An analysis of the length-weight relationship of larval fish: limitations of the general allometric model

Pierre Pepin
Department of Fisheries and Oceans
P.O. Box 5667, St. John's, Newfoundland, Canada A1C 5X1

Substantial morphological and physiological changes occur during the early ontogeny of fish. After hatching, both shape and size undergo significant alterations in association with yolk absorption and a subsequent increase in musculature. In fish, the larval stage generally consists of a period of rapid growth, which can vary substantially in duration within and among species (Sinclair and Tremblay, 1985, Ware and Lambert, 1985; Houde, 1989; Pepin, 1991). Length and weight may increase by factors of approximately 10 and 1,000, respectively, over a time interval that often spans less than 10% of a species' life time. Such high development rates are associated with high metabolic rates (Giguère et al., 1989) which can lead to substantial variation in condition as a result of fluctuations in food availability (Houde and Schekter, 1980; Werner and Blaxter, 1980). Studies of variations in growth characteristics and condition have been an important keystone in understanding early life history survival (Houde, 1987).

Changes in length or weight through time have been used to assess the general growth rates of populations. Most often, the model used to describe length-weight relationships of fish larvae is a general allometric function

$$W = aL^b, \qquad (1a)$$

where W is weight, L is length, and a and b are constants. A logarithmic transformation of Equation 1 leads to a linear relationship

$$\log W = \log a + b \log L \qquad (1b)$$

that can be estimated with minimal computing power, by using least squares, and for which the fit is generally strong (e.g. Laurence, 1978). The latter point may seem reason enough to assume that a general allometric model is an adequate description of the data. However, some inferences derived from this type of information concern variation in condition. For example, deviations from a general length-weight relationship (e.g. Fulton's (1911) index of condition [$K=W/L^3$, where W and L are the weight and length of individuals]) have been used to describe the relative state of health of individuals (e.g. Westernhagen and Rosenthal, 1981; Checkley, 1984; Ciechomski et al., 1986; Harris et al., 1986; Frank and McRuer, 1989; Drolet et al., 1991). It is therefore necessary to ensure that the model used to describe the length-weight relationship not only provides a strong fit to the data but also that it accurately describes the functional form of that relationship.

Zweifel and Lasker (1976) suggest that changes in length or weight of fish larvae through time can be described by a Gompertz model

$$L = L_0\, e^{K(1-e^{-\alpha t})} \qquad (2a)$$

$$W = W_0\, e^{K'(1-e^{-\alpha' t})}, \qquad (2b)$$

where L_0 and W_0 are the length and weight at time t=0, K and K' are the specific growth rates at time t=0, and α and α' are the rates of decay in growth rates. Only when $\alpha=\alpha'$ does the length-weight relationship reduce to the form shown in Equation 1b. Otherwise, the logarithmic length-weight relationship will exhibit a degree of nonlinearity (Laird et al., 1968; Zweifel and Lasker, 1976). Barton and Laird (1969) noted that fitting the general allometric model is relatively insensitive to slight departures from the true time relations for growth in length and weight (i.e. $\alpha\neq\alpha'$). Consequently, a general allometric relationship (Eq. 1b), with only two parameters, may be considered to provide an adequate description to the data, despite the fact that a more complex model (e.g. a Gompertz length-weight relationship) better describes the patterns of growth in length and weight. Although the importance of such subtle differences may appear to be minor, consistent departures from a general allometric model can lead to significant bias in predicting or interpreting weight at length. This can be particularly important when trying to model growth during the early life history (e.g. Rose and Cowan, 1993) or in estimating size-dependent metabolic processes (e.g. Checkley, 1984; Kiørboe, 1989; Giguère et al., 1989). Furthermore, there is potential for inaccurate inferences in instances where condition is being studied (e.g. W/L^3). Westernhagen and Rosenthal (1981) and Ciechomski et al. (1986) noted a decrease in Fulton's condition index after hatch, followed by an increase some time after first feeding. Although this pattern may be due to food deprivation, it can also arise because of a developmentally determined nonlinear allometric length-weight relationship (i.e $\alpha\neq\alpha'$).

In this study, I present evidence that, despite a strong fit to a general allometric length-weight rela-

Manuscript accepted 9 November 1994.
Fishery Bulletin 93:419–426 (1995).

tionship (Eq. 1b), the use of such a model may be inappropriate for the study of fish larvae.

Materials and methods

Ichthyoplankton samples were obtained during two surveys of Conception Bay (47°45'N, 53°00'W), Newfoundland, Canada. Cruises were held during the periods from 27 June 1990 to 15 July 1990 and from 25 September 1990 to 30 September 1990. Sampling was conducted during daylight hours (0700–1900) with a 4-m^2 Tucker trawl equipped with panels of 1,000-, 570-, and 333-µm mesh nitex. At each station, a single oblique tow of approximately 15 minutes was made at 2 knots (1 $m \cdot s^{-1}$). The net was lowered to 40 m at a rate of approximately 0.25 $m \cdot s^{-1}$ and retrieved at 0.064 $m \cdot s^{-1}$. After the net was washed, samples were preserved in 2% buffered formaldehyde. Within three to six months after collection, ichthyoplankton were sorted and identified to species or to the lowest taxonomic level possible (Atlantic Reference Centre, Huntsman Marine Science Centre, St. Andrews, New Brunswick, Canada). Sorted specimens were stored in 95% ethanol for approximately three years. Sixteen species were used in this analysis. For each species, 20 to 80 larvae were measured and weighted, depending on abundance, general condition, and the range of sizes available.

Larvae were measured to the nearest 0.1 mm by using an image analysis system mounted on a Wild M3C dissecting microscope that was equipped with an S-type mount fitted with a 0.5× objective. Each larva was placed on a preweighted aluminium sheet and dried in an oven at 65°Celsius. After 24 hours, larvae were transferred to a desiccator for no less than 1 hour and no more than 3 hours. Each larva was weighted to the nearest 0.1 µg by using a Cahn-31 microbalance.

Length-weight relationships of $\log_{10}$-transformed data were evaluated by using two models. In the first instance, a general allometric model of the form

$$\log W = a' + b \log L + \varepsilon, \qquad (3)$$

where W and L are weight and length, a' is equal to log(a) from Equation 1b, b is the exponent in Equation 1, and ε is error, was fit by using a general linear algorithm (procedure GLM, SAS, 1988). In the second case, a model of the form

$$\log W = a'' + b''(\log L)^{c''} + \varepsilon, \qquad (4)$$

where W and L are weight and length, respectively, and a", b", and c" are constants, and ε is error, was fit by using a nonlinear iterative least squares algorithm (procedure NLIN, SAS, 1988). When the value of c" is not significantly different from 1, Equation 4 reduces to the general allometric model (Eq. 3). Equation 3 is a well-recognized and general functional form used in the estimation of length-weight relationships (Ricker, 1975; Zweifel and Lasker, 1976; Cone, 1989). Equation 4 is not a common form (e.g. a Gompertz model; Laird et al., 1968; Zweifel and Lasker, 1976) but represents a first-order increase in complexity over the general allometric model (Eq. 3). I chose not to use the more complex Gompertz length-weight model, which has been used in other studies (e.g. McGurk, 1987) for two reasons. First, a Gompertz model is best suited for data that cover the entire range of sizes for a developmental stage. Such data were not available from the surveys conducted as part of this study. Second, preliminary analysis revealed that Equation 4 is numerically more stable than the Gompertz model for the data used in this study.

To establish whether there was a significant departure from loglinearity (Eq. 3), a second order polynomial was fit to the residuals (Y = a + bX + cX^2, where Y are the residuals and X is the log-transformed length). If the second order coefficient (c) is not significantly different from 0, then there is no departure from loglinearity and all other terms will also not differ from 0.

Results

Despite the wide variation in the range of information available for each species considered in this analysis (Table 1), the relationship between length and weight appears to be strong in all instances (Fig. 1). Analysis with the general linear allometric model (Eq. 3) shows a very highly significant fit for all species (Table 1). Evidence of a nonlinearity in the allometric relationship between length and weight is apparent in an analysis of the residuals from the general allometric model (Eq. 3). In 10 of 16 species, the second-order polynomial fit to the residuals in relation to log-transformed length was significant (Table 2).

The value of c" (Eq. 4) was significantly different from 1 for 11 of the 16 species used in this study (Table 3). In the case of *Ammodytes* sp., the value of c" indicates an asymptotic relationship. An exponential length-weight relationship of the log-transformed data is indicated in the 10 other species with values of c" significantly different from 1. Fitting Equation 4 to the data resulted in a decrease in residual sum of squares in 14 of the 16 species which averaged

Table 1

General characteristics of the length data for the 16 species used in this study. Three groups could only be identified to genus. Parameters of the general allometric model (Eq. 3) were estimated for the 16 species used in this analysis. The r^2, and the number of observations (n) are also provided. All relationships are significant at $P<0.001$. Values in brackets represent the standard error of the estimated parameters.

Species	Range in length (mm)	Median length (mm)	Intercept (a')	Slope (b)	r^2	n
Ammodytes sp.	7.3–28.6	18.0	−3.41	2.97 (0.14)	0.93	37
Aspidophoroides monopterygius	6.4–24.9	13.1	−2.83	2.49 (0.20)	0.89	20
Clupea harengus	6.8–28.9	9.7	−4.19	3.45 (0.11)	0.97	34
Gadus morhua	2.2–12.2	4.8	−2.68	2.65 (0.12)	0.92	40
Glyptocephalus cynoglossus	5.6–37.6	10.6	−3.12	2.63 (0.18)	0.85	40
Hippoglossoides platessoides	2.7–24.5	7.7	−3.53	3.42 (0.10)	0.94	80
Liparis atlanticus	2.8–7.5	4.0	−2.85	3.15 (0.10)	0.98	20
Liparis gibbus	5.3–12.5	7.5	−3.01	3.13 (0.20)	0.93	20
Lumpenus sp.	9.9–28.8	16.2	−3.11	2.70 (0.10)	0.95	36
Mallotus villosus	4.2–24.0	8.5	−3.55	2.79 (0.06)	0.98	40
Pleuronectes americanus	2.1–6.2	3.8	−3.08	3.11 (0.16)	0.91	40
Pleuronectes ferrugineus	1.9–14.4	3.6	−3.35	3.54 (0.09)	0.97	40
Sebastes sp.	4.4–9.5	7.5	−2.39	2.27 (0.19)	0.76	46
Stichaeus punctatus	8.8–22.0	13.5	−3.96	3.71 (0.13)	0.95	40
Tautogolabrus adspersus	3.3–9.3	5.3	−3.73	4.22 (0.25)	0.90	59
Ulvaria subbifurcata	4.5–13.3	6.4	−3.23	3.13 (0.13)	0.92	50

19% (range: 2–47%). In the cases of *Lumpenus* sp. and *Sebastes* sp., the use of Equation 4 resulted in an increase in the residual sum of squares of 15% and 8%, respectively.

Although lengths and weights were not corrected for shrinkage, Hay's (1984) and Johnston and Mathias' (1993) studies show that proportional weight loss due to preservation is greater than shrinkage in length and is proportionally greater as size of larvae decreases. If correction factors had been available, the net result would have been to increase the departure from log-linearity.

Discussion

Despite the apparently strong fit to the general allometric relationship between length and weight of larval fish, this analysis clearly shows a consistent nonlinear pattern in the log-transformed data. Although the curvature appears subtle, incorrect assumptions about model form may cause bias in the prediction of weights from lengths as well as in the interpretation of size-related variations in the physical condition of fish larvae. The significance of such inaccuracies may be minor for some aspects of the early life history (e.g. range of weights based on a mean functional relationship [Houde, 1989]) but may become more important in the calculation of metabolic processes (e.g. Checkley, 1984; Kiørboe, 1989; Giguère et al., 1989). Furthermore, the interpretation of gross measures of condition could also be influenced by the nonlinear nature of the length-weight relationship of larval fish. For example, calculation of Fulton's K, an index of condition, relies on the assumption that the general length-weight relationship of organisms follows a linear logarithmic function, specifically an isometric one (i.e. b=3). Increases or decreases in this coefficient are believed to be related to variations in condition. Not only is the general isometric assumption violated in 11 of 16 species (Table 1), but also that of linearity (Table 3). The significance of a departure from an isometric relationship in the interpretation of measures of condition relative to changes in body shape has been discussed in general terms by Cone (1989) and in relation to larval fish by Laurence (1978). As Ricker (1975) points out, Fulton's K can be used only to contrast individuals of approximately the same length. However, this is only true if the logarithmic length-weight relationship is linear and may not be appropriate when there is a significant departure from linearity, as shown in this study.

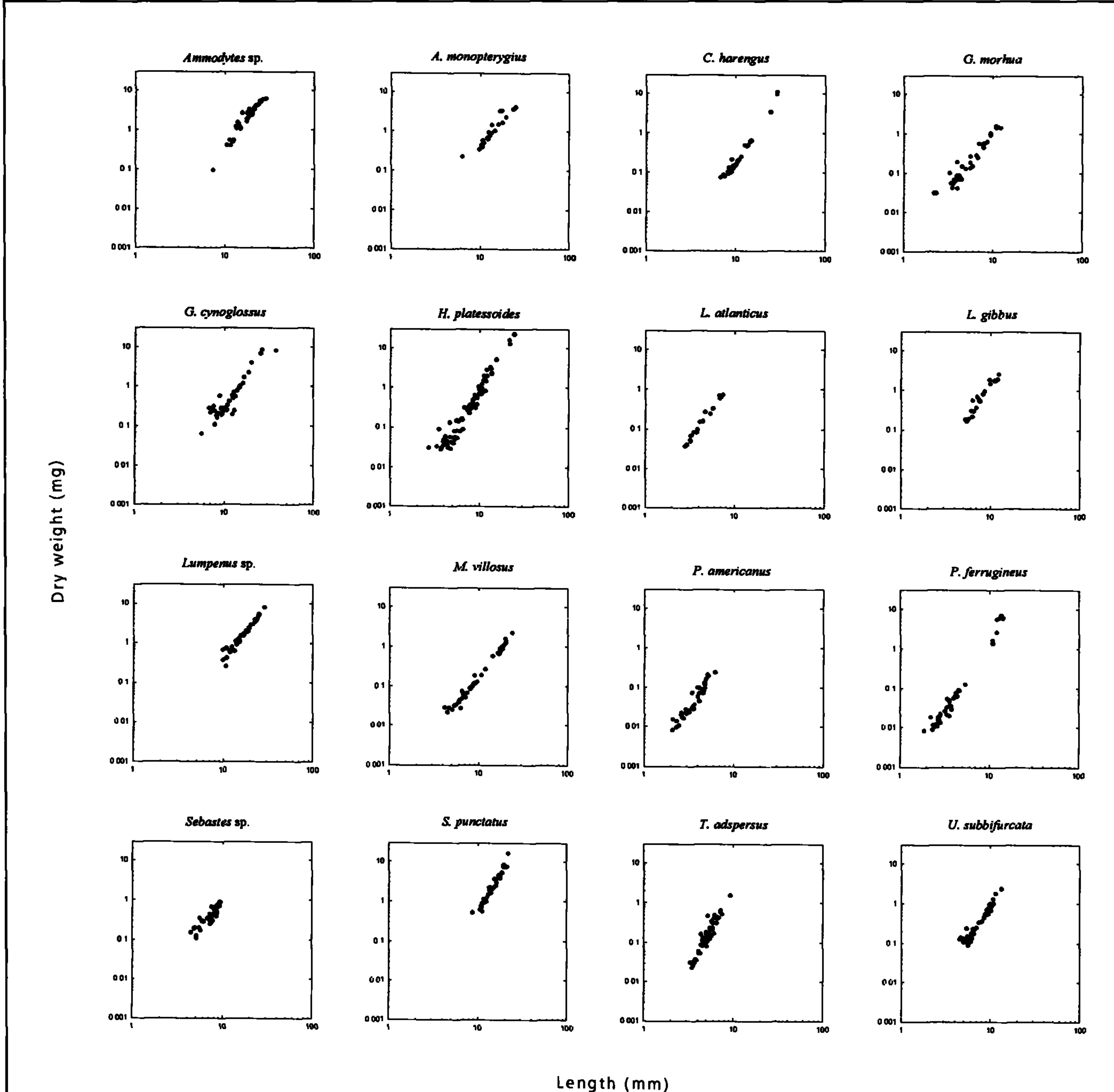

Figure 1

Logarithmic plot of the length-weight data for the 16 species considered in this analysis. Each point represents an individual larva.

Ontogenic development is characterized by notable changes in functional morphology that impact motility, foraging ability, and predator avoidance (Blaxter, 1986; Neilson et al., 1986; Olla and Davis, 1992). Developmental changes in body form or composition can result in differences in proportional growth in terms of length and weight and thus lead to a nonlinear allometric length-weight relationship. Alternatively, nonlinear variation in the length-weight relationship could be considered as evidence of changes in condition induced by some degree of food deprivation within a population of larval fish (e.g. Grover and Olla, 1986; Frank and McRuer, 1989; Drolet et al., 1991). Under such circumstances, varia-

Table 2

Estimated parameters of a second-order polynomial ($Y = a + bX + cX^2$) fit to the residuals (Y) from the general allometric model, estimated for the entire data set, in relation to log-transformed length (X). The right-most column provides the significance level of a two-tailed t-test evaluating the hypothesis that c=0.

Species	a	b	c	*P*
Ammodytes sp.	–3.21	5.45	–2.28	0.003
Aspidophoroides monopterygius	0.79	–1.43	0.63	0.54
Clupea harengus	2.79	–4.99	2.17	0.001
Gadus morhua	0.92	–22.62	1.74	0.003
Glyptocephalus cynoglossus	1.96	–3.56	1.57	0.03
Hippoglossoides platessoides	1.19	–2.83	1.59	0.001
Liparis atlanticus	–0.48	1.50	–1.13	0.23
Liparis gibbus	–2.30	5.11	–2.80	0.15
Lumpenus sp.	1.48	–2.47	1.02	0.26
Mallotus villosus	1.06	–2.19	1.08	0.001
Pleuronectes americanus	0.66	–2.56	2.37	0.05
Pleuronectes ferrugineus	0.80	–2.47	1.67	0.001
Sebastes sp.	3.70	–9.07	5.49	0.01
Stichaeus punctatus	2.57	–4.47	1.92	0.14
Tautogolabrus adspersus	–0.79	2.26	–1.58	0.26
Ulvaria subbifurcata	3.93	–9.16	5.23	0.001

Table 3

Parameter estimates for the nonlinear logarithmic length-weight relationship (Eq. 4). Values in brackets represent the asymptotic standard error of the estimated parameters. An asterisk next to the parameter in column c" denotes that the exponent is significantly different from 1 (two-tailed t-test). The right-most column provides the percent change in residual sum of squares relative to the fit provided by Equation 3. A positive value indicates an increase in the residual sum of squares whereas a negative value represents a decrease in the residual sum of squares.

Species	a"	b"	c"	Percent
Ammodytes sp.	–18.4	18.0	0.19 (0.05) *	–22
Aspidophoroides monopterygius	–1.84	1.52	1.55 (0.92)	–3
Clupea harengus	–1.92	1.15	2.44 (0.29) *	–47
Gadus morhua	–1.78	1.80	1.94 (0.33) *	–23
Glyptocephalus cynoglossus	–1.53	1.02	2.22 (0.59) *	–11
Hippoglossoides platessoides	–2.27	2.11	1.78 (0.19) *	–21
Liparis atlanticus	–4.66	4.87	0.53 (0.37)	–9
Liparis gibbus	–30.6	30.7	0.09 (0.51)	–9
Lumpenus sp.	–1.56	1.18	1.91 (0.81)	15
Mallotus villosus	–2.39	1.58	1.76 (0.23) *	–25
Pleuronectes americanus	–2.37	2.83	1.80 (0.39) *	–9
Pleuronectes ferrugineus	–2.42	2.58	1.66 (0.16) *	–47
Sebastes sp.	–0.99	0.93	3.80 (1.28) *	8
Stichaeus punctatus	–1.65	1.42	2.18 (0.59) *	–6
Tautogolabrus adspersus	–8.02	8.24	0.40 (0.51)	–2
Ulvaria subbifurcata	–1.35	1.26	3.41 (0.60) *	–29

tion in condition, or the scatter about the length-weight relationship, should be greatest at the developmental stage most vulnerable to food deprivation (i.e. yolk absorption). However, the pattern of scatter about the length-weight relationship shows little evidence of a consistent pattern associated with that stage of the early life history (Fig. 1). It is possible that the majority of larvae undergo a degree of starvation associated with the period of yolk absorption (e.g. Theilacker, 1986; Drolet et al., 1991; Marguiles, 1993), which would result in a uniform pattern in the deviation from a general allometric length-weight relationship. However, there is also evidence that suggests that only a limited fraction of a larval fish population suffers from substantial food deprivation (O'Connell, 1981; Canino et al., 1991; McGurk et al., 1992). The consistent nonlinear pattern in the length-weight relationship among a suite of species with different life histories, which could result in substantial differences in vulnerability to environmental factors (Miller et al., 1988; Pepin, 1991), suggests that developmental processes in the early ontogeny of fishes are important factors governing the form of this relationship. The degree of curvature in the logarithmic relationship (c'': Eq. 4) is not significantly correlated with size at hatch (r=0.45, P>0.05, n=14; Fig. 2), which may be a measure of vulnerability to starvation (Miller et al., 1988; but see Pepin, 1991). In fact, the positive trend is opposite that expected on the premise that species that produce small larvae should be more vulnerable to starvation.

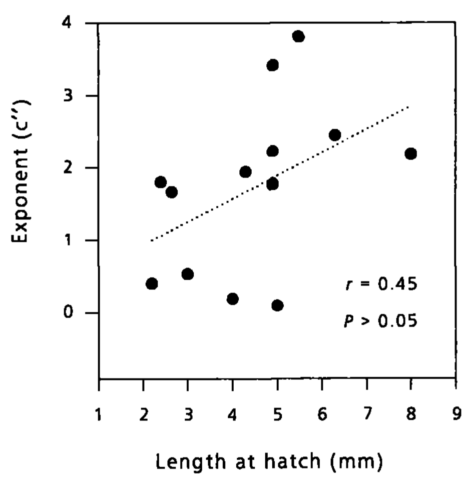

Figure 2
The value of c'' in relation to the size at hatch for 14 of the 16 species used in this study. The value of c'' provides a measure of the curvature in the logarithmic length-weight relationship. Data on size at hatch were obtained from general reference sources detailing fish life history characteristics (Fahay, 1983; Scott and Scott, 1988). Data were unavailable for *Aspidophoroides monopterygius* and *Lumpenus* sp.

Whether physiological processes rather than developmental constraints result in the nonlinear logarithmic length-weight relationship described in this study is uncertain. There are a number of approaches that may be indicative of the physiological condition of larval fish (e.g. Theilacker, 1986; Clemmensen, 1988; Fraser, 1989), but they may never the less be highly correlated with morphometric indices of condition (e.g. Theilacker, 1978; Harris et al., 1986; Setzler-Hamilton et al., 1987). Furthermore, there may remain considerable uncertainty about the interpretation of variation in such condition indices of larval fish (e.g. Bergeron and Boulhic, 1994). To interpret variation in length-weight relationships correctly, it is essential that thorough studies be conducted to establish the proper functional form and how this may vary under different feeding conditions.

Acknowledgments

I thank D. Beales and T. H. Shears for their technical assistance. Comments by E. Dalley, T. Miller, W. Warren, and two anonymous reviewers were helpful in the development of this study.

Literature cited

Barton, A. D., and A. K. Laird.
1969. Analysis of allometric and non-allometric differential growth. Growth 33:119–127.

Bergeron, J. P., and M. Boulhic.
1994. Rapport ARN/ADN et évaluation de l'état nutritionel et de la croissance des larves de poissons marins: un essai de mise au point expérimentale chez la sole (*Solea solea*). ICES J. Mar. Sci. 51:181–190.

Blaxter, J. H. S.
1986. Development of sense organs and behaviour of teleost larvae with special reference to feeding and predator avoidance. Trans. Am. Fish. Soc. 115:98–114.

Canino, M. F., K. M. Bailey, and L. S. Incze.
1991. Temporal and geographic differences in feeding and nutritional condition of walleye pollock larvae *Theragra chalcogramma* in the Shelikof Strait, Gulf of Alaska. Mar. Ecol. Prog. Ser. 79:27–35.

Checkley, D. M.
1984. Relation of growth to ingestion for larvae of Atlantic herring *Clupea harengus* and other fish. Mar. Ecol. Prog. Ser. 18:215–224.

Ciechomski, J. D., R. P. Sanchez, G. Alsepeiti, and H. Regidor.
1986. Study of the growth in weight and condition factor of larval anchovy *Engraulis anchoita*. Rev. Invest. Desarr. Pesq. 5:183–193.

Clemmesen, C. M.
1988. A RNA and DNA fluorescence technique to evaluate the nutritional condition of individual marine fish larvae. Meeresforschung Rep. Mar. Res. 32:134–143.

Cone, R. S.
1989. The need to reconsider the use of condition indices in fishery science. Trans. Am. Fish. Soc.118: 510–514.

Drolet, R., L. Fortier, D. Ponton, and M. Gilbert.
1991. Production of fish larvae and their prey in subarctic southeastern Hudson Bay. Mar. Ecol. Prog. Ser. 77: 105–118.

Fahay, M. P.
1983. Guide to the early stages of marine fishes occurring in the western north Atlantic Ocean, Cape Hatteras to the southern Scotian Shelf. J. Northwest Atl. Fish. Sci. 4, 423 p.

Frank, K. T., and J. K. McRuer.
1989. Nutritional status of field-collected haddock (*Melanogrammus aeglefinus*) larvae from southwestern Nova Scotia: an assessment based on morphometric and vertical distribution data. Can. J. Fish. Aquat. Sci. 46 (suppl. 1):125–133.

Fraser, A. J.
1989. Triacylglycerol content as a condition index for fish, bivalve, and crustacean larvae. Can. J. Fish. Aquat. Sci. 46:1868–1873.

Fulton, T. W.
1911. The sovereignty of the sea. Edinburgh and London.

Giguère, L. A., B. Côté, and J. F. St. Pierre.
1989. Metabolic rates scale isometrically in larval fishes. Mar. Ecol. Prog. Ser. 50:13–19.

Grover, J. J., and B. L. Olla.
1986. Morphological evidence for starvation and prey size selection of sea-caught larval sablefish, *Anoplopoma fimbria*. Fish. Bull. 84:484–489.

Harris, R. K., T. Nishiyama, and A. J. Paul.
1986. Carbon, nitrogen, and caloric content of eggs, larvae, and juveniles of the walleye pollock, *Theragra chalcogramma*. J. Fish. Biol. 29:87–98.

Hay, D. E.
1984. Weight loss and change in condition factor during fixation of Pacific herring, *Clupea harengus pallasi*, eggs and larvae. J. Fish. Biol. 25:421–433.

Houde, E. D.
1987. Fish early life dynamics and recruitment variability. Am. Fish. Soc. Symp. 2:17–29.
1989. Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. Fish. Bull. 87:471–496.

Houde, E. D., and R. C. S. Schekter.
1980. Feeding by marine fish larvae: developmental and functional response. Environ. Biol. Fish. 5:315–334.

Johnston, T. A., and J. A. Mathias.
1993. Length reduction and dry weight loss in frozen and formalin-preserved larval walleye, *Stizostedion vitreum* (Mitchill). Aquacult. Fish. Manage. 24:365–371.

Kiørboe, T.
1989. Growth in fish larvae: are they particularly efficient? Rapp. P.-V. Reun. Cons. Int. Explor. Mer 191:383–389.

Laird, A. K., A. D. Barton, and S. A. Tyler.
1968. Growth and time: an interpretation of allometry. Growth 32:347–354.

Laurence, G. C.
1978. Length-weight relationships for seven species of northwest Atlantic fishes reared in the laboratory. Fish. Bull. 76:890–895.

Marguiles, D.
1993. Assessment of the nutritional condition of larval and early juvenile tuna and Spanish mackerel (Pisces: Scombridae) in the Panama Bight. Mar. Biol. 115: 317–330.

McGurk, M. D.
1987. Age and growth of Pacific herring larvae based on length frequency analysis and otolith ring number. Environ. Biol. Fish. 20:33–47.

McGurk, M. D., A. J. Paul, K. O. Coyle, D. A. Ziemann, and L. J. Haldorson.
1992. Relationships between prey concentration and growth, condition, and mortality of Pacific herring, *Clupea pallasi*, larvae in an Alaskan subarctic embayment. Can. J. Fish. Aquat. Sci. 50:163–180.

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.

Neilson, J. D., R. I. Perry, P. Valerio, and K. G. Waiwood.
1986. Condition of Atlantic cod *Gadus morhua* larvae after the transition to exogenous feeding: morphometrics, buoyancy and predator avoidance. Mar. Ecol. Prog. Ser. 32:229–235.

O'Connell, C. P.
1981. Percentage of starving northern anchovy, *Engraulis mordax*, larvae in the sea as estimated by histological methods. Fish. Bull. 78:475–489.

Olla, B. L., and M. W. Davis.
1992. Phototactic responses of unfed walleye pollock, *Theragra chalcogramma* larvae: comparisons with other measures of condition. Environ. Biol. Fish. 35: 105–108.

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.

Ricker, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191, 382 p.

Rose, K. A., and J. H. Cowan.
1993. Individual-based model of young-of-the-year striped bass population dynamics. I: Model description and baseline simulations. Trans. Am. Fish. Soc. 122:415–438.

SAS.
1988. SAS/STAT user's guide, release 6.03. SAS Institute, Cary, NC, 1,028 p.

Scott, W. B., and M. G. Scott.
1988. Atlantic fishes of Canada. Can. Bull. Fish. Aquat. Sci. 219, 731 p.

Setzler-Hamilton, E. M., D. A. Wright, F. D. Martin, C. V. Millsaps, and S. I. Whitlow.
1987. Analysis of nutritional condition and its use in predicting striped bass recruitment: field studies. Am. Fish. Soc. Symp. 2:115–128.

Sinclair, M., and M. J. Tremblay.
1985. Timing of spawning of Atlantic herring (*Clupea harengus harengus*) populations and the match-mismatch theory. Can. J. Fish. Aquat. Sci. 41:1055–1065.

Theilacker, G. H.
1978. Effect of starvation on the histological and morphological characteristics of jack mackerel, *Trachurus symmetricus*, larvae. Fish. Bull. 76:403–414.
1986. Starvation-induced mortality of young sea-caught jack mackerel, *Trachurus symmetricus*, determined with histological and morphological methods. Fish. Bull. 84:1–18.

Ware, D. M., and T. C. Lambert.
1985. Early life history of Atlantic mackerel (*Scomber scombrus*) in the southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. 42:577–592.

Werner, R. G., and J. H. S. Blaxter.
1980. Growth and survival of larval herring in relation to prey density. Can. J. Fish. Aquat. Sci. 37:1063–1069.

Westernhagen, H. von, and H. Rosenthal.
1981. On condition factor measurements in Pacific herring larvae. Helgolander Meeresunters. 34:257–262.

Zweifel, J. R., and R. Lasker.
1976. Prehatch and posthatch growth of fish: a general model. Fish. Bull. 74:609–621.