*, 2012) but Morton (2012) suggested that differential energetic allocation during ontogeny explains some of the variations in growth among species based on a path model that aimed to predict larval body mass based on biochemical and histological variables. Although it is uncommon to consider variations in ontogenetic state in population studies of early life stages, it is important to bear in mind that such initiatives track organisms that are undergoing developmental events likely to have energetic consequences to an individual's capacity to feed and avoid predators and that will also reflect its history.

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