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Once upon a larva: revisiting the relationship between feeding success and growth in fish larvae

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Variations in larval fish growth rates are largely the result of variability in biotic and abiotic characteristics of the feeding environment experienced by each individual. An assessment of an individual's overall feeding success (i.e. accumulation of utilizable organic matter) can best be achieved at the time of capture when the relationships among environment, short-term feeding success as defined by gut content and long-term feeding success as defined by accumulated growth can be contrasted. Here, we investigated the relationships between average growth, feeding success, and variability in individual growth and feeding rates across a range of taxa based on a synthesis of studies in which stomach content and otolith growth were measured in the same individuals. Instantaneous measures of feeding success were highly variable and demonstrated a positive yet somewhat limited association with growth rates across all taxa. The strength of the feeding-growth relationships among taxa, and cohorts within taxa, was reflected in the autocorrelation of individual growth rates, suggesting that stable growth was achieved through consistent feeding success. However, when viewed at the individual level, faster growth was achieved in individuals with more variable growth rates, and by inference more variable past feeding success. The dichotomy in these underlying relationships may point to the importance of stochastic events in the development of exceptional individuals in a population, and may be linked to how surplus energy is allocated to individual growth rates. The positive correlation found between feeding success and growth in all taxa is consistent with the growth-survival paradigm for the larval stage of fish. However, both the correlation between feeding success and growth and the serial correlation of growth time-series was greatest in fast-growing species, suggesting that the potential for an early "critical period" regulating survival varies among species, reaching a maximum in fast-growing fish.

Keywords: early life history, gut content, otolith microstructure, recruitment, survival, trophodynamics.

Introduction

There is widespread agreement that the early life history of fish is a key stage in the life cycle that can determine both short- and longer-term variations in population abundance (Cushing, 1996; Leggett and Frank, 2008; Houde, 2009). The larval stage is generally considered one of the main bottlenecks determining relative strength of year classes within a fish stock (Anderson, 1988; Leggett and Deblois, 1994; Houde, 2008). This bottleneck can occur over a short "critical period" (*sensu* Hjort, 1914, 1926) as a result of starvation following yolk absorption, or over a more protracted period from hatch to metamorphosis (e.g. Cushing, 1990). In both instances, understanding the key factors influencing these processes involves investigating patterns of growth, either of individuals or populations, and their potential relationships with the larva's feeding environment. Some of the most significant progress in the study of growth rates has been achieved through the use of otolith microstructure, which can serve to trace the growth history of individuals (Campana, 1990) or assess which individuals are most likely to survive by comparing populations at different stages of development (e.g. Meekan and Fortier, 1996; Hare and Cowen, 1997; Robert et al., 2007).

If we are to understand variations in growth, we have to consider that a cohort consists of a collection of individuals, each of which experiences a unique feeding environment in their immediate proximity on scales <10 s of metres daily. We have to relate the characteristics of individuals to those of the population to infer how these might be altered as the environment changes. The number of prey ingested daily by an individual is a function of local productivity and the factors influencing the probability of encountering and capturing appropriate prey within the larva's search volume. Within a cohort experiencing suboptimal feeding conditions, growth rates are more variable, and the strong growth exhibited by the most successful individuals in the population is achieved through a certain degree of luck (Pepin, 2004). A comparison among cohorts revealed that as the feeding environment improves, similarly high growth can be achieved by individuals that were among the "weaker" individuals. However, the growth rates of most successful individuals within a population or cohort are greatly dependent on stochastic and infrequent events associated with high prey densities or feeding success (Pepin, 2004).

An accurate understanding of the link between an individual's feeding success or abilities and its feeding environment can generally only be achieved at the time of capture because this is the only opportunity when the larval prey field (species composition and abundance) can be measured. Recently, Dower et al. (2009) and Robert et al. (2014) demonstrated that despite a significant relationship between the relative length-at-age of individuals and the age-adjusted stomach content, there was considerable variability around these relationships and that a fast-growing species (Atlantic mackerel—*Scomber scombrus*) demonstrated a closer relationship between individual growth and stomach content than a slower-growing one (radiated shanny—*Ulvaria subbifurcata*). This suggests that lower growth may be the result of greater variability in feeding success, not necessarily lower feeding success alone. They also found similar contrasts in the level of growth autocorrelation within species, with mackerel showing greater serial correlation of individual growth rates relative to shanny, suggesting that more consistent feeding rates lead to faster growth. Although the contrasts appear logical, and it might be tempting to generalize, it remains to be determined to what extent the relationship between

feeding success and growth performance varies across taxa and ecosystems. Furthermore, do these conclusions derived at the cohort/population level hold among individuals within a given species?

In the present study, we use a synthesis of previously published (fully or partially) datasets of stomach content and otolith growth measured from the same individual fish larvae, to contrast the link between feeding and growth among populations, species, and environments. Our aims were to investigate the relationships between growth and feeding across a range of taxa and how these are reflected in the characteristics of individual larvae because it is the variance among animals upon which selective processes are likely to act.

Material and methods
Data compilation

A total of 14 population-specific datasets including both gut content and otolith growth data sampled in the same individual fish larvae were gathered for the analyses (Table 1). The datasets included a wide range of habitats, ranging from freshwater to marine and from polar to tropical areas. Arctic cod *Boreogadus saida*, Atlantic cod *Gadus morhua*, and yellow perch *Perca flavescens* were the only species that comprised replicates (i.e. several populations), although the limited number of individuals per population of *P. flascescens* did not permit us to conduct separate analyses on each. Sampling methodologies are detailed in the original publications derived from each dataset (Table 1), although one dataset remains unpublished (*Limanda ferruginea*) and two others were only partially published (*G. morhua* from Scotian Shelf—otolith growth only, and *G. morhua* from southern Gulf of St Lawrence—stomach content only). For *L. ferruginea*, samples were collected during the same surveys and analysed following similar methods as those described for *S. scombrus* (Robert et al., 2008, 2009). Gut content and otolith analyses for the two *G. morhua* populations were also performed following these methods in the same laboratory. Analyses were based on length as the basis for comparison among taxa because it is the most commonly available metric of body size and was measured for each individual used in the analysis and does not involve conversion based on estimated parameters (e.g. length–weight relationships; Houde, 1997). Metabolic processes, such as growth, may be more accurately contrasted using measurements of individual body mass, but these were not available.

Measure of feeding success

In all studies, feeding success was derived through the measure of total dry weight or carbon gut content. Larval fish guts were examined under the dissecting microscope, and each prey was measured and identified to the lowest taxonomic level possible. The contribution of each prey to total dry weight or carbon content was derived from species-specific length–weight relationships from the literature (Falardeau et al., 2014). The larvae used in our analyses were collected during periods of the day when there was clear evidence of active feeding based on the distribution of age-dependent percentile scores of total carbon ingested (see the Data analysis section).

Specimens with no food in their stomach represent a challenge to the comparison of feeding success and growth patterns because empty guts may represent true failure to effectively capture prey in the hours preceding capture or may be the result of regurgitation during sample collection, which can be affected by a number of factors (e.g. duration of speed of net tows, larval morphology, state of digestion, etc.). Because it is impossible to ascertain the

Table 1. Nature and origin of the datasets used in the present study.

Species	Common name	Area	Period	Number of larvae	Length range (mm)	Age range (d)	References
Arctogadus glacialis	Ice cod	SE Beaufort Sea	2002–2004	90	6.6–45.5	1–194	Bouchard et al. (in press)
Boreogadus saida	Arctic cod	SE Beaufort Sea	2002–2009	390	5.3–54.0	0–234	Bouchard et al. (in press)
		North Water polynya (NOW)	1998	420	4.0–16.5	2–54	Thanassekos and Fortier (2012)
		Northeast Water polynya (NEW)	1993	373	4.6–22.1	0–68	Michaud et al. (1996), Fortier et al. (2006)
Chrysophrys auratus	Australasian snapper	Port Phillip Bay	2004–2010	302	1.8–7.5	2–19	Murphy et al. (2012)
Gadus morhua	Atlantic cod	Scotian Shelf	1991–1993	127	2.9–39.2	0–154	Meekan and Fortier (1996)
		Southern Gulf of St Lawrence	1997–2000	958	3.4–46.9	0–175	Robert et al. (2011)
Istiophorus platypterus	Sailfish	Straits of Florida	2003–2004	161	2.4–34.6	3–18	Llopiz and Cowen (2008), Sponaugle et al. (2010)
Limanda ferruginea	Yellowtail flounder	Southern Gulf of St Lawrence	1997–1998	786	2.5–24.2	1–81	Unpublished results
Makaira nigricans	Blue marlin	Straits of Florida	2003–2004	198	2.4–23.0	2–20	Llopiz and Cowen (2008), Sponaugle et al. (2010)
Perca flavescens	Yellow perch	Canadian Boreal Shield Lakes	2005	308	10.9–60.0	11–57	Leclerc et al., (2011a, b)
Scomber scombrus	Atlantic mackerel	Southern Gulf of St Lawrence	1997–2000	516	3.0–16.8	2–27	Robert et al., (2008, 2009)
Thalassoma bifasciatum	Bluehead wrasse	Straits of Florida	2003–2004	91	3.3–6.9	15–27	Sponaugle et al. (2009)
Ulvaria subbifurcata	Radiated shanny	Trinity Bay, Newfoundland	2000	197	4.0–18.5	1–38	Dower et al. (2009)

cause of differences in the frequency of empty stomachs among the various species and protocols that contributed to this study, we have excluded specimens with empty guts from most of the analyses considered below. We acknowledge that differential occurrence of true feeding failure among taxa could affect the strength of the relationships presented in our analyses, but the extent to which it would affect the interpretation of our findings is well beyond the scope of this study and so we base our assessment on individuals for which we have a non-zero measure of the immediate feeding success at capture.

Daily growth history

Age and daily growth history were derived from the number and width of daily increments from the core to the edge of the otolith, except *Chrysophrys auratus*, in which age was calculated by adding 2 days to the number of increments counted, as the first increment corresponds to first feeding which occurs 2 days post-hatch (Murphy *et al.*, 2013). However, the portion of the otolith ranging from the last full daily increment to the outer edge, representing the last, incomplete day of life, was not considered in the analysis. Otoliths were mounted on slides and analysed at $400-1000\times$ using a compound microscope connected to an image-analysing system with either a video or digital camera. Average growth rates were estimated based on the slope of the length-at-age relationship of each species, population, or cohort. We also estimated the average and standard deviation of the first 15 daily increments of each individual larva.

Data analysis

Following Dower *et al.* (2009) and Robert *et al.* (2014), we used non-parametric local density estimators (Davison and Hinkley, 1997) to describe the change in variability in larval state (i.e. length, growth, and gut content) with age, to avoid potential bias from traditional linear models as a result of age-dependent individual departures from the overall response. 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 age as a covariate and surrounding observations using kernel smoothing. In our analysis, the weighting function was $w(d) = e^{-d}$, 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 each 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 days]. 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) 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. The analysis was performed for each species separately.

Relationships between feeding and growth metrics among species were investigated using Pearson's production moment

correlations (*r*), which assumes a linear relationship between variables, and Spearman's rank correlation (*r*$_s$), which evaluates whether the relationship between variables follows a monotonic trend. Application of both approaches provides an assessment of the consistency of association between variables and the potential influence that the distribution of observations may have on the outcome. In instances with a limited number of observations, the contrast between correlations may provide an evaluation of the influence of observations at the extremes of the range in the data.

Results

Length-at-age
The range in size and age of fish larvae varied widely among species (Table 1). In fast-growing scombroid species such as *Istiophorus platypterus*, *Makaira nigricans*, and *S. scombrus*, captured larvae ranged between lengths of 3–20 mm and ages 0–20 d. In contrast, larvae of the slow-growing Arctic gadids *Arctogadus glacialis* and *B. saida* measured between 5 and 55 mm and ranged in age from 0 to nearly 250 d. The relationship between length and age was mostly linear, despite a trend for non-linear growth within the older portion of some populations, such as scombroids (Figure 1). Larval stage duration was about an order of magnitude shorter in sailfish (18 d) relative to Arctic gadids (∼200 d), which was paralleled by a difference in growth rates of the same order of magnitude (0.95 mm d^{-1} for sailfish vs. 0.15 mm d^{-1} for Arctic gadids; Figure 1). The scatter of length-at-age (i.e. variation in length achieved at a given age) was relatively constant in most species but showed an increasing trend with age in *L. ferruginea*, *P. flavescens*, *S. scombrus*, and *U. subbifurcata* (Figure 1).

Stomach content at age
Carbon content of guts increased exponentially with larval age in all species (Figure 2). In populations that were sampled continuously from hatch to the late larval stage, the mean gut content generally increased by 3–4 orders of magnitude, independent of taxon and habitat. Regression of log-transformed prey mass in relation to length revealed considerable variability in the slope and fit of the relationships, but in general there was a two to threefold level of variation in stomach contents at a given length, based on the root mean square error in which specimens with empty guts were excluded from the analyses (Table 2). Past the first-feeding stage, the feeding ratio (proportion of larvae with prey in guts) was generally high, with the exceptions of the *B. saida* population from the Northeast Water polynya and *C. auratus*, which were both characterized by a large proportion of empty guts throughout the larval stage (33% for *B. saida* and 62% for *C. auratus*). The high occurrence of empty guts in those studies was inconsistent with the observations from the other studies and may be indicative of relatively high occurrence of regurgitation during capture.

When datasets were compared among species, the amount of carbon in the guts of fish larvae increased exponentially with body length (Supplementary Figure S1). The logarithm of scatter (variation in gut content at length excluding empty stomachs) varied by up to 4 orders of magnitude at a given length among all species. Fast-growing species such as *M. nigricans*, *I. platypterus*, and *S. scombrus* generally had a prey mass 2 orders of magnitude greater than that of slow-growing species such as *L. ferruginea* or *B. saida*, at a given length.

Relation between stomach content and growth
The percentile score of total carbon ingested at a given age by individual larvae [*P*(carbon|age)] was positively correlated with length-at-age [*P*(length|age)] in 13 out of the 14 populations (Figure 3). When individuals with empty guts from the Northeast Water polynya *B. saida* and *C. auratus* populations were removed from the analysis, all 14 populations were characterized by a positive correlation, indicating that in all species, larger individuals at a given age tended to have a larger prey mass in their guts relative to individuals that were smaller at age. The strength of the correlation coefficient between [*P*(carbon|age)] and [*P*(length|age)] varied from *r* = 0.14 in the slow-growing *L. ferruginea* to *r* = 0.60 in the fastest-growing *I. platypterus*.

Overall, the correlation between [*P*(carbon|age)] and [*P*(length|age)] was positively linked to average linear growth rate achieved by the different larval fish populations (all data *r* = 0.50, *p* < 0.05, *r*$_s$ = 0.32, *p* > 0.2; zeroes removed *r* = 0.55, *p* < 0.05, *r*$_s$ = 0.38, *p* > 0.1; Figure 4). This indicates that the correlation between probabilities of carbon content and length at a given age was stronger on average in fast-growing than in slow-growing species. Some populations departed from this general pattern, such as the fast-growing *M. nigricans* and *P. flavescens*, both of which only displayed moderate levels of correlation between [*P*(carbon|age)] and [*P*(length|age)], or *G. morhua* and *Thalassoma bifasciatum*, which displayed strong correlation despite relatively slow growth (Figure 4).

A consistent set of relationships were found among species between serial correlation in growth and the strength of correlation between [*P*(carbon|age)] and [*P*(length|age)]. The relationship was strongest between ages 5 and 15 d (Figure 5a; *r* = 0.70, *p* < 0.01, *r*$_s$ = 0.44, *p* > 0.1), but also remained strong over a shorter age interval ranging between 5 and 10 d (Figure 5b; *r* = 0.58, *p* < 0.05, *r*$_s$ = 0.47, 0.1 > *p* > 0.05) or when considering average autocorrelation between ages 1–5 and 10–15 d (Figure 5c; *r* = 0.59, *p* < 0.05, *r*$_s$ = 0.48, 0.1 > *p* > 0.05). This indicates that in species characterized by a strong link between [*P*(carbon|age)] and [*P*(length|age)], individuals characterized by fast growth early in life are likely to remain fast growers later in life. In contrast, for species with low correlations between [*P*(carbon|age)] and [*P*(length|age)], growth performance achieved early in life was less indicative of future growth performance.

To investigate whether the findings among taxa and ecosystems were applicable among cohorts within a species, we repeated the same analysis on different year-classes of *G. morhua* (1997–2000), *L. ferruginea* (1997–1998), and *S. scombrus* (1997–2000) from the southern Gulf of St Lawrence. There was considerable variability in the strength of the correlation between [*P*(carbon|age)] and [*P*(length|age)] for *L. ferruginea* and *S. scombrus* but limited variation for *G. morhua*. This was reflected in the pattern of variation in growth autocorrelation between 5 and 10 d and the association between age-dependent stomach content and length-at-age (*r* = 0.75, *p* < 0.05, *r*$_s$ = 0.81, *p* < 0.01; Figure 6). Species-specific trends were consistent with the general patterns demonstrated previously for *L. ferruginea* and *S. scombrus*, except *G. morhua* for which the level of variation among cohorts was considerable in terms of growth autocorrelation but not in terms of individual association between age-dependent stomach content and length-at-age.

Age-dependent patterns in serial correlation of growth rates varied considerably among taxa (Figure 7). Several species (*A. glacialis*, *B. saida*, *G. morhua*, *P. flavescens*) demonstrated little evidence that the autocorrelation in growth rates became stronger with increasing age, and although there were differences in the rate of loss in growth "inertia" among species, the similarity in an individual's growth rate dropped to negligible levels in a matter of
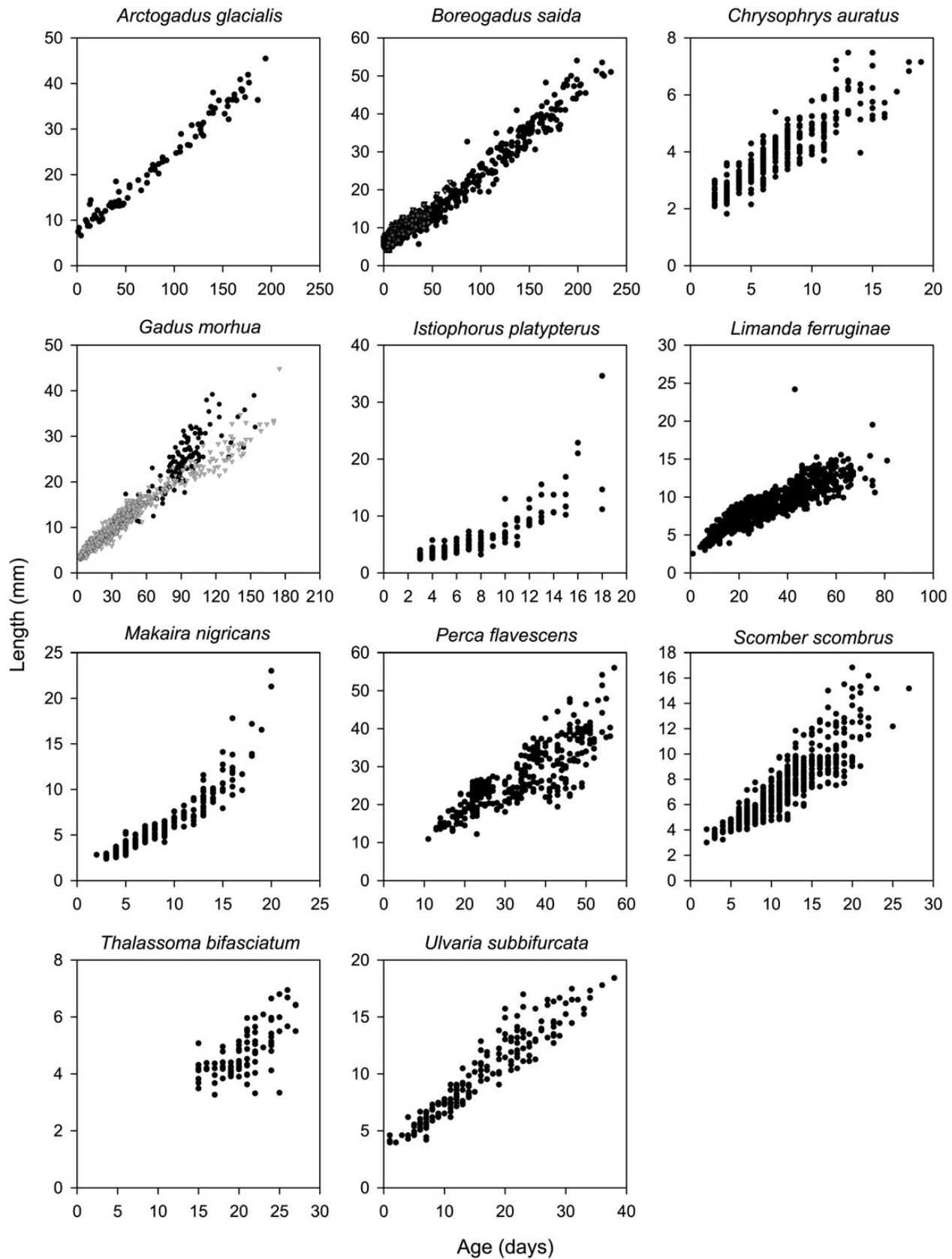
Figure 1. Standard length in relation to daily age derived from otoliths in 11 species of larval fish. Data for *B. saida* and *G. morhua* were combined in plot, but populations (shown in different shades of grey) were analysed separately.
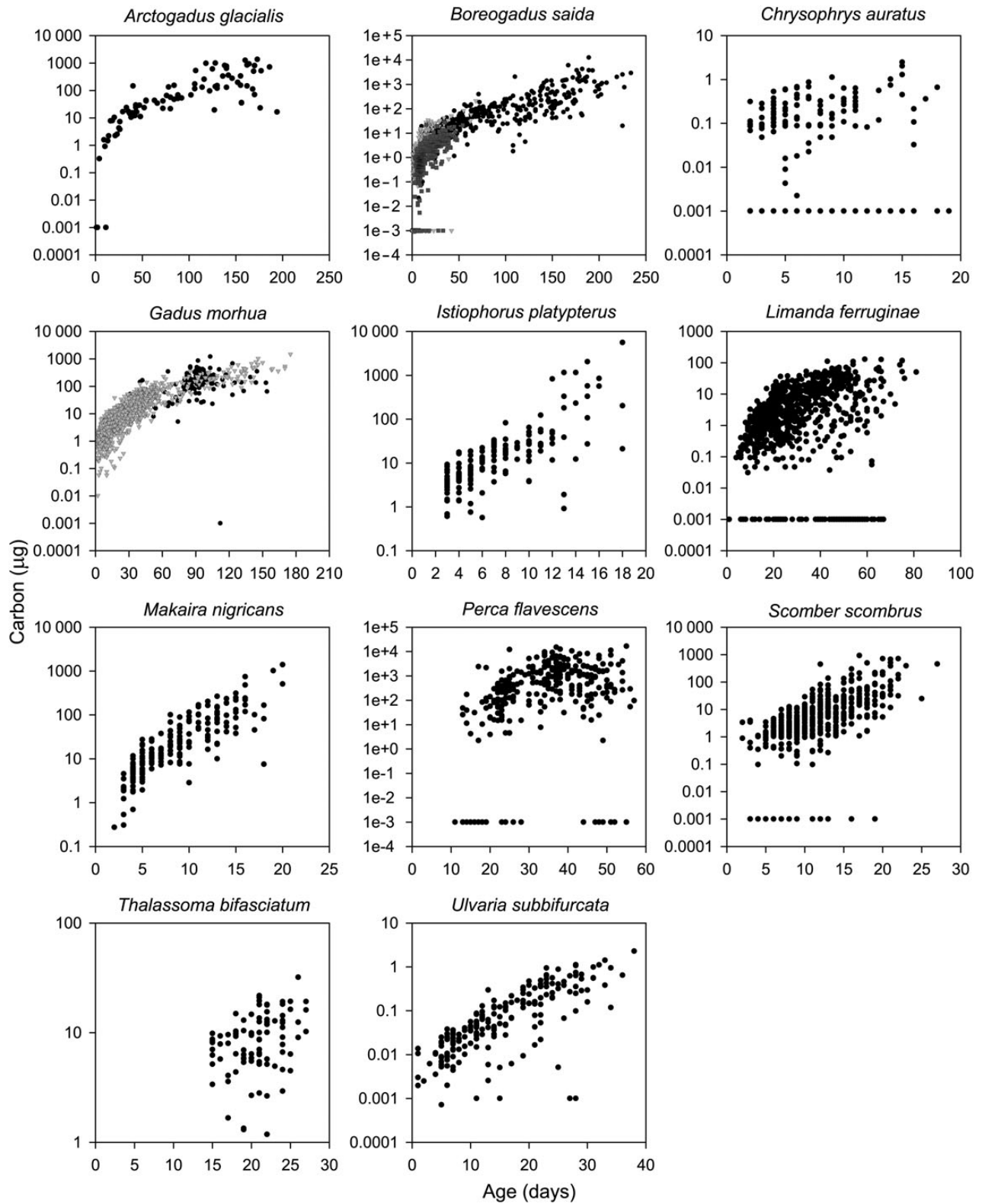
Figure 2. Total carbon content in relation to age in 11 species of larval fish. Data for *B. saida* and *G. morhua* were combined in plot, but populations (shown in different shades of grey) were analysed separately. Empty stomachs are represented by values of 0.001 μg carbon.

a few days in these taxa. In contrast, as larvae of *S. scombrus*, *T. bifasciatum*, and *U. subbifurcata* aged, the persistence of high or low growth rates became considerably stronger, indicative of an increasing differentiation of growth patterns of individuals within a cohort

over time. Growth autocorrelation of *L. ferruginea* showed a substantial increase with age, but the overall strength in serial growth correlation was much weaker than in the former three species. There may have been hints of increasing correlation of serial growth in *C.*

Table 2. Regression analysis of the $\log_{10}$-transformed relationship between total carbon content of stomach (µg C) and the length (mm) of individual fish larvae by taxa.

Species	Area	Intercept	Slope	r^2	RMSE
Arctogadus glacialis	SE Beaufort Sea	−2.66	3.29	0.71	0.44
Boreogadus saida	SE Beaufort Sea	−2.07	2.95	0.72	0.48
	North Water polynya	−4.28	4.97	0.60	0.41
	Northeast Water polynya	−3.26	3.65	0.48	0.42
Chrysophrys auratus	Port Phillip Bay	−1.66	1.58	0.17	0.45
Gadus morhua	Scotian Shelf	−0.63	2.01	0.33	0.34
	Southern Gulf of St Lawrence	−1.79	2.94	0.79	0.34
Istiophorus platypterus	Straits of Florida	−0.69	2.56	0.69	0.38
Limanda ferruginea	Southern Gulf of St Lawrence	−2.75	3.55	0.36	0.59
Makaira nigricans	Straits of Florida	−0.75	2.78	0.75	0.34
Perca flavescens	Canadian Boreal Shield Lakes	−1.53	2.92	0.20	0.71
Scomber scombrus	Southern Gulf of St Lawrence	−2.49	3.86	0.61	0.43
Thalassoma bifasciatum	Straits of Florida	−0.42	1.99	0.29	0.24
Ulvaria subbifurcata	Trinity Bay, Newfoundland	−4.42	3.38	0.71	0.37

RMSE, root mean square error.
Zero values (empty stomachs) were excluded from the regressions. All relationships are statistically significant $p < 0.001$.

auratus, and *M. nigricans*, but the limited age range over which autocorrelation could be estimated reliably both for these species and *I. platypterus*, made it difficult to evaluate to what extent the individual growth histories of taxa with rapid growth were maintained over time.

The relationship between the standard deviation and average growth increment widths of individual larvae (hereafter s.d.-to-mean) for individuals 10 d or older was statistically significant in all populations or taxa, but the slope of the relationships was highly variable. Average growth rates were a poor predictor of the slope of the s.d.-to-mean relationships, but the serial correlation was significantly correlated with this metric of individual growth histories ($r = 0.60$, $p < 0.05$, $r_s = 0.69$, $p < 0.01$; Figure 8). The strength of the $P(\text{carbon}|\text{age}) \sim P(\text{length}|\text{age})$ relationship was not significantly correlated with the slope of the s.d.-to-mean relationship ($r = 0.35$, $p > 0.1$, $r_s = 0.53$, $p < 0.1$).

Discussion
Variability in the feeding-growth relationship at the level of the cohort vs. the individual
We showed that, on average, consistent feeding success was linked significantly with a species' or cohort's ability to achieve high growth rates, a result that was reflected by serial correlations in growth histories. However, when we extended the analysis to the level of individuals, stronger serial correlations were associated with greater strength of the s.d.-to-mean relationship in individual growth rates. This means that faster growth was achieved in individuals that had more variable growth rates, and by inference, more variable feeding success. The dichotomy in the underlying relationships of growth and consistency in feeding success at the species vs. individual levels does not invalidate the growth–mortality paradigm, but rather may point to the increasing importance of stochastic events in the development of exceptional individuals within a population. In a comparison among cohorts of radiated shanny, Pepin (2004) noted that individuals in poor feeding environments that resulted in low average growth rates of the population, were likely to have more highly variable daily growth rates than those fish foraging in good feeding environments. Although the inference may be that prey patchiness is the ultimate driver of this pattern, the potential influence of behaviour (e.g. short-term satiation or pauses in foraging activity) and physiology cannot be ignored. Indeed, the distribution of observations in the plot of the relationship between the s.d.-to-mean slopes vs. autocorrelation suggests that a threshold may exist in the processes that govern the balance between foraging ability and stochastic events in determining growth rates of larval fish, comparable to the concept of surplus energy allocation (Ware, 1978). By maintaining baseline but variable feeding rates, larvae may be capable of achieving the basic energetic requirements for development. However, random events that result in encounters with high prey densities and/or high feeding success may allow larvae to enhance or sustain high growth rates for extended periods, and hence greater serial correlation, because of enhanced energy reserves.

Energy reserves in larval fish are generally stored as large, high-energy triacylglycerols (TAG, Rainuzzo *et al.*, 1997), but lipids can also be used directly in the form of short-lived transitory, small components that are energetically available (e.g. free fatty acids and diacylglycerides; Kattner *et al.*, 2007). Most studies dealing with energy storage in larval fish have focused on longer term reserves, such as TAGs that are required during periods when metabolic demands exceed intake. Intermediate metabolite lipids occur in lower concentrations than TAGs in a manner consistent with their role in physiological processes, but may also lead to an undervaluation of their role in development because of high turnover rates (Morton, 2010). To illustrate the possibility of a threshold for enhanced growth, we contrast the increment widths at ages 7 and 11 of *G. morhua* and *S. scombrus* from the southern Gulf of St Lawrence (Figure 9), two species with similar morphologies at this early stage of development. There is evidence of a non-linearity in increment widths beyond ~ 1.5 µm in *S. scombrus* that is not apparent in *G. morhua* because exceptionally high growth rates do not appear to have been reached by individual larvae. Although it is beyond the scope of this study to evaluate the possible role of enhanced energy reserves on larval growth more fully, the existence of such a process would have considerable implications for the formulation and evaluation of individual-based models (IBMs) of larval fish development. Most current IBMs do not explicitly consider the influence of energy results or the non-linear effects that stochastic feeding events may have on physiological processes (Peck and Hufnagl, 2012). However, the design of feeding-growth models that incorporate serial processes to deal with selective allocation of energy to development vs. allocation to short (hours–days) and longer (weeks–months) term energy reserves may be beyond the scope of current knowledge about the physiology of larval fish.
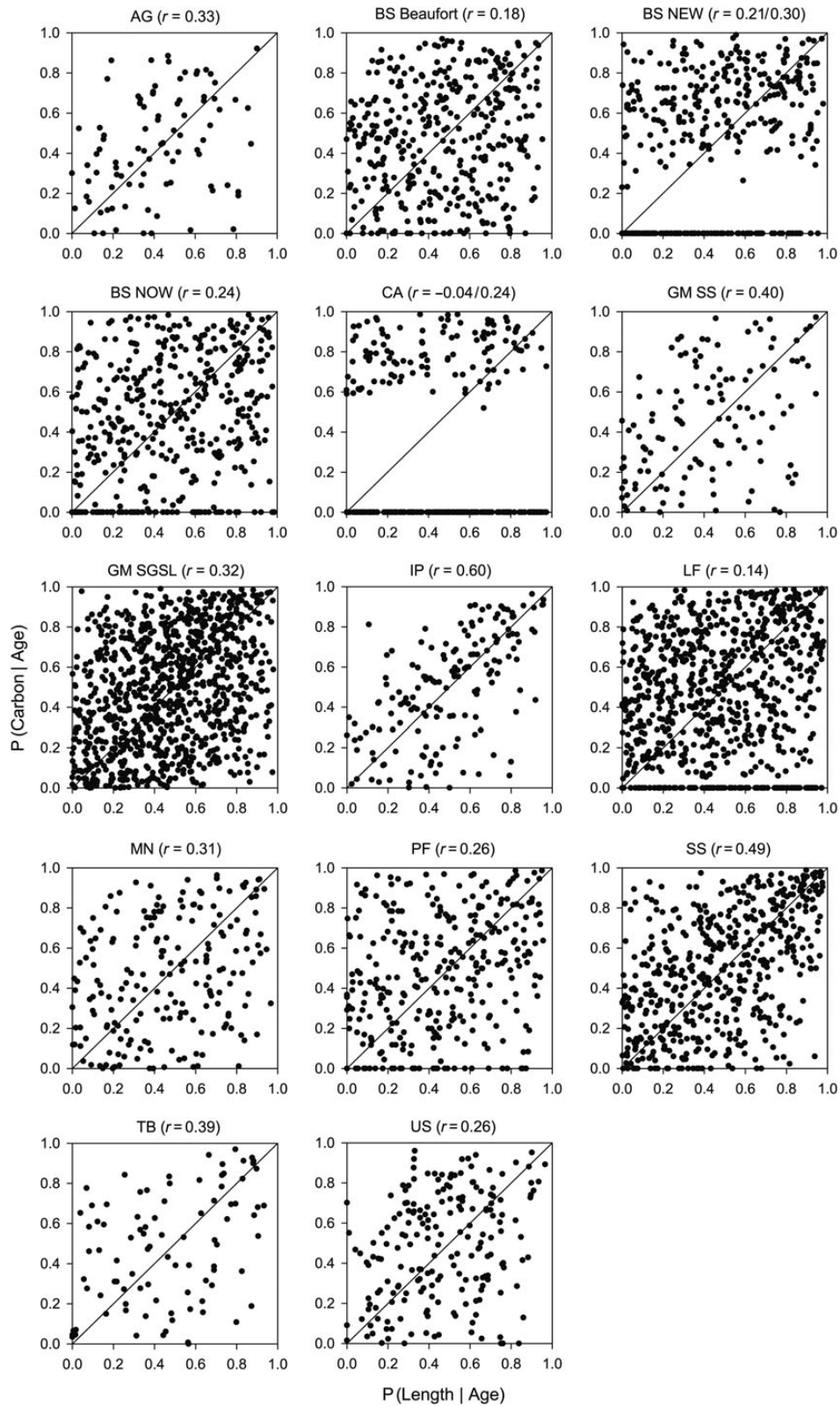
Figure 3. Age-dependent percentile score of carbon ingested in relation to percentile score of length-at-age for 14 larval fish populations. Correlation is indicated above each panel. BS NEW and CA have two correlations—the first based on all data (unrestricted) and the second based reanalysis after removing highly frequent empty stomachs. AG, *Arctogadus glacialis*; BS, *Boreogadus saida* (BS, Beaufort Sea; NEW, Northeast Water polynya; NOW, North Water polynya); CA, *Chrysophrys auratus*; GM, *Gadus morhua* (SS, Scotian Shelf; SGSL, Southern Gulf of St Lawrence); IP, *Istiophorus platypterus*; LF, *Limanda ferruginea*; MN, *Makaira nigricans*; PF, *Perca flavescens*; SS, *Scomber scombrus*; TB, *Thalassoma bifasciatum*; US, *Ulvaria subbifurcata*.
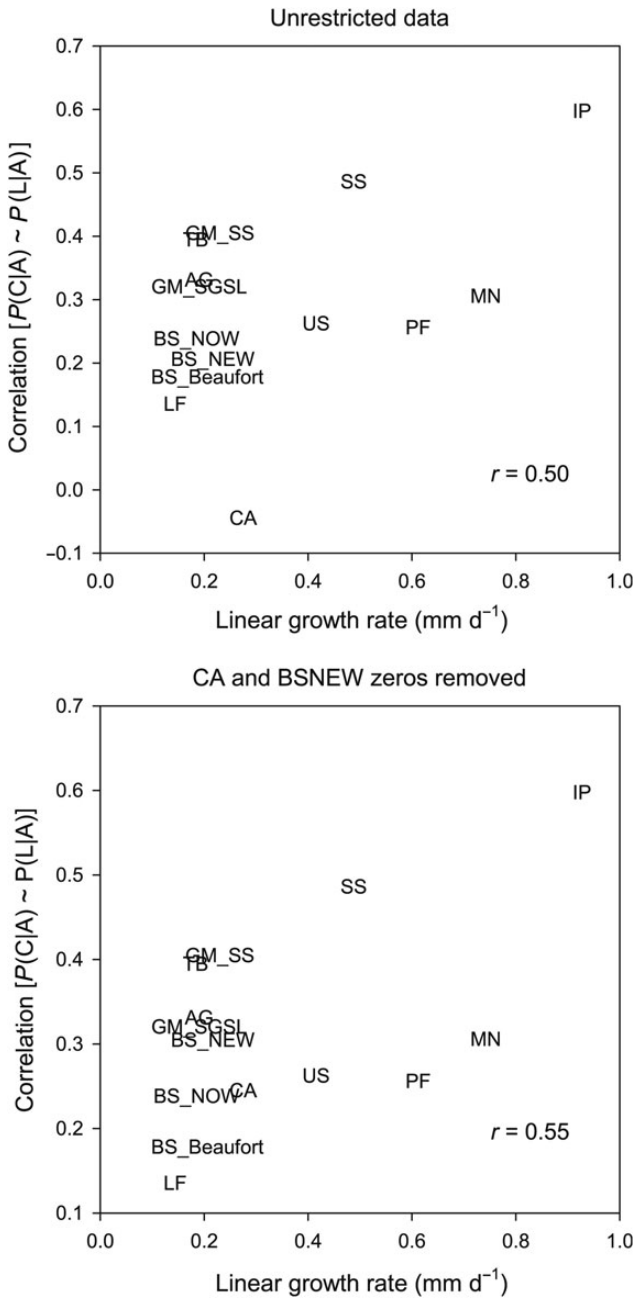
Figure 4. Relation between the correlation of age-dependent carbon ingested [P(Carbon|Age)] and length-at-age [P(Length|Age)], and linear growth rate in 14 larval fish populations. The top panel presents the unrestricted analysis, while the bottom panel presents the reanalysis after empty stomachs from BS NEW and CA have been removed. Correlations between variables are shown in the bottom right corner of each panel. See Figure 3 caption for symbol legend.

Figure 5. Autocorrelation of increments 5 and 15 (a), increments 5 and 10 (b), and average autocorrelation of increments 1 – 5 with increments 11 – 15 (c) in relation to correlation between age-dependent stomach content and length-at-age. Note that autocorrelation was calculated between increments 3 and 8 and that average autocorrelation was calculated between age intervals 1 – 5 and 6 – 10 d in *C. auratus*, *I. platypterus*, and *M. nigricans* (dark grey symbols) because older larvae were not available in sufficient numbers to provide reliable estimates of autocorrelation. See Figure 3 caption for symbol legend.

How environmental variations in prey abundance and availability are perceived and dealt with by larval fish is ultimately reflected in the growth rates that individuals can achieve (e.g. Anderson, 1988). Metabolic scope and maximal feeding rates and/or needs are dependent on environmental temperature to a great extent and so would establish the upper limit of what growth rates can be achieved in a given ecosystem (e.g. Jobling, 1997; Buckley *et al.*, 2004). Instantaneous measures of feeding success are highly variable
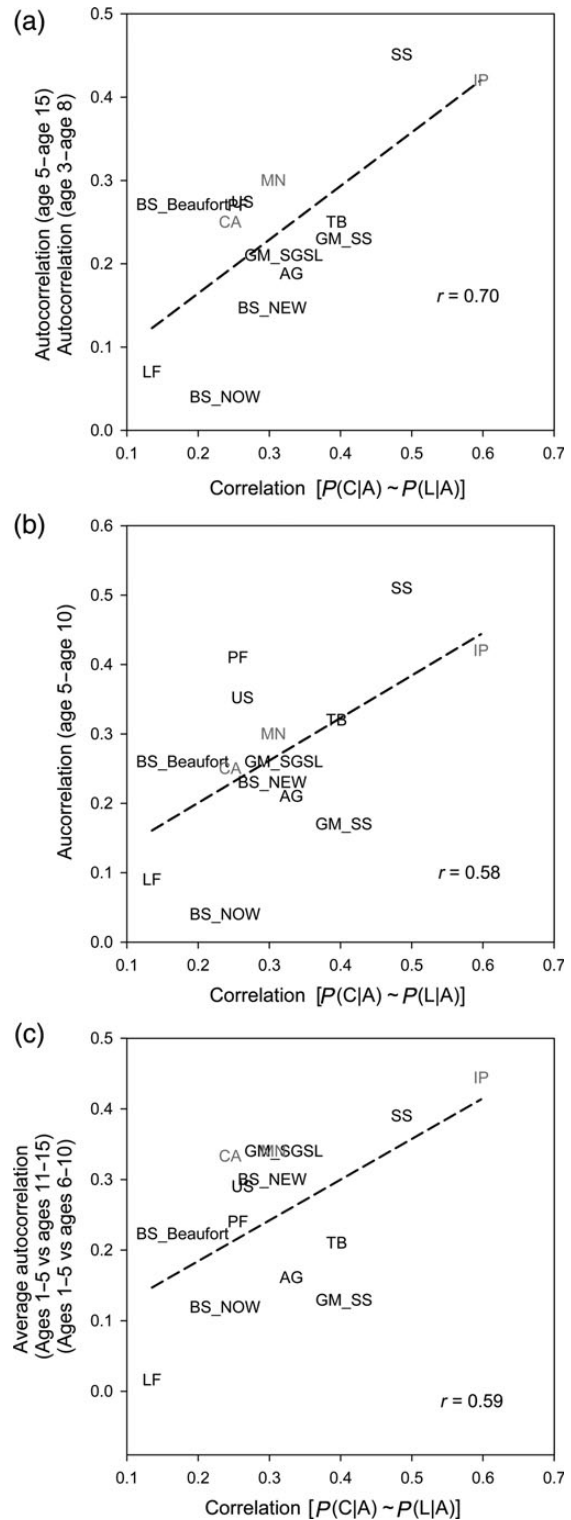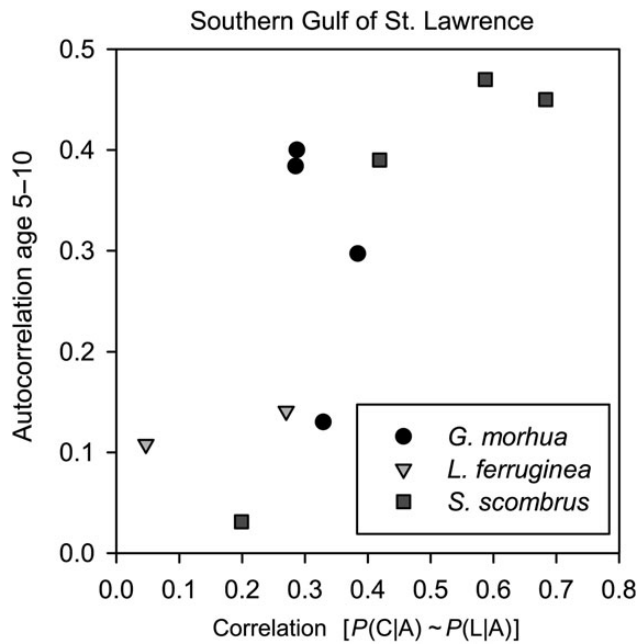
Figure 6. Autocorrelation of increments 5 and 10 in relation to correlation between age-dependent stomach content and length-at-age for different year-classes of *G. morhua* (1997–2000), *L. ferruginea* (1997–1998), and *S. scombrus* (1997–2000).

and demonstrate a positive, yet somewhat limited association with the physiological dynamics of individual larvae (e.g. Dower *et al.*, 2009; Robert *et al.*, 2014). This was evident in the link between the strength of the feeding-growth relationships and the autocorrelation of individual growth rates across a broad range of taxa, in addition to among cohorts within a species. High growth rates can be maintained by encountering high densities of prey, which will require a certain degree of luck, given the high levels of patchiness characteristic of microplankton (Owen, 1989; Lough and Broughton, 2007; Young *et al.*, 2009) and will vary in different ecosystems. However, the behavioural ability of each individual and taxon to search their environment and successfully capture sufficient prey also plays a key role in determining growth potential, as was demonstrated by the variation among taxa within a single ecosystem (i.e. *G. morhua*, *L. ferruginea*, and *S. scombrus* from the southern Gulf of St Lawrence). There may also be an effect resulting from the behavioural trade-off between feeding activity and vulnerability to predation but which we are unable to address without full consideration of growth-dependent mortality. Despite our findings, the relative contributions of the environment and the larva's ability as a predator remains difficult to tease apart because the range of environmental conditions both within and among ecosystems can easily be confounded with the differences in growth among individuals and taxa.

Measurement error may be an important consideration in the analysis of otolith microstructure, particularly when growth is slow or in very young larvae owing to the inherent uncertainty associated with the timing of first visible increment formation or with determining the precise location of an increment's edge (Meekan *et al.*, 1998; Pepin *et al.*, 2001). The impact may be significant if the goal is to reconstruct size-at-age of individuals over short time intervals (Meekan *et al.*, 1998) and may obscure the short-term effects of changes of environmental conditions on an individual's

state (Pepin *et al.*, 2001). Pepin *et al.* (2001) concluded that over time, an individual's physiological inertia (Morales-Nin, 2000) would reflect the cumulative effect of environmental variability on its growth history that could be detected from measurements of otolith microstructure. The patterns of serial correlation described in this study and their relationship with each species' effective growth rates are consistent with the cumulated effects of feeding histories on increment formation.

Our use of parametric and non-parametric correlations identified some differences in the strength of the relationships between metrics of feeding success and/or growth. The contrast in the degree of association under different assumptions about the nature of the relationships may be a reflection of differences in the time intervals that are integrated by each metric. Gut contents represent the outcome of events that occur over a few hours, while otolith increments represent the effect of events over the course of days and average growth rates summarize the entire larval phase. In most instances, the difference in the strength of the association between variables was modest and did not alter the underlying trend. The most significant difference occurred in the association between average linear growth rates and the association between the conditional stomach content (Figure 4). The linear trend was greatly influenced by the high growth rate and strong feeding success of *I. platypterus*. However, it may also reflect the dichotomy between the most instantaneous metric of feeding success and/or growth, which depends on the state of the individual and some degree of chance, and the average growth rate. The latter integrates all past events that may include the selective losses that are likely to have removed the least successful individuals. Differences in the cumulative impact of selective loss from the different taxa may also have contributed to the high degree of variability around the overall trend.

Implications for the growth-survival paradigm

A major assumption underlying the growth-survival paradigm is that within a given population, individual larvae characterized by superior growth performance (and eventually a higher rate of survival) are those that have consistently achieved higher feeding success. Adding to the evidence from *U. subbifurcata* (Dower *et al.*, 2009) and *S. scombrus* (Robert *et al.*, 2014), we observed that all the additional 12 populations (9 species) considered in this meta-analysis were characterized by a positive correlation between age-dependent probabilities of gut content and length. Populations considered in this study included a wide variety of taxa inhabiting various habitats ranging from freshwater to marine and from tropical to polar. Although the relationship between feeding success and growth was relatively weak in most species, the existence of a positive correlation between both of these vital rates (as predicted by the growth-survival hypothesis) in all species we examined in our study strongly supports the idea that identifying the determinants of larval feeding success is critical for the prediction of early growth and survival in marine fish.

In addition to confirming the general importance of the link between feeding success and growth in larval fish, our study has also revealed striking interspecific differences in the variance explained by the relationship. The correlation coefficient between probabilities of stomach content and length-at-age increased as a function of linear growth rate, ranging from 0.14 in the slowest-growing species, *L. ferruginea* (0.15 mm d^{-1}) to 0.60 in the fastest-growing species, *I. platypterus* (0.90 mm d^{-1}). Given that fast-growing species (relative to slow-growing species) were also generally characterized by stronger serial correlation in growth suggests that the relative importance of
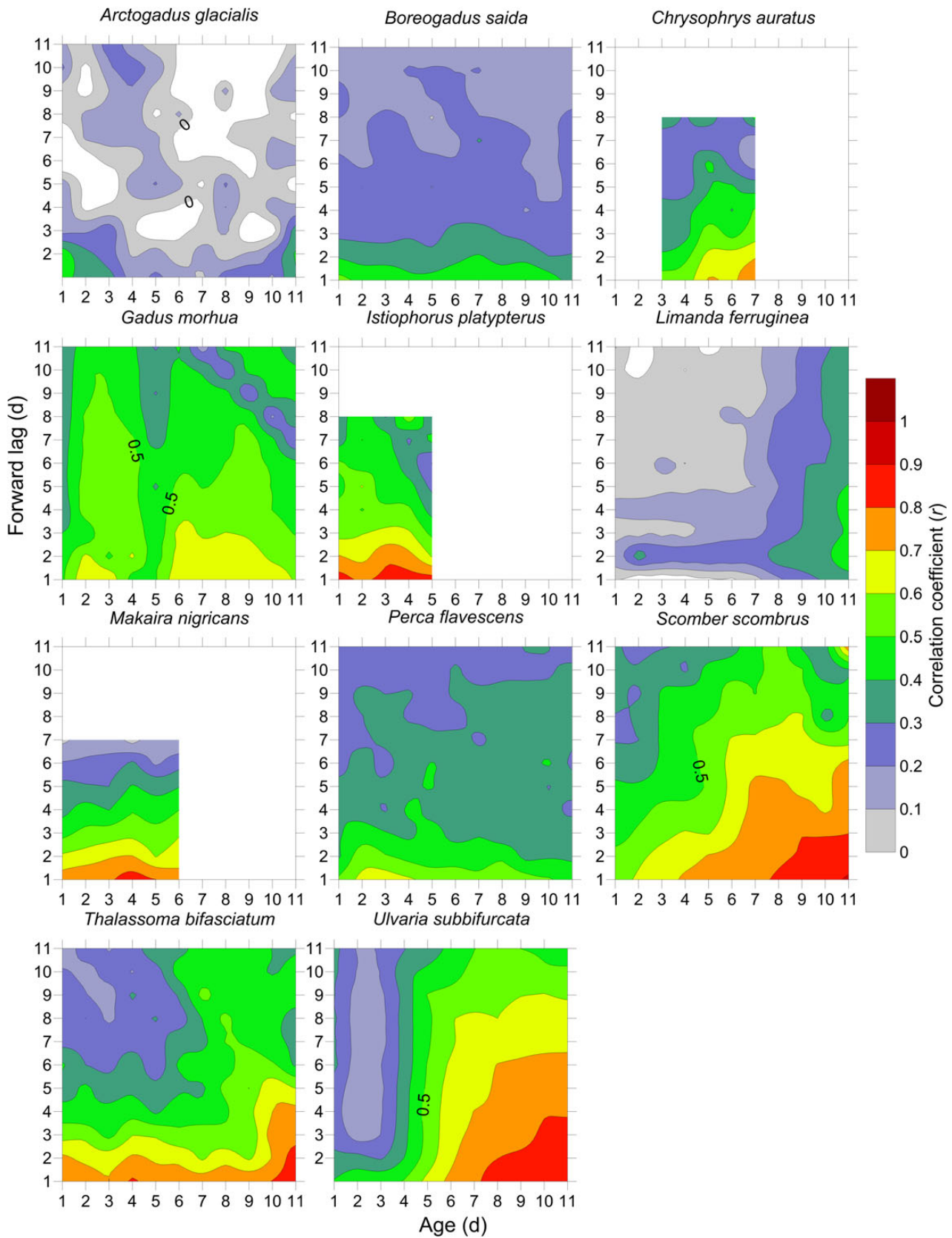
Figure 7. Age-dependent patterns in serial correlation of growth rates (*r*, value represented by the colour scale) of otolith increment widths for 11 taxa. Forward lag is the number of daily increments after a given otolith increment (age). Note that the serial correlations for *U. subbifurcata* include data from studies other than Dower *et al.* (2009).
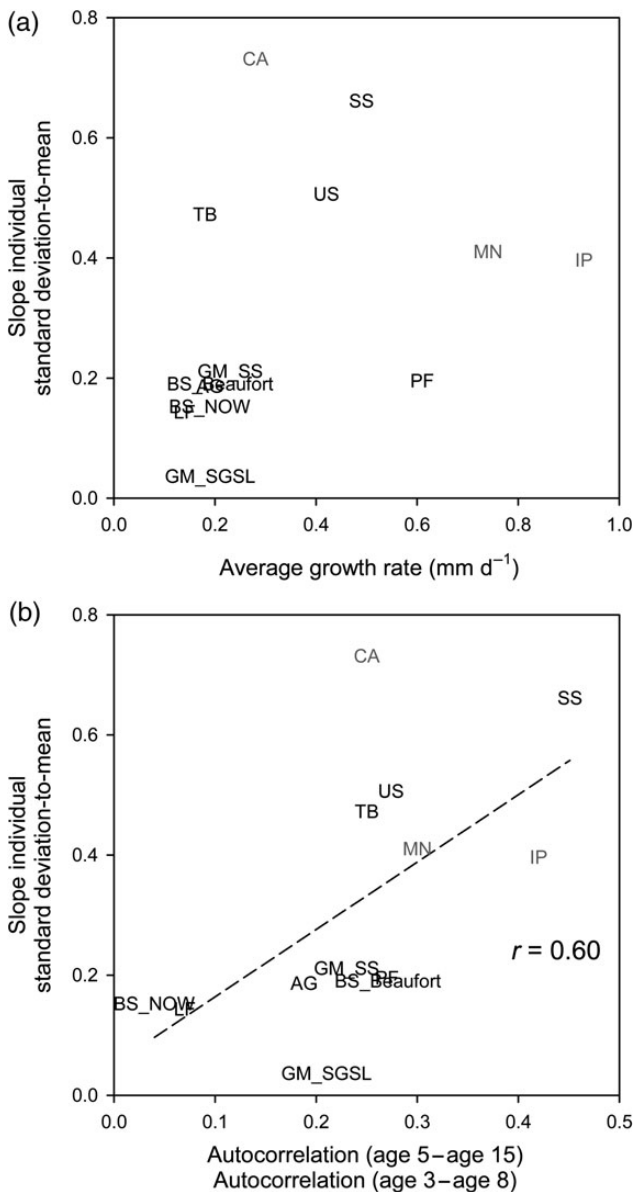
Figure 8. Slope of the standard deviation to mean increment widths estimated based on the first 15 days of life of individual larvae (age $\geq$10 days) in relation to the average growth rate (top panel) and autocorrelation of increments 5 and 15 (bottom panel; black symbols). Note that autocorrelation was calculated between increments 3 and 8 in *C. auratus*, *I. platypterus*, and *M. nigricans* (dark grey symbols) because older larvae were not available in sufficient numbers. See Figure 3 caption for symbol legend.
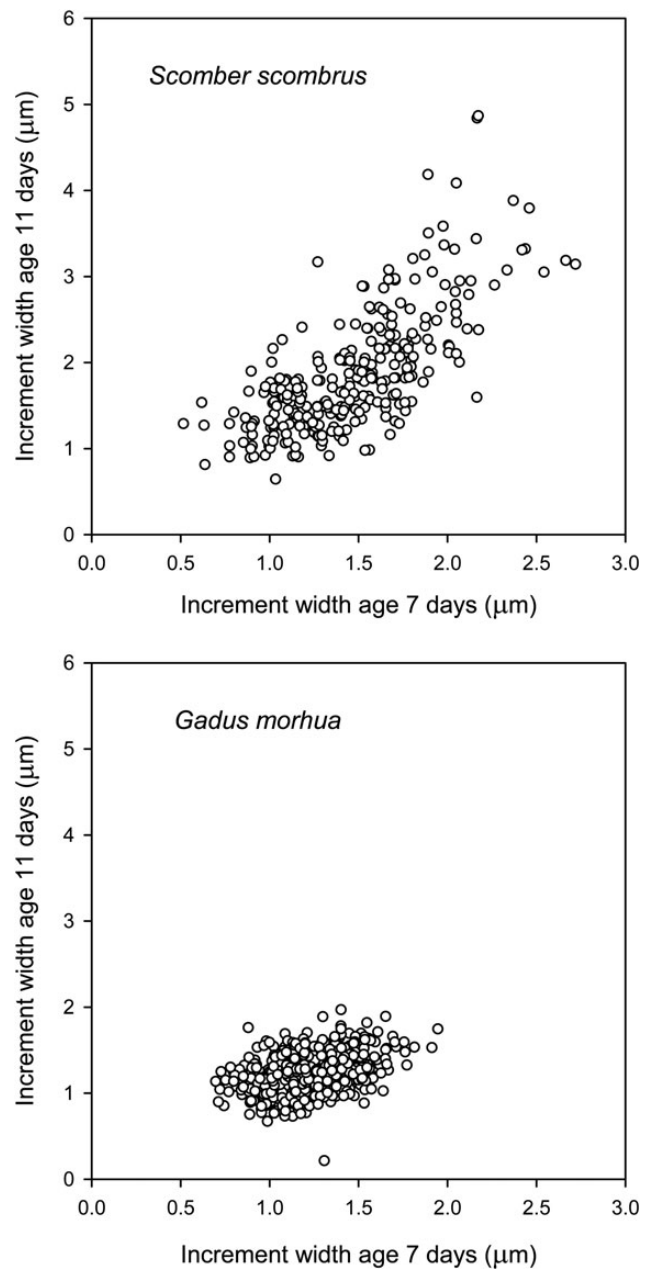

Figure 9. Increment width at age 11 d in relation to increment width at age 7 d of *S. scombrus* (top panel) and *G. morhua* (bottom panel) larvae from the southern Gulf of St Lawrence.

achieving high feeding success and growth from the early larval stage varies widely among taxa. For instance, first-feeding success in scombroid taxa-like sailfish (*I. platypterus*) and Atlantic mackerel (*S. scombrus*) appears a strong determinant of future feeding and growth performance. It has been shown that survival of scombroid fish is often linked to growth performance from the early larval stage, and the onset of cannibalism early in the larval ontogeny is thought to be a mechanism ensuring that fastest-growing individuals can sustain explosive growth rates until metamorphosis, when mortality rates decrease substantially (Peterson and Ausubel, 1984; Tanaka *et al.*, 1996; Kaji *et al.*, 2002).

In contrast, the links between feeding, growth, and serial growth correlation were relatively weak in slow-growing species such as the yellowtail flounder *L. ferruginea* and polar gadids *A. glacialis* and *B. saida*. These slow-growing species are characterized by lower food intake at a given length relative to fast-growing species and appear more resilient to episodes of poor feeding success (and growth) early in life as indicated by relatively weak serial correlation in growth. This observation is consistent with earlier work, particularly on flatfish, where many studies have reported an absence of any relationship between larval growth rate and recruitment (e.g. Bailey, 1994; van der Veer *et al.*, 2000), or even a reverse relationship (Oshima *et al.*, 2010). Flatfish larvae usually need to drift long

distances towards their nursery areas before they can successfully settle on the seabed and transform into juveniles. This ontogenetic feature combined with a juvenile stage characterized by very specific benthic requirements implies that if larval growth rate is too fast, the bulk of individuals may not have time to reach productive nursery grounds before they need to settle (Nielsen *et al.*, 1998; van der Veer *et al.*, 1998; Bailey *et al.*, 2005). For such species, settlement success seems to be a key driver of early survival and fast growth during the pelagic larval stage may not be as important as it is for other species. Similarly, production of Arctic gadoid larvae typically occurs weeks or months before the spring bloom and the bulk of larvae develop within a prey-depleted environment under the ice cover. Bouchard *et al.* (in press) speculated that in these species, a large pre-winter size at the end of the first growth season likely - constitutes a key asset for surviving through the first year of life. Hatching well ahead of the spring bloom, coupled with the ability to cope with low prey availability and slow growth, is considered the main mechanism allowing individuals to reach large pre-winter size. This unique life strategy would explain the relatively weak relationship between gut content and growth as well as the weak level of serial correlation observed in otolith growth during the early larval stage.

Variations in the patterns of serial growth correlation also have implications for the potential differentiation in growth among individuals within a cohort and the potential for growth or size selective processes to influence survival patterns. Increasing serial correlation with age will result in greater differentiation in length-at-age among individuals within a cohort and therefore provide greater variation on which selection can act. The significance of such variations in serial correlation will obviously depend on the scale of the variability relative to the nature of the selective pressure. For example, Takasuka *et al.* (2007) found growth-selective losses in the larvae of Japanese anchovy (*Engraulis japonicus*) subjected to some predators [e.g. round herring (*Etremus teres*) and jack mackerel (*Trachurus japonicus*)] but not others [e.g. amberjack (*Serolia dumerili*) and skipjack tuna (*Katsuwonus pelamis*)]. However, we must be cautious in generalizing, because the impact of any selective process will not only depend on intensity but also on the timing and duration over which it is applied. Our results could imply that because of much reduced differences in the level of variation in size and growth among individuals of Arctic species, their survival might be less affected by selective losses; however, these species have far longer larval durations than warm-temperate or tropical species in which metamorphosis can occur in only a few weeks. Thus, the overall influence of selective processes cannot be inferred without an understanding of the situation facing each species or cohort. Although variations among individuals may be slow to accumulate in cold environments, the level of differentiation among individuals will compound with increasing age. It is unclear whether environmental conditions in Arctic waters are likely to be more variable at the scale of the individual larva than in temperate or tropical ecosystems, or whether the contrast reflects inherent behavioural differences. The ability of each taxon to overcome the effects of environmental variability and/or prey patchiness differs considerably (e.g. *G. morhua*, *L. ferruginea*, and *S. scombrus* from the southern Gulf of St Lawrence) and understanding how these differences occur may be critical in contrasting the differential vulnerability to fluctuations in prey availability across taxa.

Despite our goal of assessing patterns in the feeding-growth relationship across systems and taxa, the small number of datasets that we were able to gather and limited replication did not allow an in-depth analysis of broad-scale patterns to the extent that we had hoped to achieve. The number of observations was insufficient to assess trends across systems without the risk of covariance with among-system variability in fish taxa. Future tests of the taxonomic trends observed in this study will thus require additional sampling effort (e.g. upwelling ecosystems, clupeids).

Evidence of the existence for a "critical period" during the larval stage of fish

Our results revealed that fast-growing species were generally characterized by a strong relationship between feeding success and growth, in addition to high serial correlations in otolith growth. For these species, larvae achieving high feeding success and growth at a given time were characterized by high probabilities of maintaining fast growth throughout larval life. In contrast, larvae characterized by low feeding success and growth at a given time were generally constrained to poor feeding and slow growth, implying a greater likelihood of reduced survival rates. Such negative feedback loops are also observed in slower-growing species, but were much weaker, suggesting that the spatio-temporal match with peak prey availability may not be as crucial to survival as in fast-growing species. Quantifying these characteristics can yield precious information on the nature of the mechanisms driving early survival and recruitment in fish. Recruitment theories that have been inspired by Hjort's (1914) "critical period", such as the "match–mismatch" (Cushing, 1990) or the "growth–predation" (Anderson, 1988) hypotheses do not discriminate among taxa by considering their early life biology and ecology. Our results suggest that while the existence of a "critical period" early in life likely occurs in fast-growing species, the potential for recruitment regulation through larval trophodynamics appears lower in slow-growing species. The relative importance of a match between larvae and their preferred prey would thus be a function of larval growth of a given species, with species characterized by slow growth and a protracted larval stage primarily being regulated by the abiotic environment (e.g. drift, overwintering conditions). Such variation in the presence of a critical period might explain in part the equivocal outcomes of many studies published through the 20th century that have tested predictions of theories on the link between productivity and recruitment and the absence of a strong direct link between food abundance *per se* and survival (Houde, 2008).

Serial correlation of otolith growth as a tool to assess the potential for a critical period during the early larval stage

Our quest for datasets comprising both feeding success and otolith growth trajectories in the same individual fish larvae revealed a limited number of past studies that have analysed these vital rates in the same individuals. This may be because a majority of scientists have paid more attention to the influence of vital rates on population dynamics at the cohort level, compared with the individual level. While published coupled feeding-growth data remain scarce, otolith growth datasets are numerous as otoliths have been used for the past 30 years as the main tool for ageing fish larvae and estimating their growth history. Given the linear relationship obtained between the level of autocorrelation in otolith growth and the correlation between age-dependent scores of feeding and growth, the strength of serial correlation in otolith growth could yield valuable information on early life history traits, even in the absence of data on feeding success. The assessment of otolith growth autocorrelation could thus constitute a promising avenue

for determining the relative potential for a "critical period" during the early larval stage across populations and species.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Acknowledgements

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