

Potential Use and Abuse of General Empirical Models of Early Life History Processes in Fish

By necessity, the development of principles and theory in scientific research requires inferences based on previous observations. To summarize information from a variety of sources, some investigators advocate the development of general empirical relationships (e.g., Dillon and Rigler 1974; Banse and Mosher 1980; Peters 1983). General allometric models provide a series of qualitative and semiquantitative hypotheses about size-related features of organisms and in that sense hold promise for the advancement of knowledge and understanding (Peters 1992). However, many have questioned the potential value of empirical models in terms of their accuracy (Gulland 1987) and applicability to different levels of aggregation (e.g., McLaren and Corkett 1984; Lehman 1991) or on different time scales (e.g., McQueen et al. 1992). In this comment, we reiterate the cautionary suggestions of other investigators in the use of general empirical models, with particular reference to reviews of the early life history stages of fish (Miller et al. 1988; Pepin 1991). We both feel that there are potential gains and losses to our understanding that can result from using such empirical reviews. On the negative side, we find indications that such models can be used as predictive equations or as supporting evidence for underlying assumptions in specific studies. One possible implication is that estimates provided by general relationships could be substituted either into models or into field or laboratory studies as substitutes for the measurement of appropriate parameters. For this reason, we feel it important to stress the constraints of empirical reviews and warrant the need for verification at the appropriate level of observation or aggregation.

Because of the paucity of information on the ecological processes that influence the eggs and larvae of any one species of fish, several reviews have attempted to highlight general features of these stages of the life history (Dahlberg 1979; McGurk 1986; Anderson 1988; Miller et al. 1988; Bailey and Houde 1989; Houde 1989; MacKenzie et al. 1990; Pepin 1991). Empirical studies were surveyed with the aim of developing general conceptual frameworks that would unify observations on common variables (Miller et al. 1988; Houde 1989; MacKenzie et al. 1990; Pepin 1991). In most cases, the principal independent variable was the size of the organism because this feature is easily measured, available in most reports, and has been used extensively to generalize processes across taxa (e.g., Peters 1983). In studies of early life stages of fish, size is generally measured as length because of the difficulty in obtaining accurate measurements of weight, although some have found sufficient available information on weight (e.g., Houde 1989). In fact, weight may be the most appropriate descriptor of the size of organisms because of the significance of mass in determining metabolic requirements (e.g., Giguère et al. 1989). Despite the potential limitations of length as a measure of body size, the conclusions from general empirical reviews are consistent with previous expectations derived from

simple physiological or ecological principles of allometry. For example, in comparisons between species, increases in size generally lead to increases in foraging efficiency (MacKenzie et al. 1990) and reductions in susceptibility to starvation (e.g., Miller et al. 1988) and vulnerability to predators (Folkvord and Hunter 1986; Pepin et al. 1987; Miller et al. 1988). These trends combine to increase the likelihood of surviving through a given stage of the life cycle of larger species (Pepin 1991). However, these conditions may not always be satisfied (see Pepin 1991). Given the consistency of these observations with basic expectations, one can easily be tempted to extend these interspecific relationships to intraspecific ones and conclude that increased size of any early life history stage leads to enhanced survival.

Variability in the characteristics of larval fish (e.g., growth or mortality rates) can be compared or estimated at organizational levels that range from species (e.g., Miller et al. 1988; Houde 1989; Pepin 1991) to populations (e.g., Hempel and Blaxter 1967) to cohorts (e.g., Oak and Houde 1987), to families (e.g., Chambers et al. 1988), to individuals (e.g., Chambers and Leggett 1987; DeAngelis et al. 1991). The issues addressed by studies conducted on these different hierarchical levels of organization can be very different. In a comparison between species, one is typically addressing the question "Do the features of different species represent differences in life histories?" Deviations from the general pattern become important as potential examples of a response to evolutionary pressures. In contrast, a comparison of individuals generally asks "Are survivors good or lucky?" This question is increasingly common in fisheries research, as we attempt to understand whether recruitment is controlled by selective processes during the early life history (Fritz et al. 1990; Crowder et al. 1992). Data provided by such different perspectives represent measurements on very separate levels of aggregation. Failure to recognize differing levels of aggregation is equivalent to making the assumption that size dependencies are independent of the level at which they are estimated. This is often not the case. For example, size-dependent vulnerability to starvation varies as one changes the level of aggregation from species (Miller et al. 1988; Pepin 1991) to stocks of a species (Blaxter and Hempel 1963) to families within a stock (Chambers et al. 1989) and finally to individuals within a family (e.g., P. Pepin and J.T. Anderson, unpublished data). These contrasting patterns reflect differences in the balance of life history characteristics at each level of aggregation. A similar difference in size dependency can be found in the predicted likelihood that an individual larva would survive exposure to a predator. Pepin et al. (1992) found that within experimental enclosures, larger individual larvae suffered higher predation rates than smaller ones. However, when they compared experiments, Pepin et al. (1992) found that the cumulative predation rates increased as the mean size of a cohort of larvae decreased. In this instance, apparent differences in size dependency did not come from differences in life history features but rather from differences in the manner by which the effects of encounter, attack, and capture probabilities were

being integrated. Clearly, forecasting individual survival probabilities based on the concept that increasing the size of a larva reduces vulnerability to capture by a predator (Brownell 1985; Folkvord and Hunter 1986; Pepin et al. 1987; Miller et al. 1988; Fuiman 1989) and thus leads to a reduced likelihood of dying could have produced erroneous predictions (see Litvak and Leggett 1992; Pepin et al. 1992). Similar results can also be found in comparative studies of size-selective mortality of pelagic fish eggs either between (Pepin 1991) or within (Rijnsdorp and Jaworski 1990) species. Finally, a study of growth and mortality rates among species shows that these vital rates are positively correlated (Pepin 1991) but variations in cohort survival are likely to result from fluctuations in either growth or mortality about the general relationship (Ware 1975). Depending on the level at which information is averaged, the effects of size can appear different and in some instances opposite to those at a different level.

To date, reviews of early life history characteristics have generally used the coarsest level of aggregation — comparison among species (e.g., Miller et al. 1988; Pepin 1991). The intent of our respective approaches was not to provide definitive relationships describing the various processes that are elements of the survival equation but rather to explore potential generalities emerging from the suite of studies surveyed. The empirical functions produced from the various analyses are not predictive models per se that are applicable to all species and levels of aggregation. Instead, they represent advanced *null hypotheses* that require verification, support, or rejection in future studies and at different levels of organization (aggregation). We refer to general empirical models as advanced null hypotheses because they constitute a summary of our current knowledge rather than the basic null model of no significant relationship. These advanced null hypotheses provide a perspective that can be used to forecast an unknown species' characteristics. A comparison and test of observations from previously unstudied organisms can then be used to assess a species' departure from the expectation based upon the responses of many others. A proper analysis to assess the *practical* and *statistical* significance of the deviation(s) from the general empirical model can then lead to further hypotheses about differences in other life history features or variability in reproductive success (see Chambers and Leggett 1991 for further discussion). However, the patterns emerging from inter-species comparisons may not be robust when one changes the level of organization considered. Without further testing and verification, predictions assuming that bigger is necessarily better can lead to spurious or inaccurate conclusions.

Our proposals that size can be used to describe features of development, production, and survival (Miller et al. 1988; Pepin 1991) are only two in a suite of perspectives that use this easily measured feature of organisms to compare across levels of aggregation (e.g., Bluewiss et al. 1978; Banse and Mosher 1980). The approach has been shown to be useful in a comparison between studies of different processes, species, or organizational levels (e.g., Sheldon et al. 1977; Dickie et al. 1987). But the conclusions should not be applied as general principles regardless of experimental or survey design. Furthermore, despite the appealing usefulness of simple empirical relationships in modelling growth, mortality, or survival of fish eggs and larvae, it is imperative that we note the precision of such relationships. Data used to derive general empirical models often come from studies conducted at the population level for which measurements were taken at coarse space and time scales.

The cumulative error associated with such measurements results in relationships that have broad confidence intervals (Miller et al. 1988, 1992; Pepin 1991). Consequently, the predictive power of models derived from these relationships is poor, and it is seldom possible to observe deviations either within or between species that are statistically discernable from the overall mean (Pepin 1993). General empirical models based on species comparisons provide first-order approximations to this process, but there is evidence that such coarse averages do not bear a strong association with adult abundance or future recruitment (e.g., Peterman et al. 1988).

In order to achieve an understanding of the mechanisms that determine overall survival, there is a need to develop a perspective that integrates information from several scales of observation (Crowder et al. 1992). By contrasting information on different scales of observations, we may be able to develop an understanding of how processes are being integrated relative to the population. General empirical relationships may provide the null models required to assess whether new information represents a departure from a summary of previous knowledge. However, when comparing observations from different sources, it is essential that we ask whether the accuracy and precision of the data are sufficient to detect deviations from a null model or an overall average. Although general models may serve as a tool to improve our understanding of early life history stages of fish, we feel they should not be used as substitutes for a lack of information pertaining to specific parameters — P. Pepin, *Department of Fisheries and Oceans, P.O. Box 5667 St. John's, NF A1C 5X1, Canada*, and T.J. Miller, *Department of Biology, McGill University, 1205 Avenue Dr. Penfield, Montreal, QC H3A 1B1, Canada.* (JB566)

References

- ANDERSON, J.T. 1988. Review of size-dependent survival during pre-recruit stages of fishes in relation to recruitment. *J. Northwest Atl. Fish. Sci.* 8: 55–66.
- BAILEY, K.M., AND E.D. HOUE. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. *Adv. Mar. Biol.* 26: 1–83.
- BANSE, K., AND S. MOSHER. 1980. Adult body mass and annual production/biomass relationships of field populations. *Ecol. Monogr.* 50: 355–379.
- BLAXTER, J.H.S., AND G. HEMPEL. 1963. The influence of egg size on herring larvae (*Clupea harengus*). *J. Cons. int. Explor. Mer* 28: 211–240.
- BLUEWISS, L., H. FOX, V. KUDZMA, B. NAKASHIMA, R.H. PETERS, AND S. SAMS. 1978. Relationships between body size and some life history parameters. *Oecologia* 37: 257–272.
- BROWNELL, C.L. 1985. Laboratory analysis of cannibalism by the larvae of the cape anchovy *Engraulis capensis*. *Trans. Am. Fish. Soc.* 114: 14–25.
- CHAMBERS, R.C., AND W.C. LEGGETT. 1987. Size and age at metamorphosis in marine fishes: an analysis of laboratory reared winter flounder (*Pseudopleuronectes americanus*) with a review of variation in other species. *Can. J. Fish. Aquat. Sci.* 44: 1936–1947.
- CHAMBERS, R.C., AND W.C. LEGGETT. 1991. Possible causes and consequences of variation in age and size at metamorphosis in flatfishes (*Pleuronectiformes*): an analysis at the individual, population, and species levels. *Neth. J. Sea Res.* 27: 7–24.
- CHAMBERS, R.C., W.C. LEGGETT, AND J.A. BROWN. 1988. Variation in and among early life history traits of laboratory-reared winter flounder (*Pseudopleuronectes americanus*). *Mar. Ecol. Prog. Ser.* 47: 1–15.
- CHAMBERS, R.C., W.C. LEGGETT, AND J.A. BROWN. 1989. Egg size, female effects, and the correlation between early life history traits of capelin *Mallotus villosus*: an appraisal at the individual level. *Fish. Bull. U.S.* 87: 515–523.
- CROWDER, L.B., J.A. RICE, T.J. MILLER, AND E.A. MARSHALL. 1992. Empirical and theoretical approaches to size-based interactions and recruitment variability in fishes, p. 237–255. *In* D.L. DeAngelis and M. Huston [ed.] *Individual-based approaches in ecology*. Chapman Hall, New York, N.Y.
- DAHLBERG, M.D. 1979. A review of survival rates of fish eggs and larvae in relation to impact assessments. *Mar. Fish. Rev.* 41: 1–12.

- DEANGELIS, D.L., L. GODBOUT, AND B.J. SHUTTER. 1991. An individual based approach to predicting density-dependent dynamics in smallmouth bass populations. *Ecol. Model.* 57: 91-115.
- DICKIE, L.M., S.R. KERR, AND P.R. BOUDREAU. 1987. Size-dependent processes underlying regularities in ecosystem structure. *Ecol. Monogr.* 57: 233-250.
- DILLON, P.J., AND F.H. RIGLER. 1974. The phosphorus:chlorophyll relationship in lakes. *Limnol. Oceanogr.* 19: 767-773.
- FOLKVORD, A., AND J.R. HUNTER. 1986. Size-specific vulnerability of northern anchovy (*Engraulis mordax*) larvae to predation by fishes. *Fish. Bull. U.S.* 84: 859-869.
- FRITZ, E.S., L.B. CROWDER, AND R.C. FRANCIS. 1990. The National Oceanic and Atmospheric Administration plan for recruitment fisheries oceanography research. *Fisheries* 15: 25-31.
- FUIMAN, L.A. 1989. Vulnerability of Atlantic herring larvae to predation by yearling herring. *Mar. Ecol. Prog. Ser.* 51: 291-299.
- GIGUÈRE, L.A., B. CÔTÉ, AND I.F. ST. PIERRE. 1989. Metabolic rates scale isometrically in larval fishes. *Mar. Ecol. Prog. Ser.* 50: 13-19.
- GULLAND, J.A. 1987. Natural mortality and size. *Mar. Ecol. Prog. Ser.* 39: 197-199.
- HEMPEL, G., AND J.H.S. BLAXTER. 1967. Egg weight in Atlantic herring (*Clupea harengus*). *J. Cons. int. Explor. Mer* 31: 170-195.
- HOUDE, E.D. 1989. Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. *Fish. Bull. U.S.* 87: 471-496.
- LEAK, J.C., AND E.D. HOUDE. 1987. Cohort growth and survival of bay anchovy, *Anchoa mitchilli*, larvae in Biscayne Bay, Florida. *Mar. Ecol. Prog. Ser.* 37: 109-122.
- LEHMAN, J.T. 1991. Interacting growth and loss rates: the balance of top-down and bottom-up controls in plankton communities. *Limnol. Oceanogr.* 36: 1546-1554.
- LITVAK, M.K., AND W.C. LEGGETT. 1992. Age and size-selective predation on larval fishes: the bigger is better paradigm revisited. *Mar. Ecol. Prog. Ser.* 81: 13-24.
- MACKENZIE, B.R., W.C. LEGGETT, AND R.H. PETERS. 1990. Estimating larval fish ingestion rates: can laboratory derived values be reliably extrapolated to the wild? *Mar. Ecol. Prog. Ser.* 67: 209-225.
- MCGURK, M.D. 1986. Natural mortality of marine pelagic fish eggs and larvae: role of spatial patchiness. *Mar. Ecol. Prog. Ser.* 34: 227-242.
- MCLAREN, J.A., AND C.J. CORKETT. 1984. Singular, mass-specific P/B ratios cannot be used to estimate copepod production. *Can. J. Fish. Aquat. Sci.* 41: 828-830.
- MCQUEEN, D.J., E.L. MILLS, J.L. FORNEY, M.R.S. JOHANNES, AND J.R. POST. 1992. Trophic level relationships in pelagic food webs: comparisons derived from long-term data sets for Oneida Lake (U.S.A.), New York, and Lake St. George, Ontario (Canada). *Can. J. Fish. Aquat. Sci.* 49: 1588-1596.
- MILLER, T.J., L.B. CROWDER, J.A. RICE, AND F.P. BINKOWSKI. 1992. Body size and the ontogeny of the functional response in fishes. *Can. J. Fish. Aquat. Sci.* 49: 805-812.
- MILLER, T.J., L.B. CROWDER, J.A. RICE, AND E.A. MARSCHALL. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Can. J. Fish. Aquat. Sci.* 45: 1657-1670.
- PEPIN, P. 1991. The effect of temperature and size on development and mortality rates of the pelagic early life history stages of marine fish. *Can. J. Fish. Aquat. Sci.* 48: 503-518.
- PEPIN, P. 1993. Application of empirical size-dependent models of larval fish vital rates to the study of production: accuracy and association with adult stock dynamics in a comparison among species. *Can. J. Fish. Aquat. Sci.* 50: 53-59.
- PEPIN, P., S. PEARRE JR., AND J.A. KOSLOW. 1987. Predation on larval fish by Atlantic mackerel, *Scomber scombrus*, with a comparison of predation by zooplankton. *Can. J. Fish. Aquat. Sci.* 44: 2012-2018.
- PEPIN, P., T.H. SHEARS, AND Y. DELAFONTAINE. 1992. Significance of body size to the interaction between a larval fish (*Mallotus villosus*) and a vertebrate predator (*Gasterosteus aculeatus*). *Mar. Ecol. Prog. Ser.* 81: 1-12.
- PETERMAN, R.M., M.J. BRADFORD, N.C.H. LO, AND R.D. METHOT. 1988. Contribution of early life stages to interannual variability in recruitment of northern anchovy (*Engraulis mordax*). *Can. J. Fish. Aquat. Sci.* 45: 8-16.
- PETERS, R.H. 1983. The ecological significance of body size. Cambridge University Press, Cambridge. 329 p.
- PETERS, R.H. 1992. Lessons from the size efficiency hypothesis II. The mire of complexity. *Hydrobiologia* 235/236: 435-455.
- RUNSDORP, A.D., AND A. JAWORSKI. 1990. Size-selective mortality in plaice and cod eggs: a new method in the study of egg mortality. *J. Cons. int. Explor. Mer* 47: 256-263.
- SHELDON, R.W., W.H. SUTCLIFFE, AND M.A. PARANJAPE. 1977. Structure of pelagic food chain and relationship between plankton and fish production. *J. Fish. Res. Board Can.* 34: 2344-2353.
- WARE, D.M. 1975. Relation between egg size, growth and natural mortality of larval fish. *J. Fish. Res. Board Can.* 32: 2503-2512.