



Food for Thought

Death from near and far: alternate perspectives on size-dependent mortality in larval fish

Pierre Pepin*

Fisheries and Oceans Canada, 80 White Hills Road, PO Box 5667, St. John's, NL, Canada A1C 5X1

*Corresponding author: tel: +1 709 772 2081; e-mail: pierre.pepin@dfo-mpo.gc.ca

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This essay contrasts the inferences about the patterns of size-dependent mortality in larval fish based on the traditional catch-curve approach with that achieved through the vertical life table method in an application to data from coastal Newfoundland. Although both approaches reveal that the average mortality rates decline with increasing body size, the rate of decline estimated using the vertical life table approach is much less pronounced than estimated from the catch-curve method. More important, however, is that on a case-by-case assessment the vertical life table reveals that mortality increases with increasing body size in 70% of the cases and declines in the remainder. Instances with greater rates of loss in larger individuals are consistent with larvae becoming more susceptible to the dominant planktivore in the study region. The contrasting results indicate that the patterns of change in mortality rates need to be measured over relatively short-time and/or length intervals. Such inferences have important implications for the development of studies dealing with larval fish dynamics. To be effective and applicable, comparative analyses that aim to develop macroscopic principles for the early life stages of fish must take the local food web structure into consideration to gain appropriate understanding of the trophic interactions that most strongly affect losses from larval fish populations.

Keywords: ecosystem structure, larval fish, mortality, predation, prey–predator interactions, size dependent, trophodynamics.

Introduction

Hjort (1914) was the first to propose that losses during the early life history of fishes were likely to be key determinants of patterns of entry into the fishery. Although considerable emphasis has been directed toward the critical period concept, whereby fluctuations in feeding conditions play a critical role in determining survival, Hjort stated that “all conditions which in any way affect the fish from the egg to the time when they are caught” may be at the origin of fluctuations in the renewal of fish stocks. The importance of factors that affect both growth and mortality was highlighted in sensitivity analyses which demonstrated that subtle variations of the same magnitude in either vital rate would be sufficient to result in substantial variations in survivorship and thereby recruitment (Houde, 1987; Beyer, 1989).

When contrasted with the extent of research into growth rates of larval fish, far less effort has been directed toward investigating the causes of variations in mortality rates (Govoni, 2005; Houde, 2008). There is clear evidence that temperature affects development

rates within and among species (Pauly and Pullin, 1988; Geffen *et al.*, 2006). The study of growth can be performed on individuals or by contrasting survivorship relative to birth date distributions, whereas mortality rates have to be estimated at the population or subpopulation (local) level. Estimating mortality rates requires accurate measurements of abundance and has greater statistical uncertainty than growth rates. Understanding the causes of variations in mortality has been difficult. Tracking transport of larvae out of a study area is demanding (Pepin *et al.*, 1995; Mountain *et al.*, 2008), and the rapid digestion of larval fish in the guts of predators has made the assessment of the impact of predation difficult to quantify accurately (Hunter and Kimbrell, 1980; Hallfredsson *et al.*, 2007; Hunter *et al.*, 2012).

Peterson and Wroblewski (1984) provided an ecological foundation detailing how mortality rates should change during larval development based on regularities in the size-dependent distribution of biomass in marine ecosystems, under the assumption that losses were attributable primarily to predation. The prediction

that mortality should decline with increasing body size has proven consistent with syntheses of larval fish vital rates (Houde, 1989; Pepin, 1991). For mortality to decline consistently with increasing body size, foodweb structure from plankton to upper trophic levels must be stable across all ecosystem types, and the effects of changes in production or fluctuations in abundance of a species or group, such as could result from overexploitation, are compensated for by changes in others. Of particular importance for fish eggs and larvae, variations in the abundance and diversity of meso- and macrozooplankton (e.g. predatory copepods, euphausiids, and cnidarians) (e.g. Brodeur *et al.*, 2002), forage fish (e.g. anchovies, sardines, capelin, and herring) (e.g. Pedersen *et al.*, 2009), and small scombroids (e.g. mackerel and tunas) (e.g. Takasuka *et al.*, 2007) should determine sequential changes in predation pressure from spawning to metamorphosis. Vulnerability of early life history stages to predators peaks when prey is $\sim 10\%$ of the predator's body length and declines on either side of this ratio (Bailey and Houde, 1989; Paradis *et al.*, 1996). Therefore, non-uniformity in biomass from small to large planktivores, as a result from low macrozooplankton abundance or elevated densities of forage fish (or *vice versa*), could cause departures from a trend of constantly declining mortality rates with increasing body size. Foodweb structure and state then become important elements to consider in evaluating how mortality rates should vary through development.

Reviews by Houde (1989) and Pepin (1991) confirming size-dependent patterns of loss were based on studies in which mortality rates were estimated from the slope of the abundance-at-length relationship (catch-curve) and the midpoint of the length intervals over which the estimates were derived. The underlying assumption is that length is a good proxy for age because length-at-age relationships are often close to linear (e.g. Pepin *et al.*, 2015). The general concept of declining mortality with increasing development has been demonstrated among life stages (e.g. Houde, 1997). However, I previously raised concerns that estimates of mortality rates from length-based catch-curves could be biased as a result of changes in the range of lengths used to derive the estimates (Pepin, 1993). The catch-curve model that assumes that the mortality rate is constant for the length interval over which the estimate is derived is in itself inconsistent with the concept that mortality rates decline with increasing length, and the syntheses which provide evidence to demonstrate it. In this essay, I contrast patterns of size-dependence that emerge from estimates of larval fish mortality rates derived from catch-curves (Houde, 2002) relative to those obtained using a ratio estimator (Aksnes and Ohman, 1996) based on the analysis of several datasets from coastal Newfoundland, Canada. My aim is to get researchers who deal with the drivers that affect early life stages to place greater consideration on parsing this phase of the life cycle into a sequence of stages that better match to the time scales and processes relevant to the organisms under study.

Models and data

Catch-curves (CC) are based on the change in abundance of larval fish in relation to age, with the latter often being derived from length-at-age relationships. A log-linear regression equation serves as the basis for the estimated mortality rate based on length frequency distributions (Z_{CC})

$$\ln N_t = \ln N_0 - Z_{CC}t = \ln N_0 - Z_{CC}f(L), \quad (1)$$

where the abundance $N_t = qC_t$ depends on the sample catch of larvae (C_t) with catchability q , and time t is estimated from an age

(in d) length (L) relationship ($f(L)$), such as can be derived from analysis of otolith microstructure (Houde, 2002), with abundance at hatch (N_0) representing the smallest age class sampled. In many instances, length is simply treated as equivalent to age and therefore “time” (Pepin 1991, 1993).

The ratio (R) method is often referred to as a “vertical life table” approach and has been commonly applied to the study of copepods (Aksnes and Ohman, 1996; Aksnes *et al.*, 1997). It is based on estimates of abundance of two adjacent life stages (N_i and N_{i+1} —in the case of larval fish I considered the stages as adjacent 1 mm length intervals) and the time (D —duration) required for individuals to move from one stage (length class) to the next. The approach assumes that the mortality rate of the two stages is identical (i.e. $Z_{R,i} = Z_{R,i+1} = Z_R$), which leads to the formula

$$\frac{N_i}{N_{i+1}} = \frac{e^{Z_R D_i} - 1}{1 - e^{-Z_R D_{i+1}}}. \quad (2)$$

An estimate for Z_R is derived using an iterative solver for equation (2). For the purpose of the analyses presented below, I considered stage duration to be equal for all circumstances and set the value of D to 1 because growth rates were not available for most species included in the analyses. This resulted in estimates per unit (mm) length interval, which made the units comparable with those of Z_{CC} .

The two estimation methods provide very different perspectives on the patterns of change in larval fish mortality rates and size-dependence. In the case of the catch-curve method, estimates of Z_{CC} derived from several studies and species are evaluated in relation to the midpoint of the length range over which mortality rates were estimated. Comparison of mortality rates from the catch-curve approach contrasts how average rates of loss change in relation to length but as stated previously each estimate assumes a constant mortality rate for each species and study. In the case of Z_R , there are two perspectives to assessing size-dependence. First, the general trend across all species and studies can serve to evaluate the overall pattern of variation. Second, the trend of Z_R in relation to length for all pairs of 1 mm length intervals is evaluated for each study and survey and species to assess case-specific variations in mortality rates. In contrast to the catch-curve, the vertical life table estimator allows a more thorough comparison of mortality rates among studies and species.

Measurement error, in terms of both sampling variability (Cyr *et al.*, 1992; Pepin and Shears, 1997) and handling and preservation effects on the measurement of individual (Hjorleifsson and Klein-MacPhee, 1992; Pepin *et al.*, 1998), will have significant effects on the accuracy and precision of each approach. Sampling variability, caused by changing patchiness during development (Hewitt, 1981; Matsuura and Hewitt, 1995) and avoidance, will result in increasing uncertainty in estimates of abundance with increasing larval length. Preservation and handling will have a greater relative effect on smaller length classes because the differential bias of relative changes of individual measurements are more likely to affect the “time” interval represented by adjacent length classes, and therefore the estimated mortality rates. Consequently, estimates of Z_{CC} are likely to be lower and less variable than estimates of Z_R because the former approach represents an average over several size (age) classes relative to the latter but it may be difficult to identify changes in patterns of loss over longer length intervals because of reduction in the signal-to-noise ratio for larger length classes.

Data used to contrast the outcome from the two approaches were derived from 18 different studies conducted in coastal areas of Newfoundland, Canada (e.g. Pepin, 1993; Pepin *et al.*, 1995, 2002, 2003). The studies were primarily carried out from June to August but in a few circumstances sampling occurred in April, May, and September. The average surface temperature ranged from 1.7 to 14°C among surveys based on *in situ* measurements. Ichthyoplankton were generally sampled using a 4 m² Tucker trawl with variable mesh size (333, 570, and 1000 µm, representing cross-sectional areas of 5.9, 23.6, and 100% of the mouth) (Pepin and Shears, 1997) during most studies but in five surveys paired 60 cm bongo nets with 333 µm mesh were used to collect larval fish. All larvae from a sample (up to 200 individuals of a species) were identified to the lowest taxonomic level possible and measured to the nearest millimetre. The analyses were restricted to larvae from 3 to 20 mm standard length. Survey designs differed among studies but for each I was able to derive an estimate of average abundance (m⁻²) for 1 mm length intervals of larval fish from 4 to 17 species, depending on the location and time of year. The survey grids were sampled from 1 to 3 times during the course of a study, and each sampling period was treated independently to derive mortality estimates in the same manner as large-scale population surveys that are commonly used in process studies.

Catchability is an unknown that is often assumed to be constant in most studies in which mortality rates are estimated. Changes in catchability with body size will affect mortality estimates. Extrusion of small larvae through the mesh will cause a reduction in estimated mortality rates as a result of lower estimates of abundance near the origin. Increasing avoidance ability as larvae grow will cause increased size-dependence with increasing length because of lower estimates of abundance at the distal end of the catch-curve. These two patterns of change in catchability are contrary to the general patterns of change in mortality rates reported in the following section. Furthermore, an extensive comparative study of the fishing capacity of the bongo and Tucker trawls revealed that the relative catchability of the two gear types for larvae from 4 to 20 mm was not significantly different from 1 (Pepin and Shears, 1997). Consequently, catchability should not affect the robustness of the inferences discussed below.

Pareto models (Lo, 1986; Butler, 1991) could have provided a metric of the rate of decline in mortality with increasing length (development). However, I chose not to apply this method for several reasons. First, the model inherently assumes that mortality rates decline during development and therefore does not allow an objective assessment of the patterns of change in mortality that may violate this assumption. Second, the model's parameters are not intuitively obvious to many, unless one integrates survival rates over the entire larval stage, and differ substantially from previous syntheses of early life stage mortality patterns (Houde, 1989; Pepin, 1991). Finally, the Pareto model has flaws similar to the catch-curve method in that it provides a single estimate of the pattern of loss over the entire length range considered in the analysis. This limits our ability to investigate changes in the patterns of loss at the developmental resolution necessary to infer what processes and predators are affecting larval fish as will be demonstrated below.

Observations

Mortality estimates derived using the catch-curve approach (Z_{CC}) rely on cases in which there is a steady decline in the abundance of successive length classes; there were 299 cases in which data from at least three length classes were available and which resulted in

estimates of "loss" from the species sampled. I did not assess the statistical significance of each regression, only whether the slopes indicated a reduction in the number of larvae across length classes. In another 135 cases, application of the catch-curve approach yielded estimated increases in abundance of larvae. Such a situation is generally considered to be in violation of the method's assumption that egg production is at a steady rate or that spawning has been completed. These were discarded from the analyses. Removal of these observations is not ideal but it allows an assessment of size-dependence that is consistent with syntheses by Houde (1989) and Pepin (1991): results that yield mortality estimates that do not represent losses are generally not reported in the literature.

Estimates of Z_{CC} decline as the midpoint of the length interval of estimation increases (Figure 1). There is greater variance in smaller larvae than in larger ones. Regression of the log-transformed data, which serves to provide a basis for comparison with Houde (1989) and Pepin (1991), demonstrates that the effect of length on mortality rates is highly significant ($\ln(Z_{CC}) = 0.163 - 1.49 \cdot \ln(L)$, $r^2 = 0.30$, $p < 0.001$). This translates into an ~96% decline in the average mortality rate from 3 to 20 mm. Addition of a temperature term to the regression did not have a statistically significant effect on mortality estimates ($p > 0.5$), in marked contrast with the findings of Houde (1989) and Pepin (1991).

The vertical life table estimator yielded 1233 mortality estimates in which a loss was recorded from one length class to the next (Figure 2). As in the case of the catch-curve approach, there is greater variability in smaller size classes than larger ones. Regression of the log-transformed data from all species and surveys reveals that the average mortality rate decreases significantly with increasing body length ($\ln(Z_R) = -0.269 - 0.391 \cdot \ln(L)$, $r^2 = 0.026$, $p < 0.001$), which results in an ~52% decrease in average mortality rates from 3 to 20 mm length. Temperature did not significantly affect mortality rates ($p > 0.5$).

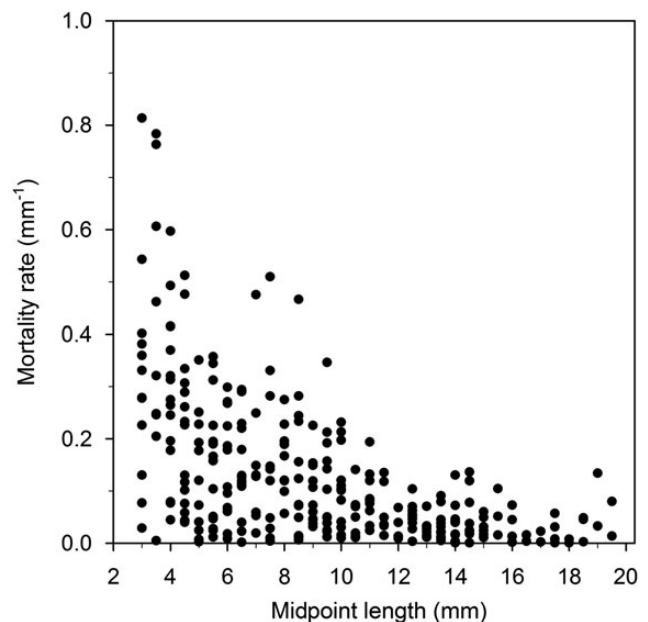


Figure 1. Larval fish mortality rate estimates in relation to the midpoint of the length range over which the catch-curve approach was applied.

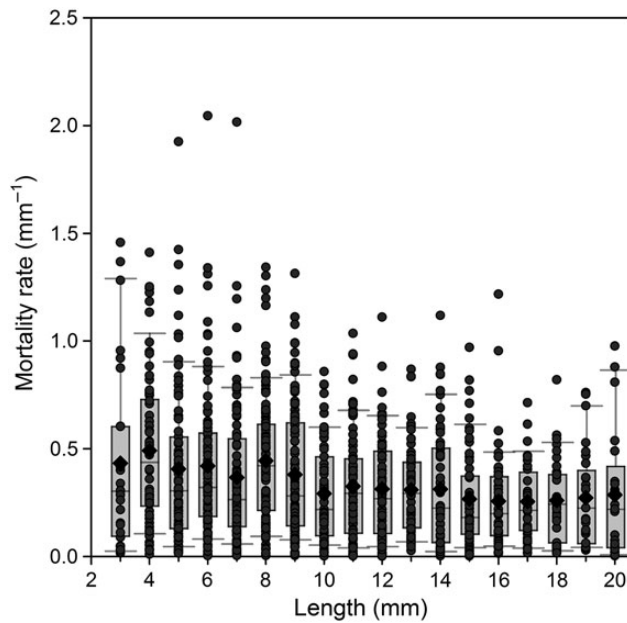


Figure 2. Larval fish mortality rate estimates based on the vertical life table estimator in relation to length for each 1 mm interval. Dark grey symbols represent individual estimates. Box whisker plot showing the distribution of estimated mortality rates are shown in the background. Thin box lines represent the 25th, 50th, and 75th percentiles of the observations; error bars represent the 5th and 95th percentiles; black diamonds represent the mean.

In contrast to the catch-curve approach, vertical life table estimator (Z_R) provided mortality estimates for all pairs of adjacent length classes that allows an assessment of the patterns length-dependence of mortality rates on a case-by-case basis (i.e. the slope of $\ln(Z_R)$ vs. Length for each survey and species combination) (Figure 3). This proved highly revealing because in 69 cases mortality rates increase with increasing length ($n = 36$, $p > 0.1$; $n = 6$, $0.1 > p > 0.05$; $n = 27$, $p < 0.05$), whereas a decline in mortality rates was apparent in only 29 cases ($n = 19$, $p > 0.1$; $n = 1$, $0.1 > p > 0.05$; $n = 8$, $p < 0.05$). The general features of these results are not affected if the analyses are restricted to data for larval lengths ≤ 15 mm (59 positive; 28 negative) or ≤ 11 mm (52 positive; 19 negative). This demonstrates that removal of length classes which could be affected by increased avoidance (and hence reduced catchability) does not alter the findings. Fewer cases were available for this analysis than in the application of the catch-curve approach because the vertical life table estimator required a greater number of length categories than the former to identify trends in size-dependence. The increase in mortality rate with increasing length is steepest in smaller larvae than in larger ones in cases where the slope of the regression is positive, whereas there is no apparent length-dependence among the cases in which mortality declines with increasing length. Modelling the slope in relation to length and temperature reveals highly significant declines in the slope with increasing length and temperature (Slope $_{Z_R-\text{length}} = 0.82 - (0.041 \times L) - (0.030 \times \text{temperature})$, $r^2 = 0.22$, $p < 0.001$, $\text{s.e.}_L = 0.0082$, $\text{s.e.}_{\text{temperature}} = 0.011$). The effect of declining slope with increasing body length is obvious but the decline with increasing temperature implies that there is less difference in mortality rates of adjacent length classes as temperature increases.

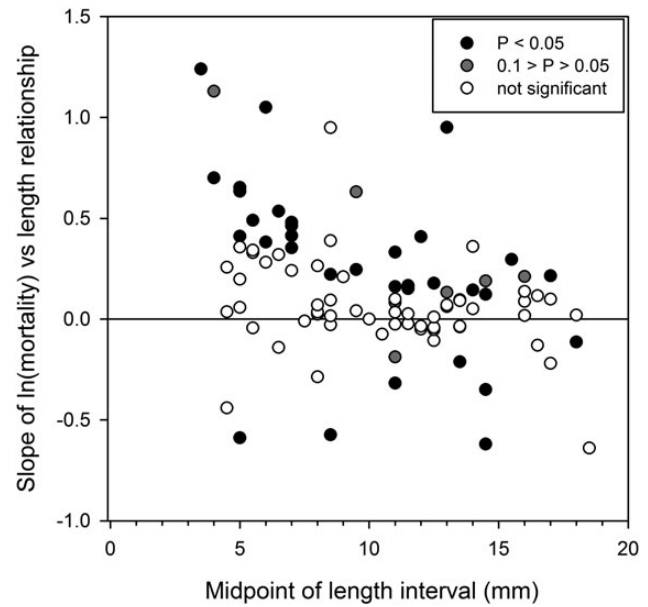


Figure 3. Slope of $\ln(\text{mortality})$ – length relationship in relation to the midpoint of the length range for case-specific instances in which there were three or more observations of mortality rates across a range of length categories. A positive slope indicates that mortality rates are increasing with increasing body length while a negative slope indicates that mortality rates are declining as length increases. Open symbols represent slopes that were not statistically significant, grey symbols represent marginally significant slopes, and black symbols represent statistically significant slopes.

Discussion

Differences in the patterns of size-dependency in larval fish mortality rates derived from the two approaches have important implications for the interpretation of ecological processes that affect the dynamics of larval fish. Although both approaches indicate a decline in average mortality rates with increasing body length, differences in the strength (30% (Z_{CC}) vs. 2.6% (Z_R) of explained variance) and magnitude (96% (Z_{CC}) vs. 52% (Z_R) decline from 3 to 20 mm) of the relationships were substantial. Part of the contrast between methods is likely a reflection that catch-curves provide averages over the length interval considered, whereas the vertical life table estimator gives a perspective for each pair of length interval, and is therefore more likely to be subjected to the effects of sampling variability (Gentleman *et al.*, 2012). However, the contrast likely also reflects the ability of the vertical life table approach to detect changes in the processes that are affecting larval fish through development that is not possible when a single estimate of the rate of loss is derived for the entire population, as in the catch-curve approach. This becomes evident in the case-by-case investigations using the vertical life table approach which demonstrated an increase in mortality with increasing body length in 70% of cases, while the remaining 30% revealed declining loss rates in larger larvae. If predation is the principal cause of mortality in marine ecosystems, then differences in size-dependent relationships should reflect differences in the principal predators affecting each species or cohort of larval fish.

Bailey and Houde (1989) and Paradis *et al.* (1996) concluded that vulnerability to predation followed a general domed-shaped relationship that peaked when prey were $\sim 10\%$ of the predator's body length, and that planktivorous fish had a greater likelihood

of capturing larvae than did carnivorous zooplankton. For cases in which mortality appears to increase with body length, there was a significant deceleration in the size-dependency as larvae approach 15–20 mm suggesting that the key predator in those instances should be of the order of 150–200 mm in length but smaller predators may also have contributed to losses. The high occurrence of increasing mortality with larger body size is consistent with the foodweb structure of the study region. The Newfoundland ecosystem consists of a wasp-waist foodweb in which capelin (*Mallotus villosus*) represents a keystone species in the transfer of energy from lower trophic levels to demersal fish, birds, and marine mammals (Carscadden *et al.*, 2002; Lilly *et al.*, 2013; Buren *et al.*, 2014). Although carnivorous zooplankton are widespread in the region (Pepin *et al.*, 2011), their potential impact on the survival of larval fish in coastal areas appears limited relative to that of capelin (Paradis and Pepin, 2001). Whether the patterns identified in this study region hold in warmer ecosystems, where invertebrate carnivores are more diverse and abundant (Rombouts *et al.*, 2009; Korhonen *et al.*, 2010; Yasuhara *et al.*, 2012), will require further investigation to assess whether there is a latitudinal cline in size-dependent mortality relationships.

Foodweb structure represents an important element in the assessment of patterns of mortality in marine ecosystems but details of potential trophic interactions are seldom considered in evaluating patterns in size- or stage-specific loss in larval fish. Pope *et al.* (1994) highlighted the significance of discontinuities in the biomass spectrum on determining the life history strategies adopted by species reproducing in ecosystems with strongly seasonal production cycles that result in a wave of energy passing through a succession of trophic levels. Although when averaged over extended periods, the size-spectrum may be approximated by the distribution of equal biomass per logarithmic interval of body size, the circumstances specific to the conditions encountered by cohorts of larval fish and the resulting pattern in mortality rates may not follow the simplified concepts that serve as the basis of the theory developed by Peterson and Wroblewski (1984). It is essential to disaggregate information on body size and trophic interactions to accurately predict changes in mortality rates across trophic levels in marine ecosystems relationships (Blanchard *et al.*, 2009). Although information disaggregation is not possible using the traditional catch-curve method commonly applied to larval fish, one has to question why previous reviews (Houde, 1989; Pepin, 1991) are consistent with the predictions by Peterson and Wroblewski (1984).

Body size of larval fish is widely considered as representative of development state and age because there is often a linear or near-linear relationship between age and length (Figure 4a) when estimated based on analysis of otolith microstructure. It seems therefore reasonable to assume that age and length can be considered interchangeable, converted from one to another based on a simple functional relationship. This might be suitable in the case where length is derived from age because there is no significant change in the variability (measured as the SD) in length-at-age with increasing age (GLM analysis: $r^2 = 0.44$, $F_{\text{species}} = 7.28$, $p < 0.001$, $F_{\text{age}} = 3.40$, $p > 0.05$ based on Type III sum of squares; Figure 4b). However, the highly significant increase in variability in age-at-length with increasing length (GLM analysis: $r^2 = 0.60$, $F_{\text{species}} = 3.51$, $p < 0.05$, $F_{\text{age}} = 24.9$, $p < 0.001$ based on Type III sum of squares; Figure 4c) results in broadening and flattening of the age distribution with increasing length and implies that length cannot be treated as equivalent to age. This could explain why increasing the

range in length used to estimate mortality leads to a strong decline in values as a result of increasing bias in the correspondence of age with length, as previously suggested (Pepin, 1993). Mortality estimates derived over a short length interval result in a much weaker trend in average size-dependent rates of loss, partly because of the small differences in the variance in age of larvae between adjacent

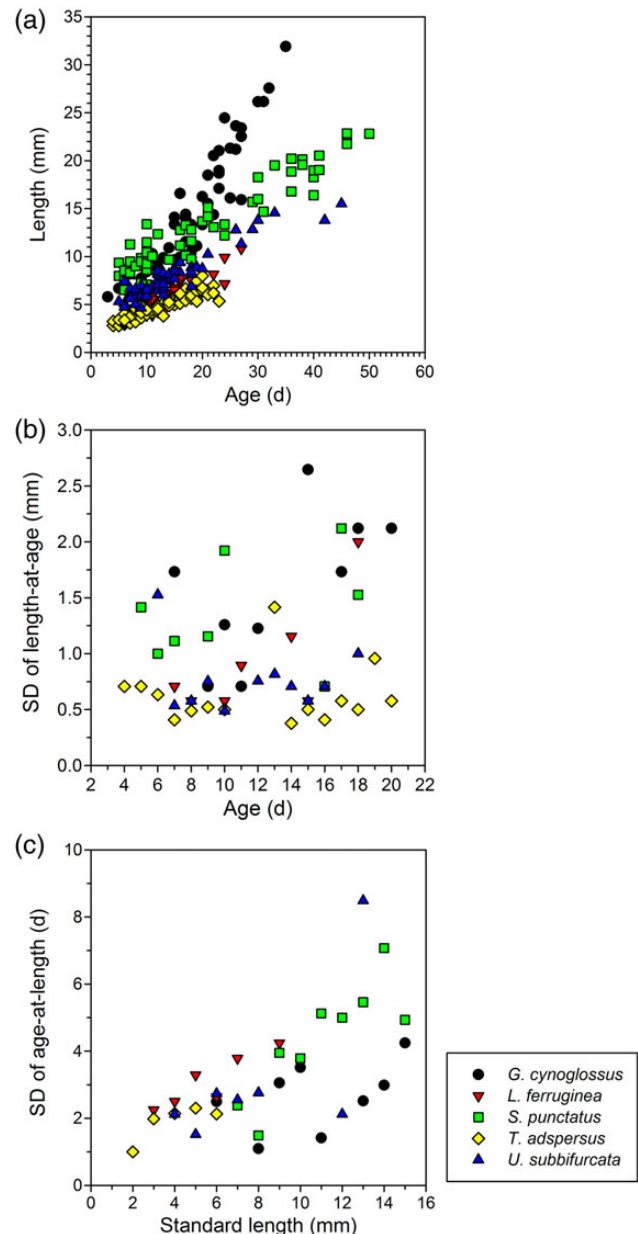


Figure 4. (a) Length-at-age relationship, (b) SD of length-at-age in relation to age, and (c) SD of age-at-length in relation to length (based on 1 mm intervals) for five species of larval fish from Conception Bay, Newfoundland, Canada. Age was determined from the analysis of sagittal otoliths and length measurements obtained using an optical imaging system. Larvae were measured immediately after capture and before preservation. Otoliths were embedded in epoxy resin, ground to near the sagittal plane with a series of graded silicon carbide sanding papers before polishing with alumina powder. The methods applied to otolith analysis were similar to those used by Baumann *et al.* (2003) and Dower *et al.* (2009).

length classes. Regardless, the contrasting patterns of variance in age-at-length and length-at-age indicate that the conversion of one to the other must, at the very least, be based on the proper application of age-length keys (Francis *et al.*, 2005; Kimura and Dorn, 2006) when attempting to estimate mortality rates.

Differences in the influence of variations in growth rates on the two approaches may also contribute to the general lack of temperature-dependency in the general trends in mortality rates using both approaches. In contrast, the negative effect of temperature on case-by-case patterns of size-dependency likely reflects of the direct influence of temperature on development (growth) rates (e.g. Buckley *et al.*, 2004, 2008). Increasing temperature will result in faster development so the time needed to growth between adjacent size classes will decline and result in smaller differences in mortality rates between length classes at higher temperature. The lack of influence of temperature on Z_{CC} mortality rates suggests that the confounding effects of variability in age-at-length overwhelms any potential impact of temperature on physiological processes whereas the absence of an effect on Z_R estimates indicates that the variability in trophic interactions specific to each survey/species are stronger than are the effects variation in temperature among the case studies.

Development of macroscopic principles, based on a combination of theoretical constructs and empirical evidence, provides the foundation of predictive capacity in ecology (Peters, 1983; Gaston and Blackburn, 2000; McGill and Collins, 2003). Often, empirical relationships rely on a comparisons across a broad range of environmental settings (ecosystems) to identify or confirm the effect key predictive variables, or because insufficient observations (or an insufficient range of environmental conditions) are available for any given system or for a taxa to achieve statistical reliability relationship. The application of macroscopic functional relationships derived over a broader range of environmental conditions than we can expect a cohort of larvae to experience may give us the ability predict the subtle level of variability in survivorship necessary to significantly affect recruitment and population dynamics. However, the strength of macro-ecological theories rests on how reliably they can be applied at different scales (e.g. spatial, temporal, and taxonomic) with the level of accuracy required to derive effective predictions of the state of organisms, communities, or ecosystems (Pepin and Miller, 1993; Lawton, 1999).

The regularity in the distribution of biomass in relation to body size has served as a foundational principle in the study of processes that govern the flow of energy among trophic levels as well in assessing the consequences of human activities on the state of communities across a broad range of ecosystems (Heath, 1995; Jennings and Blanchard, 2004; Pope *et al.*, 2006; Andersen *et al.*, 2009; Ho *et al.*, 2013). When we consider the strong dependency of physiological processes (e.g. basal metabolism, respiration) on body size and environmental temperature across a broad range of taxa (Frangoulis *et al.*, 2005; Glazier, 2009), the potential importance of these variables as key macro-ecological drivers on the early life stages of fish is clearly well founded. Although factors affecting growth can be evaluated from the individual to the population level (Buckley *et al.*, 2010), principles governing the patterns of variation in mortality rates have generally required comparison across taxa and ecosystems because there are few instances in which individual vulnerability has been assessed under differing circumstances (e.g. Takasuka *et al.*, 2007). The contrast in the results of this case study with those of earlier syntheses (Houde, 1989; Pepin, 1991) may have important consequences on the feasibility of comparing vital

rates across taxa and environments in the absence of knowledge concerning differences and similarities in ecosystem structure. In many macro-ecological syntheses, temperature often serves to contrast different regions or ecosystems rather than to identify variations in local environmental conditions, although there are exceptions (e.g. Planque and Fredou, 1999). One must question whether patterns identified in empirical syntheses reflect differences in trophic structure and interactions among regions rather than in the underlying temperature-driven turnover rate of each ecosystem.

There is little doubt that temperature has been demonstrated to affect mortality rates of planktonic organisms based on analyses within ecosystems (Hirst *et al.*, 2007; Plourde *et al.*, 2009; Dvoretzky, 2012). However, even within those systems the potential role of temporal shifts in predator abundance or trophic interactions should be considered (e.g. Garrison *et al.*, 2000; Hirst *et al.*, 2007). Comparative ecology relies on metrics that are commonly available across studies, such as body size and temperature, and is therefore often forced to proceed without the basic knowledge of the trophic and community structure of the different environments included in the analysis, essentially assuming a degree of consistency across time and among ecosystems. A potential problem arises when the principles derived from comparative analyses are considered as validated evidence and are applied as inferential tools in the interpretation of unmeasured variables or processes. The repeated extrapolation across studies may lead to retrogression or stagnation within a field of research because the underlying uncertainties are unlikely to be effectively addressed in the design of new initiatives (Hare, 2014; this study). The importance of lengthy observational time-series, coupled with novel approaches to the evaluation of variations in growth and mortality (e.g. Fassler *et al.*, 2011; Payne *et al.*, 2013) cannot be overemphasized if we are to test general ecological principles and advance our understanding of the drivers of recruitment variability and population production potential. To gain an appropriate understanding of the trophic interactions that most strongly affect losses from larval fish populations, analysis of the patterns of mortality rates must be based on observations taken over relatively short time and/or length intervals while taking the local foodweb structure into consideration. Reliance on Peterson and Wroblewski's (1984) size-dependent model and subsequent reviews (McGurk, 1986; Houde, 1989; Pepin, 1991) to infer or interpret selective patterns of loss during prerecruit stages of fish populations may have contributed to the limited progress toward explaining the causes of recruitment variability in the last century (Houde, 2008; Pepin, 2015).

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