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AGE AND SIZE AT FIRST REPRODUCTION OF FISHES: PREDICTIVE MODELS BASED ONLY ON GROWTH TRAJECTORIES

JI X. HE[1] AND DONALD J. STEWART

State University of New York, College of Environmental Science and Forestry, 103 Illick Hall,
1 Forestry Drive, Syracuse, New York 13210, USA

Abstract. Age and size at first reproduction have broad implications for studying population and community ecology. From general functions of body growth we developed models for estimating both age and size at first reproduction when growth trajectories are the only reliable information. We evaluated our models using empirical data, including 85 species of marine and freshwater fishes, with 235 populations or sex groups. From the data set, we found the following two sets of relations. (1) There is a nonlinear negative relation between the von Bertalanffy growth coefficient (K) and the age at first reproduction (T_r). (2) The ratio of body length at first reproduction (L_r) to asymptotic body length (L_{inf}) may increase in two possible ways: one is increases in K and, consequently, decreases in L_{inf}; the other is increases in T_r and delay of the age at first reproduction. Our model integrates the above complex relations into a simple linear function. The set of life-history invariants summarized by E. Charnov and by A. L. Jensen is a special case of our model. The pattern of life-history diversification demonstrated by K. O. Winemiller and K. A. Rose is similar to our model implication and the results of our data analysis. Additional information about other complex traits such as mortality and fecundity are not needed in our models, so our models provide an independent basis for testing life-history theories and for applying those theories to modeling population dynamics.

Key words: age and size at first reproduction; body growth; fishes, marine and freshwater; life histories, patterns and theories; life-history parameters; population dynamics; sexual maturity; von Bertalanffy growth function.

INTRODUCTION

Changes in age or size at first reproduction are related, in complex ways, to variations in body growth (Alm 1959, Trippel 1995, Jennings et al. 1998). As the asymptotic size increases, body size at first reproduction may increase (Beverton 1992), decrease (Chen and Harvey 1994), or not change noticeably (Beverton 1987). With each of the above three cases, age at first reproduction may increase, decrease, or remain the same. Those complexities differ in qualitative ways, so it is a challenge to develop a general model for quantitative predictions.

There have been three theoretical approaches for studying age or size at first reproduction. In the first, a combination of body growth, sexual maturity, fecundity, and mortality is regarded as an optimum solution for a given organism to maximize its fitness in a given environment (Roff 1984, Stearns and Koella 1986, Kozlowski 1996). In this approach, every life-history trait seems to be critical for understanding and predicting age or size at first reproduction. Among those life-history traits, the most complex one is mortality. It may include natural mortality, predation mortality, and fishing mortality, and is often difficult to estimate accurately (Vetter 1988).

The second approach suggests that, for a given group of fishes, there may be a constant ratio between body length at first reproduction and the asymptotic body length (Beverton and Holt 1959). According to that approach, it should be a simple exercise to estimate body length at first reproduction directly from growth trajectories. Except for Beverton's (1992) own effort, however, the hypothesis rarely has been evaluated specifically against data. Recent studies have tried to find the linkage between Beverton and Holt's hypothesis and the above-mentioned evolutionary theory about life history (Charnov and Berrigan 1991, Charnov 1993, Jensen 1996). Jensen suggested that first reproduction should occur at the peak of yearly body-mass growth. There have been empirical supports for that suggestion (Holt 1962, Jensen 1985), but Jensen's model is not sufficiently flexible to address the full complexity mentioned above.

The third approach attempts to address the linkages between life histories and ecosystem processes. Following the landmark work of MacArthur and Wilson (1967), Winemiller and Rose (1992) suggested that there may be three major types of life histories in various environmental conditions: opportunistic, equilibrium, and periodic. There is no clear boundary among those three major types of life histories. To make quan-

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[1] E-mail: jhe@mailbox.syr.edu

titative predictions of both age and size at first reproduction, a promising approach may be to focus on growth trajectories that change according to both environmental conditions and taxonomic groups.

We suggest that the relation between growth trajectories and each of the major life-history traits (e.g., mortality, fecundity, age and size at first reproduction) should be quantified separately. Such an analytical practice will facilitate an ultimate synthesis of interactions among all life-history traits. In this paper we focus on estimation of both age and size at first reproduction when various growth trajectories are the only reliable information. The recent study of Shuter et al. (1998) was toward that same large goal. They have documented an empirical expression for only one species, lake trout (*Salvelinus namaycush*).

We propose that a general form of the linkage between body growth and first reproduction can be derivable from general growth functions, although parameter values may change according to environmental conditions or distinctive features of particular taxonomic groups. A recent study has suggested that there was no reason to use von Bertalanffy's (1957) growth function (VBGF) for studying the relation between body growth and sexual maturity, apparently because post-mature growth and immature-stage growth are different (Day and Taylor 1997). We maintain that the VBGF is still one of the best models for expressing a growth pattern over the life span of a fish. Like Iles's (1974) and Pauly's (1984) previous works, our study is based on observations that sexual maturity may not change the trajectory of body growth (see also Reznick 1983). However, whenever a growth trajectory changes significantly, the age or size at first reproduction will change.

EMPIRICAL DATA

We collected growth data from published studies, including 85 species with 235 populations or sex groups (see the Appendix). Each of the collected von Bertalanffy growth functions (VBGFs) was accompanied with data on age or size at first reproduction for a given population or sexual group. When data for size at age were not synthesized into a VBGF, or a proposed VBGF does not fit its accompanied empirical growth pattern, we estimated or re-estimated two VBGF parameters: growth coefficient (K) and asymptotic body length (L_{inf}). Our method for those estimations is the standard calculation from a Ford-Walford plot (Walford 1946, Ricker 1975). All data for our analysis treated the first annulus as age 1 in the VBGF. If a given author treated the first annulus as age 0 and provided data for size at age, we added 1 to reported ages and re-estimated the VBGF parameters (K and L_{inf}) using Ford-Walford plots. For the complete data set, the asymptotic body length (L_{inf}) ranged from 2.85 to 440 cm. The values for body length at first reproduction (L_r) were from 2.4 to 322 cm. The ages at first reproduction (T_r) ranged from 0.5 to 35 yr. Values for the VBGF growth coefficient (K) ranged from 0.026 to 6.11.

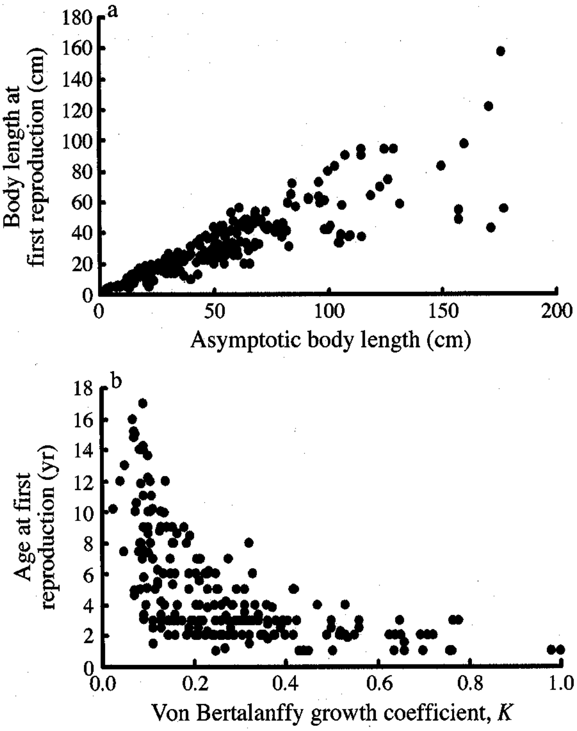

FIG. 1. Relations between age and body size at first reproduction and von Bertalanffy growth function parameters. (a) Mean body length at first reproduction (L_r) vs. the asymptotic body length (L_{inf}) in a von Bertalanffy growth function (VBGF). Seven data points with asymptotic size >200 cm are not shown. (b) Mean age at first reproduction (T_r) vs. the VBGF growth coefficient (K). Three data points with age at first reproduction >20 yr, and ten data points with K value >1.0 are not shown.

When data for size at age were available, we also calculated specific growth rates based on body length at successive ages ($G = [L_{t+1} - L_t]/L_t$). Then we calculated linear regressions for $\log_e(G)$ vs. $\log_e(L_t)$. The regression parameters were transformed to parameter values for the widely used power function of body-length growth (see next section). This subset of data included 60 populations or sex groups. Of the 60 regression lines, 57 were significant at $P < 0.05$, 45 were significant at $P < 0.005$ (Procedure REG, SAS Institute 1996).

We plotted data to explore relations between VBGF parameters and age or size at first reproduction. Our findings are as follows: (1) There was no general relation between body length at first reproduction (L_r) and asymptotic body length (L_{inf}) (Fig. 1a). The upper boundary of the scatter plot has a slope of about 0.8, while the bottom boundary has a slope of about 0.3. (2) The relation between age at first reproduction (T_r) and VBGF growth coefficient (K) appears to follow a negative power function, but variations in that relation do not allow for a useful predictive model (Fig. 1b).

TABLE 1. Results of a principal components analysis of growth and maturity parameters for 235 fish populations or sex groups (based on the correlation matrix shown here).

Correlation matrix

	L_{inf}	L_r	K	T_r	L_r/L_{inf}	$L_r/(KL_{\text{inf}})$	$L_r/(T_rL_{\text{inf}})$
L_{inf}	1.0000						
	0.0000						
L_r	0.9386	1.0000					
	0.0001	0.0000					
K	−0.2821	−0.2220	1.0000				
	0.0001	0.0006	0.0000				
T_r	0.3678	0.4126	−0.3099	1.0000			
	0.0001	0.0001	0.0001	0.0000			
L_r/L_{inf}	−0.0763	0.1879	0.3996	0.1909	1.0000		
	0.2441	0.0038	0.0001	0.0033	0.0000		
$L_r/(KL_{\text{inf}})$	0.4407	0.4246	−0.3564	0.9544	0.0330	1.0000	
	0.0001	0.0001	0.0001	0.0001	0.6153	0.0000	
$L_r/(T_rL_{\text{inf}})$	−0.3633	−0.3016	0.8042	−0.5060	0.2916	−0.5229	1.0000
	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0000

Eigenvectors

	PRIN1	PRIN2	PRIN3
K	0.759079	−0.126232	0.638643
T_r	−0.291796	0.810978	0.507119
L_r/L_{inf}	0.581940	0.571297	−0.578763
Proportion of variance explained	0.4752	0.3942	0.1306

Notes: T_r is the age when 50% of individuals attain first reproduction, K is the von Bertalanffy growth coefficient, L_r is the body length at which 50% of individuals attain first reproduction, and L_{inf} is the asymptotic body length when age is infinity.

THE DERIVATION OF GENERAL RELATIONS

A growth trajectory can be described either by the von Bertalanffy growth function (VBGF) (Ricker 1975),

$$dL/(Ldt) = K(L_{\text{inf}} - L)/L \tag{1}$$

or a simple power function,

$$dL/(Ldt) = xL^{-y} \tag{2}$$

where L is body length; L_{inf} is the asymptotic body length; K is von Bertalanffy growth coefficient; t is age (in years); x and y are regression parameters. With respect to body length rather than age, the first derivatives of Eqs. 1 and 2 are as Eqs. 3 and 4, respectively:

$$G' = -KL_{\text{inf}}L^{-2} \quad \text{or} \quad L^2 = -KL_{\text{inf}}/G' \tag{3}$$

$$G' = -xyL^{-(y+1)} \quad \text{or} \quad L^{(y+1)} = -xy/G' \tag{4}$$

where G is the specific growth rate $dL/(Ldt)$, and G' is the rate of change in G as body length (L) increases.

When 50% of the individuals attain first reproduction, G' can be expressed as G_r' and L can be expressed as L_r. If growth trajectories change, age and size at first reproduction also may change. To predict those potential changes, we note that G_r' has the dimension of $(L \cdot L^{-2} \cdot t^{-1})$, and $1/G_r'$ has the dimension of (tL). To understand that dimensional feature, we hypothesize that $1/G_r' = -(a + b\,T_r)L_r$, where T_r is the age when 50% of individuals attain their first reproduction, a is a parameter with the dimension of time (in years), and b is a nondimensional positive parameter. The negative sign is necessary because G decreases as body length increases and G_r' has negative values. If the above hypothesis is valid, from Eqs. 3 and 4, we should see two linear relations as follows:

$$L_r = (a_1 + b_1T_r)(KL_{\text{inf}}) \quad \text{or}$$

$$L_r/(KL_{\text{inf}}) = a_1 + b_1T_r \tag{5}$$

$$L_r^y = (xy)(a_2 + b_2T_r) \quad \text{or}$$

$$L_r^y/(xy) = a_2 + b_2T_r. \tag{6}$$

Those linear relations are not linear approximations of nonlinear growth models such as Eqs. 1 and 2. Our hypothesis and model derivation can be summarized into three key points as follows. (1) First reproduction must occur at a given point on a given growth trajectory. (2) At that point, there is a general linear linkage between age and size regardless of changes in growth pattern or growth parameters (Eqs. 5 or 6). (3) We can always find such a kind of linear function regardless of the form of a growth model.

THE BIOLOGICAL IMPLICATIONS

In this section, we focus on Eq. 5 to address the underlying biological implications. The left side of Eq. 5 has the structure of $L_r/(KL_{\text{inf}})$, where the ratio of L_r/L_{inf} has significant positive correlation with L_r (the body length at first reproduction), but the negative correlation between L_r/L_{inf} and L_{inf} (the asymptotic body length) is not significant (Table 1). For studying relations between body growth and sexual maturity, the ratio of L_r/L_{inf} may be more important than separate values of L_r and L_{inf} (Beverton 1992).

Another possible parameter combination is KL_{inf}.

Gallucci and Quinn (1979) have suggested that KL_{inf} represents the potential maximum yearly growth (see Eq. 1). Such a notation has been widely accepted but has not been evaluated fully. The growth coefficient (K) is from the slope of the Ford-Walford line, which is a plot of body length at age $t + 1$ vs. body length at age t (i.e., $K = -\log_e$ slope; Walford 1946). The asymptotic body length (L_{inf}) is a combination of the intercept and the slope (i.e., $L_{\text{inf}} =$ intercept/[1 − slope]; Ricker 1975). The combined parameter (KL_{inf}) uses the information of K twice. Because the first year of fish life and their life after the first year are different, the maximum yearly growth (KL_{inf}) is over-aggregated and confounds the effects of two life stages. In Eq. 5, we emphasize the ratio of L_r/L_{inf} rather than KL_{inf}.

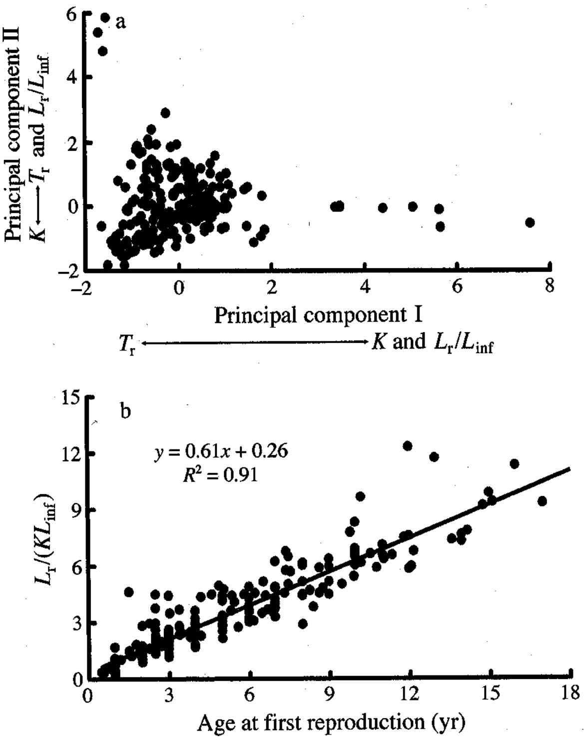

FIG. 2. A relation between body growth and first reproduction for 235 fish populations or sex groups. a) Distribution of the fish populations or sex groups relative to axes defined by the first two principal components, PC (Table 1). K is the von Bertalanffy growth coefficient, T_r is the age at which 50% of individuals attain first reproduction, L_r is the body length at which 50% of individuals attain first reproduction, and L_{inf} is the asymptotic body length when age is infinity. For the x-axis, a large T_r leads to negative values of PC I; for the y-axis, a large K leads to negative values of PC II. b) A linear relation between $L_r/(KL_{\text{inf}})$ and T_r for those populations or sex groups. Parameters are defined in Eqs. 1 and 5. Three data points with age at first reproduction >20 yr were included in the regression but not shown on the graph. Regressions were done using procedure REG (SAS Institute 1996).

There are significant positive correlations between K and L_r/L_{inf} and between T_r and L_r/L_{inf}; the correlation coefficients are 0.40 and 0.19, respectively (Table 1). There is also a significant negative correlation between K and T_r and that correlation coefficient is −0.31 (Table 1). The interesting point is that both K and T_r are related positively to L_r/L_{inf}, but K and T_r are related negatively to each other. Those intriguing relations suggest a necessary integration. Thus, we find that the correlation coefficient between T_r and $L_r/(KL_{\text{inf}})$ is 0.95. Such a high positive correlation supports the structure of Eq. 5, which is $L_r/(KL_{\text{inf}}) = a_1 + b_1T_r$. Similarly, the correlation coefficient between K and $L_r/(T_rL_{\text{inf}})$ is 0.82, slightly less than 0.95. The difference between the last two correlation coefficients can also be explained by Eq. 5. T_r is a function of $L_r/(KL_{\text{inf}})$, but we cannot solve for K alone as a function of $L_r/(T_rL_{\text{inf}})$.

The simple linear relation of Eq. 5 has the following implications. For a given set of constants a_1 and b_1, a fish may increase the ratio L_r/L_{inf} in two possible ways. One is to have a large K and, consequently, a small asymptotic body size (Table 1); the other is to have a large T_r and delay its first reproduction. Because K and T_r are negatively related to each other (Table 1, Fig. 1b), the two possible ways actually represent different strategies. Such a divergence may relate to classical r-/K-selection life-history theory (MacArthur and Wilson 1967), but the difference and linkage between the two extremes have never been addressed clearly based on individual growth. The negative relation between K and T_r does not mean that rapid growth leads to early age at first reproduction. A large K means to approach asymptotic size rapidly (Eq. 1), but there is a negative relation between K and L_{inf} (Table 1). A large K does not necessarily mean to grow rapidly in the sense of increases in body length per unit time.

A constant ratio of L_r/L_{inf} is a possible case under the relation of Eq. 5. Following Beverton and Holt's (1959) initial effort, Charnov (1993) and Jensen (1996) have summarized three life-history constants: $MT_r = C_1$, $M/K = C_2$, and $L_r/L_{\text{inf}} = C_3$, where M is natural mortality. Such a set of constants represents a special case of Eq. 5, where a_1 equals zero and the constants of C_1 and C_2 provide a new constant: $KT_r = C_1/C_2 = C_3/b_1 = C_4$.

To illustrate the biological implications of Eq. 5 with the above-analyzed correlations, we conduct a principle components analysis (PCA) using variables K, T_r and the ratio of L_r/L_{inf} (Table 1). The first principal component represented the trend that increases in the ratio L_r/L_{inf} is related to increases in K. The second principal component represented the other trend that increases in L_r/L_{inf} is related to increases in T_r. Those two principal components explained 87% of total variation. The third principal component represented contradictions between the above two principle components, because there are nonlinear negative relations between K and T_r (Table 1, Fig. 1b). Plotting the second principal component vs. the first one reveals a triangle-shaped distribution (Fig. 2a). It clearly indicates that a fish may increase the ratio L_r/L_{inf} in two possible ways; one is to have a large K and another is to have a large T_r. Even if we ignore the samples with extreme K or T_r values, the triangle-shaped distribution still exists.

The purpose of our PCA is to illustrate biological implications of Eq. 5 with the overall distribution pattern of fishes. Detailed data for those 85 species with 235 observations are given in the Appendix. In the triangle-shaped distribution, the first or the lowest end point is characterized with the lowest values of L_r/L_{inf}. Typical examples in our data set are carps and other minnows. The second or upper-left end point is characterized with the largest values of L_r/L_{inf} and late maturity (large T_r) . A typical example is spiny dogfish (*Squalus acanthias*). The third or right end point is characterized with the highest values of L_r/L_{inf} and large K. Typical examples are fishes from temporary waters in southwestern Australia.

Along the left side between the first two end points, fishes are typical marine sit–wait predators such as righteye flounders, cods, and goosefishes. Along the bottom side between the first and third end points, fishes are from seasonal environments such as temporary streams, temporary pools, mountain streams, estuaries, and coastal ocean. In the middle of the triangular distribution, most fishes are from freshwater lakes and non-seasonal streams. Relatively small-sized fishes in the middle group are mostly close to the bottom side of the distribution. Relatively large-sized fishes in the middle group are mostly close to the left side and upper-right side of the distribution. The inclination of the inverted-triangle-shaped distribution indicates that there are not clear boundaries among the above-mentioned three endpoints or three sides. A fish may increase both K and T_r and increase the ratio of L_r/L_{inf}. Consequently, the PCA does not provide a basis for grouping fishes discretely. The overall distribution pattern, however, is meaningful and illustrates clearly the biological implications of Eq. 5.

MODEL VERIFICATION

According to Eq. 5, we plotted $L_r/(KL_{inf})$ vs. T_r and found a clear linear pattern (Fig. 2b). With 235 observations, R^2 for that relation was 0.91. If we exclude three data points with the age at first reproduction >20 yr, R^2 still would be 0.86. Variations in the plot may include three major components. The first is related to potential differences in slope and intercept among species or taxon groups. The second is related to environmental differences among ecosystems. The third is related to a variety of procedures for ageing fish, for determining age and size at first reproduction, and for estimating von Bertalanffy growth function (VBGF) parameters.

To improve the accuracy of predictions, it may be useful to focus on a given species or a group of closely related species. From the data set summarized in the Appendix, we were able to provide nine examples (Fig. 3), including: (1) sharks, (2) sillagos, (3) seven populations of marine Perciformes, (4) sculpins and olive rockfishes, (5) cods, grenadier, and goosefish, (6) American plaice (*Hippoglossoides platessoides*), (7) carps and other minnows, (8) lake trout (*Salvelinus namaycush*), and (9) walleye (*Stizostedion vitreum*) and yellow perch (*Perca flavescens*). When males and females had different growth patterns represented by different values for VBGF parameters, we treated males and females as discrete observations within a group (see the Appendix). When males and females shared a single VBGF, we only used maturity data for females.

For only two of the nine groups, sharks and sculpins, the asymptotic body length (L_{inf}) alone might be a good predictor of the size at first reproduction, and the VBGF growth coefficient (K) alone might be a good predictor of the age at first reproduction (regressions are not shown). In the previous section, we indicated that a set of life-history constants summarized by Charnov (1993) and Jensen (1996) is a special case of our Eq. 5. Sharks and sculpins studied here represent empirical examples for that special case. Those two groups met two necessary criteria: (1) the intercepts of their regression lines equal zero, and (2) the product of K and T_r appears to be a constant in those two groups. In each of the two groups, data points that apparently deviate from the regression lines are those whose products of K and T_r deviate noticeably from group mean and group mode.

In practice, when either age or size at first reproduction is known, it is a simple exercise to calculate the other using the commonly used form of the VBGF:

$$L_t = L_{inf}(1 - e^{-K(t - t_0)}) \qquad (7)$$

where t is age and t_0 is a coefficient with the dimension of time (in years). With Eq. 5 for a group of fishes and Eq. 7 for a changed or new growth trajectory, we can estimate both T_r and L_r when neither of them is known. To make the procedure clear, we rearrange Eq. 5 and define:

$$\Delta = L_t/(KL_{inf}) - (a + bt) \qquad (8)$$

where all parameters are from Eqs. 5 or 7. Setting Δ equal to 0, we can solve L_t and t with Eqs. 7 and 8. There may be two sets of solutions. One of them will often have a negative t value or a t value far less than possible values for T_r. That set of solutions is not biologically meaningful and can be identified easily. The second set of solutions provides values for L_r and T_r. If data for size at age have not been synthesized into a complete VBGF like Eq. 7, a Ford-Walford plot can be used to estimate K and L_{inf}. Then, plotting Δ vs. age (t) can provide similar results.

In Fig. 3, R^2 values have a range of 0.82–0.98. When the R^2 value is >0.9, most predictions are very close to observed values. If required data are obtained using standard or consistent methods, R^2 values around 0.95 or even higher are attainable. From that perspective, Eq. 5 may provide a basis for future long-term com-

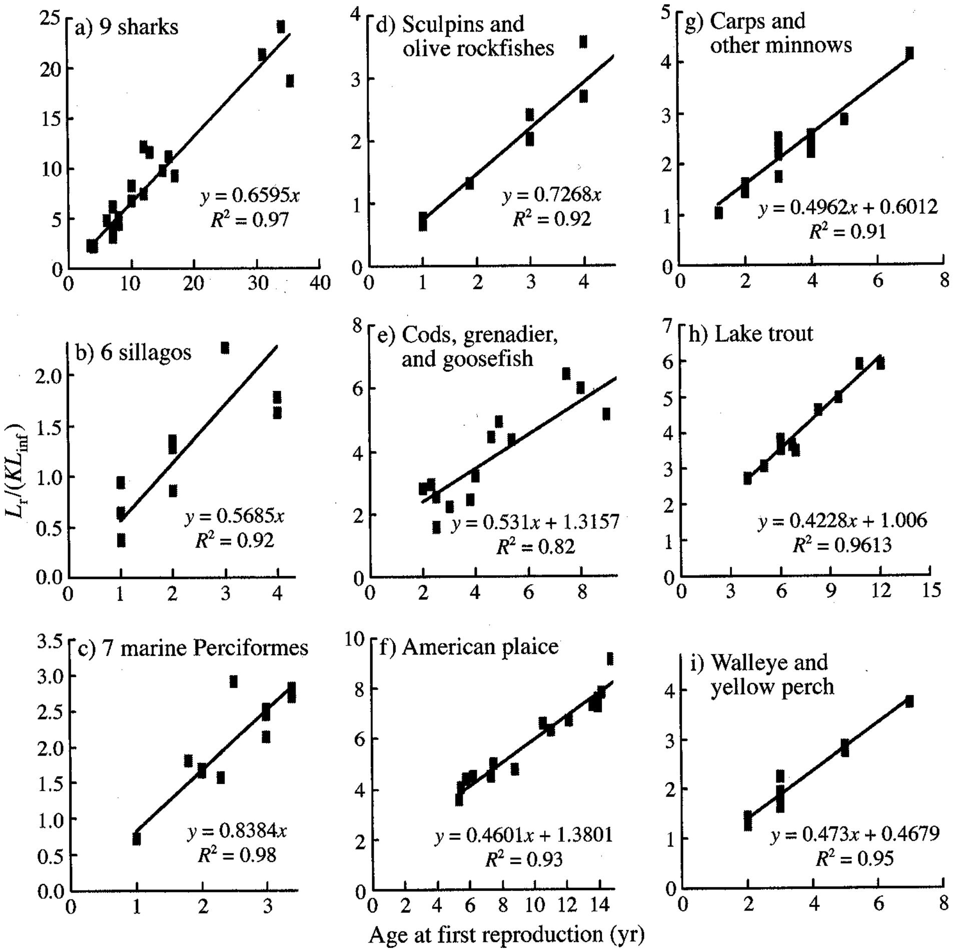

FIG. 3. $L_r/(KL_{inf})$ vs. T_r for nine groups of fishes (see Fig. 2 for symbol definitions). Detailed data for those fishes are presented in the Appendix. Regressions were done using the REG procedure (SAS Institute 1996). The regression line for sharks is not significantly different from those for sillagos, marine Perciformes, or sculpins (based on analysis of covariance). The regression line for sillagos, however, is significantly different from those for marine Perciformes and sculpins. Regression lines for the two groups of marine sit–wait predators (i.e., groups e and f) are not significantly different from each other, nor are regression lines for carps, lake trout, and walleye/yellow perch significantly different from each other.

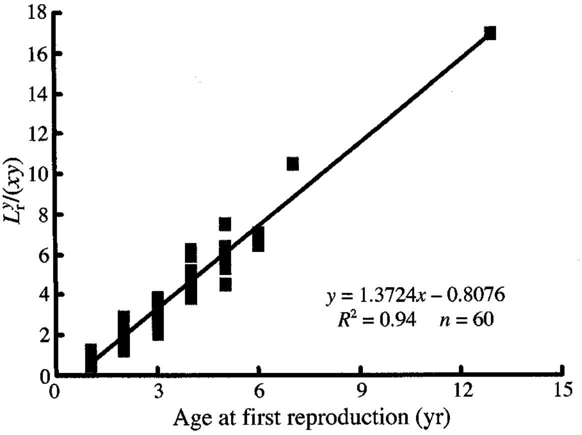

FIG. 4. $L_r^y/(xy)$ as a function of T_r (age at first reproduction) for a subset of data with 60 observations. Parameters are defined in Eqs. 2 and 6. Regressions were done using the REG procedure (SAS Institute 1996).

parative studies and for applications to modeling fish population dynamics.

Plotting $L_r^y/(xy)$ vs. T_r reveals another linear relation (Fig. 4), which is suggested by Eq. 6. The underlying biological principle is the same as Eq. 5. The age and size at first reproduction are related to the pattern that length-specific growth rate decreases as body length increases. The linear linkage between age and size at first reproduction does not depend on a particular growth model.

DISCUSSION

There have been many studies that tried to explain age or size at first reproduction based on growth of early life stages (Trippel and Harvey 1989, Henderson et al. 1996, Hutchings 1997). Our models suggest that the pattern of specific growth rates ($dL/(Ldt)$) vs. body size is most important, while the absolute value of a growth rate (dL/dt) or a specific growth rate ($dL/(Ldt)$) in a particular growth period is relatively less important. A similar conclusion has been implied by experimental studies (e.g., Rijnsdorp 1993). For synthesizing this type of studies, Eq. 6 based on a simple power function may be more convenient than Eq. 5 based on a von Bertalanffy growth function (VBGF).

There are four major life-history traits: growth trajectory, size-dependent fecundity, mortality, and age or size at first reproduction. The first two components have been formulated based on solid empirical observations (Ricker 1975, Bagenal 1967), while the formulations for the last two components remained ambiguous. When mortality was assumed to be a constant for a given fish population, the age or size at first reproduction could be estimated (Roff 1984, Stearns and Koella 1986, Koslowski 1996, Shuter et al. 1998). Some studies represented mortality as a simple negative power function of body size, but that function may be realistic only for early life stages. Our model estimates both age and size at first reproduction based only on growth trajectories. Such an independent relation provides a new basis for testing and applying life-history theory.

From a different approach, our study provided results that were similar to those of Winemiller and Rose (1992). One side of our triangle (Fig. 2a) corresponds to fishes living in temporary environments with short growth period and rapid growth (see also Conover 1990). That side may correspond to an end point of Winemiller and Rose's triangle ("opportunistic strategy"). Another side of our triangle is efficient lifestyle in open ocean or deep waters and may correspond with Winemiller and Rose's second end point of "equilibrium strategy." Along the upper-right side and in the middle of our triangle, fishes are between the above two relatively extreme "strategies." Winemiller and Rose (1992) defined their third end point as "periodic strategy" and attributed most fishes to that group. Their model included life-history traits such as mortality and fecundity. Our results were consistent with theirs, but our analysis did not include fecundity and mortality. The two studies provided similar results because, probably, mortality and fecundity are functions of body size and our analysis was based on trajectories of body growth.

When a growth trajectory changes, there will be two dimensions for potential changes in sexual maturity. One is the size at first reproduction and the other is age at first reproduction. Some empirical studies demonstrate a constant size at first reproduction, while others demonstrate a constant age at first reproduction. Both cases were valid in certain circumstances (Bernardo 1993). Beverton and Holt's hypothesis emphasized only one dimension (Beverton and Holt 1959, Beverton 1992). Our model simply combined two dimensions of potential changes. Such a general relation between fish body growth and the age or size at first reproduction should be applicable broadly to studies on population dynamics. In particular, it provides a basis for dynamically modeling both age and size at first reproduction whenever a change in a growth trajectory is known or predicted. We expect that similar relations might be found for other animal groups.

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APPENDIX

A table presenting data for 85 species of marine and freshwater fishes with 235 populations or sexual groups that we used to develop our model for the relations between growth and maturity is available in ESA's Electronic Data Archive: *Ecological Archives* E082-006.