Differences between marine and freshwater fish larvae: implications for recruitment

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Differences in the dynamics (growth and mortality) and energetics properties of marine and freshwater fish larvae have important implications for determining the life stages at which year-class size is established. After correcting for temperature effects, marine fish larvae, which typically weigh less at hatch, can be shown to experience higher mortality rates, have higher metabolic requirements, and have longer larval stage durations than do freshwater fish larvae. Growth rates and growth efficiencies are similar for the two categories of larvae. The difference in body size between typically small marine and typically large freshwater fish larvae is an important factor affecting their dynamics and energetics. Predicted mean survivorship to metamorphosis of a cohort of freshwater fish larvae is 5.30%, while that of marine larvae is only 0.12%. The probability of significant density-dependent regulation during the larval stage could be relatively high for marine species, based upon their life-history properties. The probability that episodic mortalities of larvae will have significant impacts on recruitment may be higher for freshwater fish than for marine fish. Starvation mortality is more probable for marine larvae, primarily because of their small body size, associated high metabolic demands, and possibly higher ingestion requirements. Because expected mean survivorship of freshwater larvae is 44 times higher than that of marine larvae, juvenile-stage dynamics will be relatively important in controlling/regulating recruitment levels of freshwater fishes. In contrast, properties of marine species indicate that larval-stage dynamics will have a greater influence on recruitment success.

Key words: larval fish, dynamics, energetics, marine, freshwater, recruitment mechanisms.

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Introduction

Research on fish early life stages has proliferated in recent years, particularly on marine species. The high fecundities of fishes ensure high larval abundances, which are subject to: (1) density-independent controls that are believed to be a primary cause of recruitment variability; and (2) possible density-dependent regulation, which will tend to stabilize recruitment levels (Cushing, 1974a,b; Rothschild, 1986). Growth rates, mortality rates, stage durations, and energetics properties of teleost larvae, when compared across taxa and ecosystems (Houde and Zastrow, in press), have many similarities, but they also show significant differences that have implications for the recruitment process, as well as for development of fishery research and management plans.

Fishes in both marine and freshwater habitats exhibit diverse morphologies and behaviors. This diversity extends to the larval stages in which morphologies and ontogenies vary widely (Balon, 1981). Development during the larval stage may be brief or protracted, resulting in either short- or long-stage durations. Because of the variability in morphologies and body sizes of larvae, as well as stage durations, it is not surprising that many biological properties differ substantially among species (Miller *et al.*, 1988; Pepin, 1991; Pepin and Myers, 1991). The vital rates (mortality rates, growth rates, stage durations) and energetics of larvae are strongly affected by temperature (Houde, 1989a; Morse, 1989). Temperature and body size probably are the main variables affecting egg and larval stage dynamics (Pepin, 1991) and prey consumption rates (Mackenzie *et al.*, 1990). Their effects on larval-stage durations may have had important consequences in the evolution of teleost life-history modes (Houde, 1989a).

There are taxa-specific as well as ecosystem-specific differences in vital rates and energetics properties of fish larvae (Houde and Zastrow, in press) that could affect

recruitment levels, in addition to influencing dynamics and energetics of older life stages. Houde and Zastrow (in press) noted some probable differences in larval-stage properties of marine and freshwater fish larvae in a broader analysis across aquatic ecosystems and taxa. In the present paper, I critically compare averaged properties of larvae from the combined marine ecosystems with properties of larvae from freshwater ecosystems and discuss the potential for regulation and control of recruitment during the larval and juvenile stages in each system.

Methods

Data on larval dynamics (vital rates) and energetics, categorized by ecosystems and by taxonomic groups, were compiled by Houde and Zastrow (1991, in press). Those reports included data on both freshwater and marine teleost larvae, but the analysis and interpretations did not focus on implications for recruitment in freshwater and marine ecosystems. Here, the analysis is extended explicitly to examine and compare the relationships between size at hatching and vital rate parameters in the two categories of larvae. Recruitment levels in each case are predicted for mean values of rates estimated during larval life, and simple simulations are run to demonstrate the extent to which average dynamics in the larval stage must vary to precipitate important changes in recruitment levels.

Most teleost taxa for which published data were available are included in the analysis. Exceptions were a few taxa of principally freshwater fishes with unusually large, precocial (*sensu* Balon, 1981) hatchlings that have either a curtailed or absent larval stage, e.g. Salmonidae, Acipenseridae, Ictaluridae. The variables that were considered are: W_o = dry weight at hatching (μg); W_{met} = dry weight at metamorphosis (μg); G = weight-specific growth coefficient (μg μg^{-1} day^{-1}); Z = instantaneous mortality coefficient (day^{-1}); D = larval-stage duration (day); i.e. days to grow from W_o to W_{met}; QO_2 = weight-specific oxygen uptake (μl O_2 mg^{-1} h^{-1}); I = weight-specific food ingestion (day^{-1}), i.e. fraction of larval body weight consumed daily; and K_1 = gross growth efficiency, defined as G/I.

Temperature-adjusted mean values of each parameter for larvae from five marine ecosystems and freshwater, and from nine broad taxonomic groups, were estimated (Houde and Zastrow, 1991, in press). Adjustments for the substantial temperature effects were accomplished via analysis of covariance. Mean values that are reported here for data from pooled marine ecosystems and from freshwater systems are those compiled by Houde and Zastrow (in press), except for minor differences resulting from a few additions or changes to the earlier data set. These values are referred to as "typical" or "average" for larvae

from marine or freshwater systems, acknowledging that such characterization does not recognize species which are atypical and whose life histories may deviate significantly from the norm. Differences between means were judged to be significant at $\alpha = 0.10$, rather than at 0.05, to increase the power of the tests to detect probable differences in these quite variable data, which often were based upon few observations.

Regression statistics relating G, Z, D, and QO_2 to W_o were calculated to determine if these variables were dependent upon weight at hatching, and if the dependence differed between freshwater and marine larvae. Expected numbers of metamorphosed survivors, at mean values of vital rates and ontogenic attributes, were calculated for fishes from freshwater and marine ecosystems, based upon the relationship:

$$N_{met} = P \times N_o e \left[\frac{-\bar{Z}(\log_e \bar{W}_{met} - \log_e \bar{W}_o)}{\bar{G}} \right], \qquad (1)$$

where N_{met} = number of metamorphosed survivors; N_o = initial number of larvae; and P = probability of surviving "episodic" mortality events.

The ratio of $N_{met\text{-}FW} : N_{met\text{-}MAR}$ for equal N_o was calculated to indicate relative stage-specific survivorship. By varying Z, G, and P in Equation (1), the changes in rates or episodic loss probabilities were calculated that are required to equalize survivorship at metamorphosis in the marine and freshwater ecosystems. Effects of initial egg or larval numbers (i.e. variability in N_o), caused by differences in mean fecundities between marine and freshwater fishes, and the consequences for survivorship at metamorphosis, were considered. Teleost fecundity data compiled by Winemiller and Rose (1992) were used for this purpose.

The potential for density-dependent regulation of larval survival via growth-rate responses to initial larval abundances was compared for marine and freshwater fish larvae by simulating responses of N_{met} in Equation (1) to variability in $\bar{G}$ and N_o. In an example, $\bar{G}$ was reduced by 10, 25, or 50% per five-fold increase in N_o. Then, the expected survivorships were compared for marine and freshwater larvae to determine their sensitivities to density-dependent growth.

Results

Marine fish larvae, on average, are smaller at hatch, suffer higher mortality rates, have higher weight-specific respiration rates, and have longer stage durations than do freshwater larvae (Table 1). The 10-fold difference in mean weight at hatching potentially has important consequences for larval-stage dynamics and recruitment. Weight-specific growth rates do not differ significantly, nor do gross growth efficiencies, although the database for the latter is small. The calculated mean,

Table 1. Temperature-adjusted (by analysis of covariance) means of dynamic and energetics properties of marine and freshwater fish larvae. Symbols for variables are defined in text (see Methods). Significance indicates $p \leqslant 0.10$, n = number of taxa, S.E. = standard error of the mean.

Variable	Marine			Freshwater			Significance
	$\bar{X}$	S.E.	n	$\bar{X}$	S.E.	n	
W_o	37.6	6.4	77	359.7	72.8	20	sig.
W_{met}	10 845.6	953.0	77	9276.9	1604.3	16	n.s.
G	0.200	0.011	80	0.177	0.019	26	n.s.
Z	0.239	0.021	26	0.160	0.040	7	sig.
D	36.1	1.1	79	20.7	1.1	15	sig.
QO_2	5.90	0.38	15	2.79	0.38	15	sig.
K_1	0.29	0.03	14	0.32	0.03	8	n.s.
I	0.57	0.07	14	0.46	0.09	8	n.s.

Table 2. Expected energy budgets (cal mg^{-1} day^{-1}) of marine and freshwater fish larvae. (a) Temperature-adjusted mean energy budgets (from Houde and Zastrow, in press). (b) Temperature-adjusted energy budgets, standardized to one unit of growth. (Note that no standardization was required for marine larvae whose mean budget by coincidence was 1.0 for the growth component.) (c) Temperature-adjusted energy budgets, standardized to one unit of ingestion.

Category	Ingestion	=	growth	+	metabolism	+	urine	+	feces
(a) Marine	3.44	=	1.00	+	0.98	+	0.24	+	1.21
Freshwater	2.78	=	0.89	+	0.47	+	0.19	+	1.23
(b) Marine	3.44	=	1.00	+	0.98	+	0.24	+	1.21
Freshwater	3.13	=	1.00	+	0.53	+	0.22	+	1.39
(c) Marine	1.00	=	0.29	+	0.29	+	0.07	+	0.35
Freshwater	1.00	=	0.32	+	0.17	+	0.07	+	0.44

weight-specific ingestion rates, which were derived from the growth rate and growth efficiency data, are 0.57 for marine larvae and 0.46 for freshwater larvae. These values were not found to differ significantly at the $\alpha = 0.10$ level.

Weight-specific growth rates (G) for the pooled data of marine and freshwater larvae, and of the freshwater larvae alone, are significantly correlated with W_o (Fig. 1a), but no relationship between G and W_o is apparent for the marine larvae over the relatively small range of W_o that is represented. No significant relationship between instantaneous mortality rate (Z) and W_o was demonstrated (Fig. 1b), although the highest rates are reported for some of the smallest marine larvae. There is also no significant correlation between larval-stage duration (D) and W_o (Fig. 1c), but the longest-stage durations were estimated for some of the smallest marine larvae. The quite strong relationship between weight-specific oxygen uptake (QO_2) and W_o, which was reported previously for combined marine and freshwater larvae by Houde and Zastrow (in press) is illustrated (Fig. 1d). In the present analysis, the QO_2 vs. W_o relationship was significant for the freshwater larvae, but not for the marine larvae.

Applying mean values (Table 1) in Equation (1) indicates that relative survivorship at metamorphosis of a "typical" cohort of freshwater fish is expected to be 44 times higher than that of a "typical" cohort of marine fish. At metamorphosis, 5.30% of an initial freshwater cohort is expected to be alive compared to only 0.12% of a marine cohort. Thus, a much larger fraction of a typical freshwater, larval cohort will survive to enter the juvenile stage.

Quite large changes in either Z or G are necessary to equalize expected survivorships at metamorphosis of marine and freshwater fish larvae. A 2.3-fold increase in $\dot{Z}$ or decrease in $\bar{G}$ by a typical cohort of freshwater larvae is necessary to reduce its survival at metamorphosis to 0.12%, the estimated survivorship of a typical cohort of marine larvae. Exactly the opposite applies to marine larvae; a typical cohort of marine larvae would need to experience 2.3-fold lower $\dot{Z}$ or higher $\bar{G}$ to support survivorship of 5.30% at metamorphosis, the expected level for a typical freshwater cohort.

If episodic mortalities of larvae i.e. weather-related events, are more prevalent in freshwater than in marine environments, such losses would tend to equalize
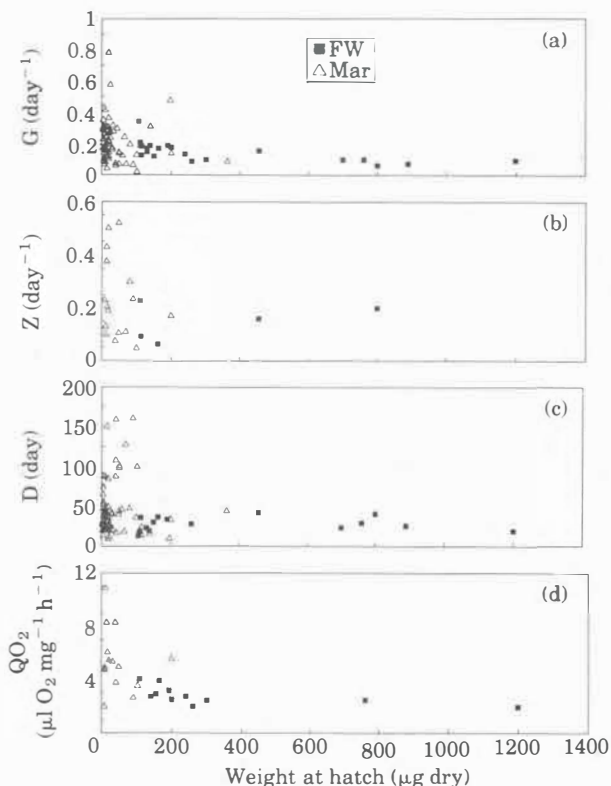
Figure 1. The relationships between dry weight at hatching and (a) weight-specific growth rate, (b) instantaneous mortality rate, (c) larval stage duration, and (d) weight-specific oxygen uptake for marine and freshwater fish larvae.

expected survivorships at metamorphosis in the two systems. But, at the mean Z and G levels of freshwater fish larvae (Table 1), additional episodic losses [P in Equation (1)] would have to reduce initial cohort abundance by 97.8% to match the expected survivorship of a typical cohort of marine larvae. If episodic mortalities, e.g. caused by aberrant transport or storm events, are an important element contributing to mortality of marine fish larvae, any such losses would tend to reduce further their expected survivorship at metamorphosis, and thus widen the gap even more between expected survivorships of freshwater and marine larval cohorts.

Decreases in growth rate, if density-dependent, potentially could have relatively strong effects of survivorship at metamorphosis of marine fish larvae compared to freshwater larvae (Fig. 2). The potential for regulation of abundance of marine larvae via density-dependent growth is relatively high because their stage durations are long, their ratio of G:Z is low, and their ratio of $W_{met}:W_o$ is high. Reductions in weight-specific growth rate of <25% per five-fold increase in initial larval abundance will induce a strong density-dependent response in relative survival of marine larvae. But, considerably greater

reductions in G are required to generate a similar response in freshwater larvae. The result indicates that survival of marine fish at metamorphosis not only is relatively more sensitive to external controlling factors that affect mortality rates and stage durations, but that marine species also have more potential to regulate their abundance in the larval stage.

The expected energy budgets for marine and freshwater fish larvae, calculated from the temperature-adjusted mean growth rates, ingestion rates, and weight-specific oxygen uptakes, are similar in most respects (Table 2a). After standardizing budgets to one unit of growth (Table 2b), the budgets differ principally in the metabolism component, which is nearly two times higher for the smaller marine larvae. Budgets standardized to one unit of ingestion (Table 2c) show that metabolism is 29% of ingested energy for marine larvae but is only 17% for freshwater larvae. Average assimilation efficiencies [(Ingestion − Feces) ÷ Ingestion] apparently are higher for marine (65%) than for freshwater fish larvae (56%), primarily because marine larvae have a higher metabolic level, not because they grow faster or more efficiently.

Discussion

It has been presumed since the important contribution by Hjort (1914) that dynamics in the early larval stage play a dominant role in controlling or regulating year-class strengths of marine fishes. Numerous studies of conceptual, theoretical, and applied nature have supported this assumption (Jones, 1973; Jones and Hall, 1974; Cushing, 1974a, 1990; Lasker, 1978; Beyer, 1989; Heath, 1992). Less emphasis on larval-stage dynamics is apparent in the literature on freshwater fishes. Results of the present analysis suggest that larval-stage dynamics generally will have less influence on control or regulation of year-class strengths in freshwater fishes, and that trophic interactions, competition for resources, and such factors as overwinter mortality during the juvenile stage, may be the predominant factors affecting their recruitment levels (Forney, 1976; Mills et al., 1987; Post and Evans, 1989; Shuter et al., 1989).

The relatively large size at hatching, short-stage duration, and low mortality rate of freshwater fish larvae favor the probability that recruitment level will be controlled during the juvenile stage. In contrast, marine fish hatch at relatively small size, have longer-stage durations, and suffer higher larval mortality rates, indicating a higher probability that recruitment levels are controlled primarily in the larval stage. Minor variability in larval growth and mortality rates are likely to register bigger effects on recruitment potential of marine fishes because, on average, the larval stage duration is 15 days longer in marine species (Table 1). Mean survival through the
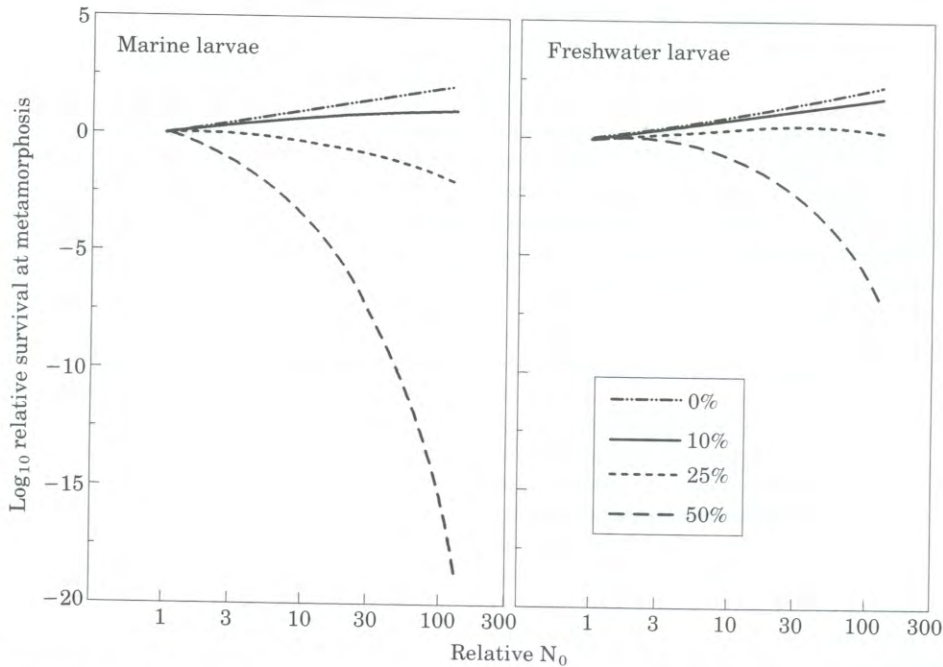
Figure 2. The effect of density-dependent growth on relative recruitment potential, indexed as relative survivorship at metamorphosis for marine and freshwater fish larvae. In the simulations, weight-specific growth rates were allowed to remain constant (0% decline) or were reduced by 10, 25, and 50% per five-fold increase in initial larval numbers.

larval stage is only 0.12% for a typical cohort of marine fish, but is 5.30% for a typical cohort of freshwater fish, suggesting that substantially less scope for control and regulation of abundance may exist in the juvenile stage of marine fishes.

Larvae of teleost fishes are as diverse as are adult teleosts, presenting a spectrum of larval sizes, morphologies, and ontogenies. But, freshwater species that have been studied have larvae which hatch at dry weights exceeding 100 μg (appendix A in Houde and Zastrow, in press), while relatively few marine larvae hatch at more than 100 μg. The difference in initial sizes between freshwater and marine larvae is in part attributable to spawning modes. Virtually all freshwater species are demersal spawners, producing relatively few but large eggs, while marine species usually are pelagic spawners, producing many but small eggs (Duarte and Alcaraz, 1989). If freshwater fishes that were excluded from this analysis, e.g. Salmonidae, Acipenseridae, and Ictaluridae, which have large and precocious larvae, had been included, the differences that were demonstrated between freshwater and marine species (Table 1) would have been magnified.

If survival through the larval stage were inversely proportional to fecundity, then the differences in larval stage survivorship between marine and freshwater species might not be significant on a "per adult spawner" basis. Winemiller and Rose (1992) reviewed data on "clutch sizes" and "spawning bouts" in fishes. Their data indicate that marine fishes, on average, are approximately 11 times more fecund than freshwater fishes. Data illustrated in Duarte and Alcaraz (1989) also suggest at least 10-fold higher fecundity, on average, in marine fishes. Even with such a large difference in fecundity, expected survival per adult spawner at the end of the larval stage [calculated from Equation (1) with N_o set at 11 and 1 for marine and freshwater species, respectively] still is four times higher for freshwater fishes. The tentative conclusion remains that control of recruitment during the juvenile stage is more probable for freshwater than for marine fishes.

The differences in population dynamics and energetics properties of marine and freshwater fish larvae are partly attributable to their differences in body size. Peterson and Wroblewski (1984) and McGurk (1986) demonstrated that mortality rates of marine organisms, including fish eggs and larvae, decline as size increases. Miller *et al.* (1988) and Werner and Gilliam (1984) indicated that many ontogenetic and behavioral properties of fish larvae are strongly related to body size. They suggested, and Beyer (1989) argued, that size-dependent mortality and growth are the decisive factors that control the recruitment process in fishes. Neither Pepin (1991) nor Houde (1990) was able to demonstrate that size at hatch of marine fish larvae had a significant effect on cumulative or instantaneous mortality during the larval stage, but

neither study included freshwater fish larvae, which generally are larger than larvae of marine fishes. Pepin and Myers (1991) did show that recruitment variability in marine fish stocks is positively correlated with the difference in size between hatching and metamorphosis (ΔL), which they argued was a measure of stage duration. This result, if extended to include freshwater fishes, suggests that recruitment variability in freshwater species, which have relatively small ΔL and short larval-stage durations, should be lower than in marine species. This hypothesis remains to be tested.

Starvation mortality is predicted to be more likely for marine than for freshwater fish larvae when food resources are scarce. If the prediction is correct, the probability of death by starvation may be highest for marine larvae that develop at high temperatures (Houde, 1989a). Mean weight-specific ingestion, while not demonstrated to be significantly lower for freshwater larvae in my analysis, may in fact be lower (Tables 1, 2). Higher required ingestion by marine larvae is expected because higher metabolic demands are imposed by their small body sizes, and because neither their weight-specific growth rate nor gross growth efficiency differed from those characters in freshwater larvae.

Houde and Zastrow (in press) found that mean weight-specific oxygen uptake (QO_2) of marine fish larvae was nearly twice that of freshwater larvae. The regression slopes of the relationships between QO_2 and temperature were the same for the marine and freshwater larvae, but the elevation of the regression was twice as high for the freshwater species. There also was a strong relationship between QO_2 and weight at hatch (Houde and Zastrow, in press) which indicated that freshwater larvae had lower QO_2 because of their relatively large sizes.

Episodic mortalities of early life stages, often associated with weather events, are more likely to be significant for freshwater fish. Freshwater nursery habitats generally are relatively small, often shallow, and vulnerable to sudden changes in temperature, water levels, pH, oxygen level, and chemical constituency. Marine nurseries, in a relative sense, are less vulnerable to events that may promote episodic mortalities, except for unfavorable advection which may cause losses of eggs and larvae. The impact of large episodic mortalities on recruitment level is often lower than effects due to modest changes in daily growth or mortality rates (Houde, 1989b). The shorter-stage durations of freshwater fish larvae, while reducing the temporal window within which episodes can occur, perhaps more importantly reduce the period of time over which vital rates may vary to affect survivorship. A contrasting situation prevails in marine nurseries, i.e. the temporal window within which a low-probability episode might occur increases, but the longer-stage durations of marine fish larvae magnify the probability that control or regulation will act through modest variability in vital rates.

Regulation of larval stage abundances, via density-dependent effects on growth and mortality, is proposed to be more likely for marine fish larvae than for freshwater larvae. The longer-stage durations of marine fish larvae imply that even small reductions in growth rates in response to increasing larval densities could have a powerful regulatory effect on recruitment (Ware, 1975; Shepherd and Cushing, 1980). The timeframe over which that effect operates will determine the magnitude of its impact. Houde (1989b) simulated effects of density-dependent growth on some species of marine and estuarine fish larvae and found that the biggest effects on recruitment level were for species with high W_{met} to W_o ratios and low G to Z ratios. In the present analysis, the mean $W_{met}{:}W_o$ for marine fish larvae is 288.4, while that for freshwater larvae is only 25.8. The mean G:Z for marine fish larvae is 0.83, while that for freshwater larvae is 1.12. On average, cohorts of marine fish larvae lose biomass during the larval stage ($G/Z < 1.0$), suggesting that they are potentially more limited by food resources than are freshwater larvae. In contrast, freshwater larval cohorts accumulate biomass ($G/Z > 1.0$) relatively fast during a short-stage duration, which may restrict the potential for density-dependent regulation in the larval stage.

Because the relative numbers (per egg or per female) surviving to enter the juvenile stage are higher in freshwater fishes, their potential for significant adjustment of year-class sizes during the juvenile stage is relatively great. On average, the relative abundances of freshwater juveniles will be higher and their stage durations longer than those of marine species. Consequently, either coarse or fine controls that are density-independent, or subtle density-dependent regulation acting on freshwater juveniles, will have a relatively big impact on recruitment levels. This prediction does not exclude the possibility of significant control and regulation during the juvenile stage of marine fishes (Sissenwine, 1984), but it suggests that juvenile-stage dynamics will be relatively more important in determining recruitment levels and variability of freshwater fishes, while larval-stage dynamics will be more important in marine species.

Acknowledgments

References

Balon, E. K. 1981. Saltatory processes and altricial to precocial forms in the ontogeny of fishes. American Zoologist, 21: 573–596.

Beyer, J. E. 1989. Recruitment stability and survival – simple size-specific theory with examples from the early life dynamics of marine fish. Dana, 7: 45–147.

Cushing, D. H. 1974a. The natural regulation of fish populations. *In* Sea fisheries research, pp. 399–412. Ed. by F. R. Harden-Jones. J. Wiley & Sons, New York. 510 pp.

Cushing, D. H. 1974b. The possible density-dependence of larval mortality and adult mortality in fishes. *In* The early life history of fish, pp. 103–111. Ed. by J. H. S. Blaxter. Springer-Verlag, New York, Heidelberg, Berlin. 765 pp.

Cushing, D. H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Advances in Marine Biology, 26: 250–293.

Duarte, C. M., and Alcaraz, M. 1989. To produce many small or few large eggs: a size-independent reproductive tactic of fish. Oecologia, 80: 401–404.

Forney, J. L. 1976. Year-class formation in the walleye (*Stizostedion vitreum vitreum*) population of Oneida Lake, New York, 1966–73. Journal of the Fisheries Research Board of Canada, 33: 783–792.

Heath, M. R. 1992. Field investigations of the early life stages of marine fish. Advances in Marine Biology, 28: 1–173.

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 20: 1–228.

Houde, E. D. 1989a. Comparative growth, mortality and energetics of marine fish larvae. Fishery Bulletin, US, 87: 471–495.

Houde, E. D. 1989b. Subtleties and episodes in the early life of fishes. Journal of Fish Biology, 35 (Suppl. A): 29–38.

Houde, E. D. 1990. Temperature-dependent and size-dependent variability in vital rates of marine fish larvae. ICES CM 1990/L:3, 15 pp.

Houde, E. D., and Zastrow, C. E. 1991. Ecosystem-specific and taxa-specific growth, mortality and energetics relationship of teleost larvae. ICES CM 1991/L: 35, 11 pp.

Houde, E. D., and Zastrow, C. E. Ecosystem- and taxa-specific dynamic and energetics properties of fish larvae assemblages. Bull. Mar. Sci., 53.

Jones, R. 1973. Density dependent regulation of the numbers of cod and haddock. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 164: 156–173.

Jones, R., and Hall, W. B. 1974. Some observations on the population dynamics of the larval stage in the common gadoids. *In* The early life history of fish, pp. 87–102. Ed. by J. H. S. Blaxter. Springer-Verlag, New York–Heidelberg–Berlin. 765 pp.

Lasker, R. 1978. The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 173: 212–230.

Mackenzie, B. R., Leggett, W. C., and Peters, R. H. 1990. Estimating larval fish ingestion rates: Can laboratory derived values be reliably extrapolated to the wild? Marine Ecology Progress Series, 67: 209–225.

McGurk, M. D. 1986. Natural mortality of marine pelagic fish eggs and larvae: Role of spatial patchiness. Marine Ecology Progress Series, 34: 227–242.

Miller, T. J., Crowder, L. B., Rice, J. A., and Marschall, E. A. 1988. Larval size and recruitment mechanisms in fishes: Toward a conceptual framework. Canadian Journal of Fisheries and Aquatic Sciences, 45: 1657–1670.

Mills, E. L., Forney, J. L., and Wagner, K. J. 1987. Fish predation and its cascading effect on the Oneida Lake food chain. *In* Predation. Direct and indirect impacts on aquatic communities, pp. 118–131. Ed. by W. C. Kerfoot and A. Sih. University Press of New England, Hanover and London. 386 pp.

Morse, W. W. 1989. Catchability, growth and mortality of larval fishes. Fishery Bulletin, US, 87: 417–446.

Pepin, P. 1991. The effect of temperature and size on development, mortality and survival rates of the pelagic early life history stages of marine fish. Canadian Journal of Fisheries and Aquatic Sciences, 48: 503–518.

Pepin, P., and Myers, R. A. 1991. Significance of egg and larval size to recruitment variability of temperate marine fish. Canadian Journal of Fisheries and Aquatic Sciences, 48: 1820–1828.

Peterson, I., and Wroblewski, J. S. 1984. Mortality rate of fishes in the pelagic ecosystem. Canadian Journal of Fisheries and Aquatic Sciences, 41: 1117–1120.

Post, J. R., and Evans, D. O. 1989. Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*): laboratory, in situ enclosure, and field experiments. Canadian Journal of Fisheries and Aquatic Sciences, 46: 1958–1968.

Rothschild, B. J. 1986. Dynamics of marine populations. Harvard University Press, Cambridge, Massachusetts. 277 pp.

Shepherd, J. G., and Cushing, D. H. 1980. A mechanism for density-dependent survival of larval fish as the basis of a stock recruitment relationship. Journal du Conseil International pour l'Exploration de la Mer, 39: 160–167.

Shuter, B. J., Ihssen, P. E., Wales, D. L., and Snucins, E. J. 1989. The effects of temperature, pH and water hardness on winter starvation of young-of-the-year smallmouth bass, *Micropterus dolomieui* Lacépede. Journal of Fish Biology, 35: 765–780.

Sissenwine, M. P. 1984. Why do fish populations vary? *In* Exploitation of marine communities, pp. 59–94. Ed. by R. M. May. Springer-Verlag, Berlin. 366 pp.

Ware, D. M. 1975. Relation between egg size, growth, and natural mortality of larval fish. Journal of the Fisheries Research Board of Canada, 32: 2503–2512.

Werner, E. E., and Gilliam, J. F. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics, 15: 393–425.

Winemiller, K. O., and Rose, K. A. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. Canadian Journal of Fisheries and Aquatic Sciences, 49: 2196–2218.