Abstract.–We studied phenotypic variation in larval and juvenile growth and development, using laboratory-reared winter flounder, *Pleuronectes americanus*. Larvae were reared individually to metamorphosis and beyond and were measured at weekly intervals. Growth in length was rapid until 30 d but slowed thereafter until metamorphosis. Standard length peaked and often declined as metamorphosis approached, and notochord length decreased during flexion. Length at 30 d (an index of larval growth rate) was inversely related to age at metamorphosis, confirming previous assertions that larvae that grow rapidly also develop most rapidly. The relation between growth rate and larval-period duration, however, was not straightforward. The time from the day of peak larval length until metamorphosis (7–35 d) appeared to be inversely related to larval growth rate. Juvenile growth rates during the first 3 weeks following metamorphosis were unrelated to length at 30 d. Additional juveniles, reared in groups as larvae and tracked as individuals following metamorphosis, showed no change in growth rates during the first 4 weeks of the juvenile period in relation to increasing age at metamorphosis or larval growth rates. These results are consistent with earlier findings that size at age does not diverge continually throughout the larval and juvenile periods. Compensatory juvenile growth among fish that grew slowly as larvae was observed but not to the same extent as previously reported. We emphasize the utility of the individual-based approach for identifying patterns of phenotypic variability in growth and development during the early life stages in fishes.

Individual variation in growth and development during the early life stages of winter flounder, *Pleuronectes americanus*

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Mechanisms controlling survival and recruitment of fishes operate at the level of the individual (Crowder et al., 1992). Further, small initial differences among individual larvae and juveniles within fish populations may have disproportionate effects on the probability of their survival (Crowder et al., 1992; Rice et al., 1993). Consequently, research programs in fisheries have begun to focus on phenotypic variability within cohorts in an effort to identify particular traits that may be unique to the small minority of survivors (Fritz et al., 1990; Taggart and Frank, 1990). If survivors are not random subsets of the original cohort, interpretations of recruitment processes based upon analyses of population averages are likely to be misleading (Pepin and Miller, 1993). Consequently, individual-based approaches are increasingly favored (Crowder et al., 1992). However, there have been few quantitative measurements of either individual variation in early life history traits of fishes or in their survival consequences (but see Rosenberg and Haugen, 1982; Rice et al., 1987; Chambers et al., 1989; Chambers and Leggett, 1992; D'Amours, 1992; Bertram and Leggett, 1994; Lochmann et al., 1995; Miller et al., 1995). In theory, longitudinal data can be obtained from sequential

measurements of individuals or from back calculations of size at age from otolith microstructure.

Variation in larval growth rates is widely believed to be a central feature in year-class formation in fishes (Leggett and Deblois, 1994). Traditionally, growth parameters are estimated from a restricted number of samples of the population. Each sample includes a range of fish lengths and ages. Importantly, each fish provides only a single estimate of length at age. Such data are termed cross-sectioned. The calculated growth parameters represent composite pictures and cannot reveal variability among the growth patterns of individuals simply because they aggregate data at a level higher than the individual. Chambers and Miller (1995) have discussed the effects of the level of aggregation of data on the inferences that can be made. In addition, composite growth curves

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are subject to several potential biases (Chambers and Miller, 1995). For example, composite curves are not accurate in cases where mortality of individual age classes are biased towards small or large individuals (Litvak and Leggett, 1992; Pepin et al., 1992). Hence, if the survival consequences of variability in growth rates are to be evaluated adequately, individual phenotypic variability in growth must be quantified (Lynch and Arnold, 1988; Chambers, 1993). This requires that longitudinal data based upon repeated measures of individuals be collected. These problems are illustrated in the following example. Consider a cohort of 220 larvae with an average size of 5.5 mm and a uniform size distribution of 20 larvae in each of ten 0.1-mm size classes from 5 to 6 mm. In a hypothetical 7-d interval, no larval growth occurs, but a gape-limited predator consumes all larvae less than 5.5 mm, leaving 120 larvae with an average size of 5.75 mm. If only cross-sectional data were available, the larval growth rate was estimated as 0.11 mm/d for the 7-d interval. However, if longitudinal data were available (i.e. measurements of survivors at the beginning and end of the week), it would be clear that no growth had occurred.

Bertram et al. (1993) have argued that the dynamics of larval and juvenile growth rates should be examined in unison, rather than separately. Using laboratory-reared winter flounder, *Pleuronectes americanus*, they have shown that size-at-age trajectories do not diverge continually during the larval and juvenile periods. In fact, juvenile size-at-age trajectories converge because fish that grew slowly as larvae compensated for their slow growth by growing rapidly as juveniles. However, Bertram et al. (1993) assumed that larval growth was linear; therefore juvenile fish used in their experiments were pooled into groups. This approach precluded the study of individual phenotypic variability. The objectives of the present study were 1) to provide estimates of the individual variability in growth rate in fish during early life stages because it is upon this individual variability that phenotypic selection acts and 2) to evaluate the validity of previous estimates of larval growth rate. Also, we explore how individual variation in larval growth affects growth during the subsequent juvenile period.

Methods

Rearing protocol

The research in this study was conducted at the Huntsman Marine Science Centre, St. Andrews, New Brunswick, during summer 1991. In May, adult win-

ter flounder were collected from Passamaquoddy Bay with a bottom trawl and held at ambient seawater temperature (7–8°C). When ripe, eggs from individual females were combined with sperm pooled from three males to create half-sibling families. Families were maintained separately throughout the study. Fertilized eggs were placed in a slurry of diatomateous earth for 12 h following fertilization to prevent clumping. Incubation temperature was 7 (±0.5)°C (mean ± SD). At approximately 24-h after fertilization, the eggs were immersed in solutions of penicillin (0.0158 g/L) and streptomycin (0.02 g/L) for 24 h. Filtered, UV-sterilized seawater was replaced every 2–3 d until hatching commenced at approximately 14 d after fertilization.

Upon hatching, 118 larvae from two families (families 1 and 2) were individually stocked into black cylindrical 0.4-L containers (15 cm diameter × 6.5 cm high) with clear plexiglass bottoms. Water temperature was maintained at 10 (±0.5)°C in a temperature controlled room with a 16:8 day:night photoperiod. At weekly intervals, 75% of the water was removed from each container and replaced with UV-sterilized filtered seawater. Additional "reserve" larvae from the same families were reared in groups under identical conditions in 18-L cylindrical, black plastic containers. Individual larvae that died within the first 3 weeks were replaced with siblings from the appropriate reserve group.

Larvae were also reared in groups in 38-L aquaria covered externally with black plastic. Five aquaria were each stocked with four-hundred 1-d-old larvae drawn from another half-sibling family (family 3). Temperatures in the aquaria were maintained at 10 (±0.5)°C. At weekly intervals, 3 liters of water were removed from each aquarium and replaced with UV-sterilized filtered seawater. Dead larvae were siphoned regularly from the tank.

All larvae were fed *Brachionus* sp. at 2 /(mL·d) until the end of week 7. Rotifers were cultured by using *Isochrysis* sp. and *Chaetoceros* sp. Twenty-four hours prior to being fed to larvae, rotifers were provided with Microfeast artificial plankton (Provesta Corporation) to enhance their nutritional quality. From the end of week 5 onwards, larvae were also offered *Artemia* nauplii (0.25/[mL·d]). Nauplii were enriched with Microfeast 24 h prior to use.

At metamorphosis, larvae from family 3, which had been reared in groups, were individually stocked into 0.4-L rearing containers (see above) to examine juvenile growth. To standardize the developmental stage of individuals used in this study, we used only fish whose left eye had just crossed the midline on its migration to the right side of the body (stage H of Seikai et al., 1986). All fish that metamorphosed on

the same day were treated as a discrete cohort. The creation of these cohorts was repeated at intervals of 3–8 d until all fish had metamorphosed. Table 1 summarizes the rearing conditions for the 3 families used in the study.

At weekly intervals, length data on individual larvae were recorded by using a dissecting microscope linked to a video system at 6× magnification. Larvae were filmed without being removed from their rearing containers. Fish were not anesthetized at any time. Larval movement was restricted by confining larvae within a 6-cm diameter plexiglass ring placed within the rearing container. Length data were collected only when fish were in the horizontal plane. To account for variation in the position of the larvae in the vertical plane, we constructed a small set of "stairs" with a plastic ruler segment attached at each level. After filming each larva, we immediately calibrated the image against the ruler segment that was in focus. For fish that were close to, or past, metamorphosis, the process of filming was simplified because these fish generally remained motionless on the bottom of the container. Following metamorphosis, individual juveniles were filmed weekly for up to 4 weeks, when rearing was terminated. Standard lengths of all fish were obtained by using an image analysis system (Optimus vers. 3.11, Bioscan Corporation, Seattle, WA). We used the image analysis system to "capture" two images for each fish for estimating standard length at age and used the largest value in all analyses.

Analysis

We constructed individual growth trajectories for larvae that survived until metamorphosis, using spline functions fitted to repeated measures of size at age. Individual larval growth trajectories were based on between 3 and 9 weekly observations per larva. Individual growth trajectories were examined quantitatively by using four indexes: 1) larval size at 30 ±1 d (roughly midway through the development period, an index of larval growth rate [e.g. Travis, 1981]); 2) average larval growth rates, defined as the difference between the length at metamorphosis and the mean length at hatching for the family divided by the time elapsed between the two events; 3) latency period, defined as the time between the age at which maximum larval length was attained and the time of metamorphosis; and 4) larval-period duration, defined as the age at metamorphosis. Correlation analyses (Pearson's correlation coefficient) were used to examine the relationships among pairs of the above variables for individual larvae. Variables were

Table 1

Summary of rearing conditions and filming schedules for the 3 families used in the study.

	Family 1	Family 2	Family 3
Larval container size (L)	0.4	0.4	38
Number of larvae/container	1	1	400
Weekly measures of larvae	Yes	Yes	No
Juvenile container size (L)	0.4	0.4	0.4
Number of juveniles/container	1	1	1
Weekly measures of juveniles	Yes	Yes	Yes

tested for normality with normal probability plots (Wilkinson, 1990). When heteroscedasticity was detected with techniques outlined in Zar (1984), variables were log-transformed. For comparison with the individual growth trajectories, we also constructed a composite size-at-age plot by using data for all larvae used in the study.

We checked for size-dependent mortality during the first part of the larval period by comparing the length of those fish that lived until their next weekly measurement with those that died during that time, using t-tests for independent samples. Size-dependent analyses were conducted for larvae after hatching (1–2 d); week 1 (8–9 d); week 2 (15–16 d); and week 3 (22–23 d). Group-reared larvae that were used as replacements for fish that died during the first 3 weeks were not included in the analysis.

Individual juvenile growth rates were estimated from the slope of a least squares fitted to weekly measures of individual size at age from metamorphosis to week 3 of the juvenile period. Thus, growth estimates were based upon up to 4 size-at-age measurements. Growth parameters were not calculated when less than 3 size-at-age measurements were available. We examined the correlations between juvenile growth rates and both age at metamorphosis and length at 30 d. Juvenile growth rates were also examined in relation to Bertram et al.'s (1993) measure of average larval growth rate estimated as the difference between the mean length at metamorphosis for fish that metamorphosed on the same day and the mean size at hatching for the family, divided by the number of days between the 2 events.

For comparison with the work of Bertram et al. (1993), we restricted the analysis of juvenile growth to weeks 1 through 4 for fish that had been reared together as larvae. The relation between juvenile growth rates and age at metamorphosis was examined by using regression and correlation analyses. Similar analyses were performed to examine the re-

lationship between juvenile growth rates and average larval growth rate. For fish that had metamorphosed early, measurements of size at age were available until week 7 of the juvenile period. For these individuals we compared growth rates during weeks 1–4 with those during weeks 5–7, using a paired t-test.

Results

Individually reared larvae

Thirty-two individually reared fish, 31 of which were from a single family (family 1), survived until metamorphosis. For 5 of these fish, weekly measures were available from hatching to metamorphosis. For the remaining 27 larvae weekly measures began at day 22. We could not detect size-dependent mortality in the weeks following: hatching (t=1.83, df=116), week 1 (t=0.18, df=87), week 2 (t=1.4, df=32), or week 3 (t=0.21, df=11). Data from the 32 fish provided estimates of individual larval growth trajectories (Fig. 1A). The trajectories exhibited considerable phenotypic variation in size at age, maximum larval size, size at metamorphosis, latency period, and the duration of the larval period (Fig. 1A). To demonstrate the loss of information introduced by basing growth parameters on cross-sectional data, we treated the original individual-level longitudinal data as cross-sectional. When individual larval sizes were depicted in this composite fashion (Fig. 1B), mean larval length at age increased rapidly from day 1 until day 30 and then leveled off. Important information, however, can be obtained only from cross-sectional data. For example, coefficients of variation (CV) for length at age increased from 0.07 on day 1 to 0.12 on day 30 but declined subsequently and leveled off at approximately 0.08.

The largest larvae at 30 d were also largest at 22 d (r=0.66, n=18, P=0.03) and at 36 d (r=0.5, n=18, P=0.034), indicating positive covariance in size at age for individually reared larvae that were alive at each of those ages. There was a significant positive relationship between larval length at 30 d and maximum larval size (r=0.6, n=27, P=0.001). However, larval length at 30 d and age at metamorphosis were negatively correlated (n=27, r=–0.589, P=0.001; Fig. 2A). The negative correlation coefficient between size at 30 d and age at metamorphosis was larger than correlation coefficients calculated for all other age classes. Average larval growth rate and length at 30 d were positively correlated (n=25, r=0.49, P=0.01; Fig. 2B).

The age of maximum larval size (log-transformed) was negatively correlated to length at 30 d (r=–0.71, n=27, P<0.001; Fig. 3A). The latency period (range:7–
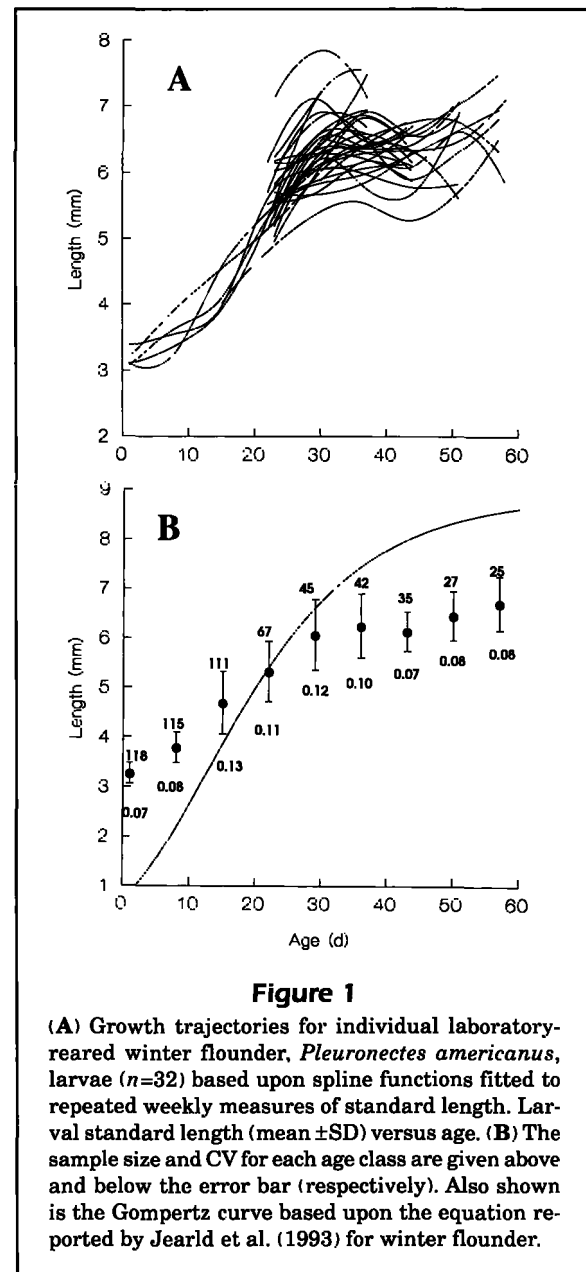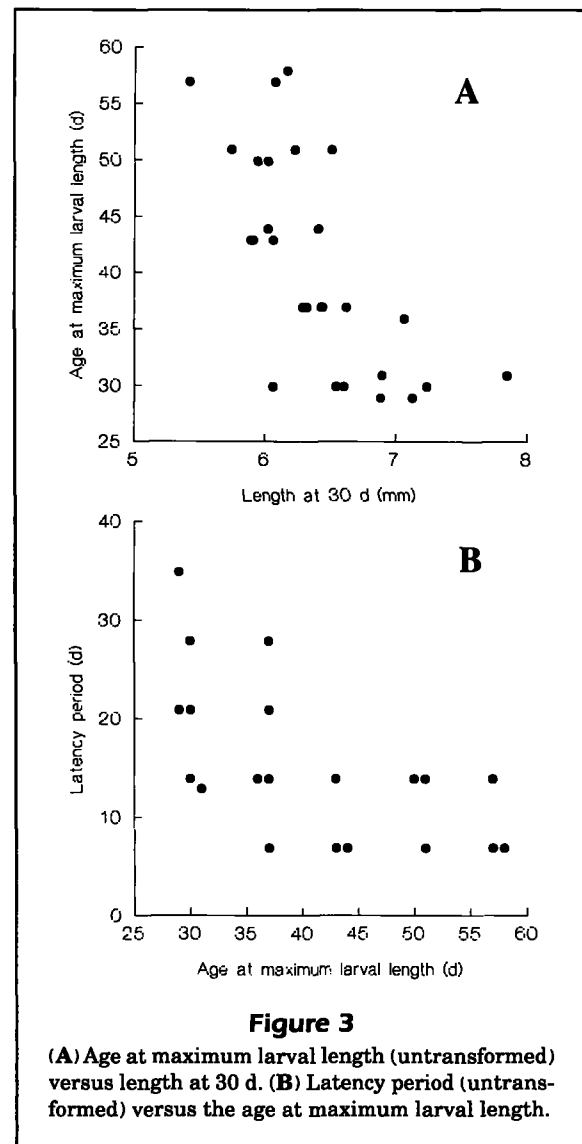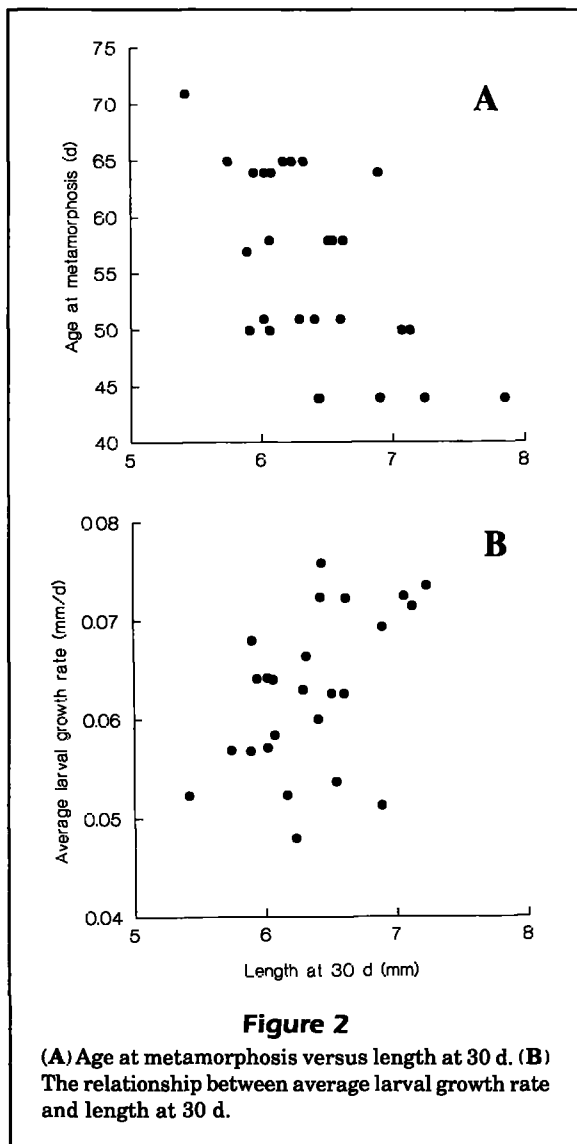

Figure 1

(A) Growth trajectories for individual laboratory-reared winter flounder, *Pleuronectes americanus*, larvae (n=32) based upon spline functions fitted to repeated weekly measures of standard length. Larval standard length (mean ±SD) versus age. (B) The sample size and CV for each age class are given above and below the error bar (respectively). Also shown is the Gompertz curve based upon the equation reported by Jearld et al. (1993) for winter flounder.

35 d; 14.4 ±7.5 d, n=31)(log-transformed) was inversely related to age of maximum larval size (r= –0.58, n=31, P=0.001; Fig. 3B). In contrast, the latency period showed a positive trend with increasing length at 30 d, but the relationship was not significant (r=0.2, n=26, P=0.38). Age at metamorphosis ranged from 44 d to 71 d (55.2 ±7.9 d). Length at metamorphosis ranged from 6.1 mm to 7.5 mm (6.6 ±0.3 mm). Length and age at metamorphosis were positively correlated for individually reared larvae (r=0.46, n=29, P=0.012).

Among individually reared larvae, subsequent juvenile growth rate during the first 3 weeks of the juvenile stage bore no relation to age at metamor-
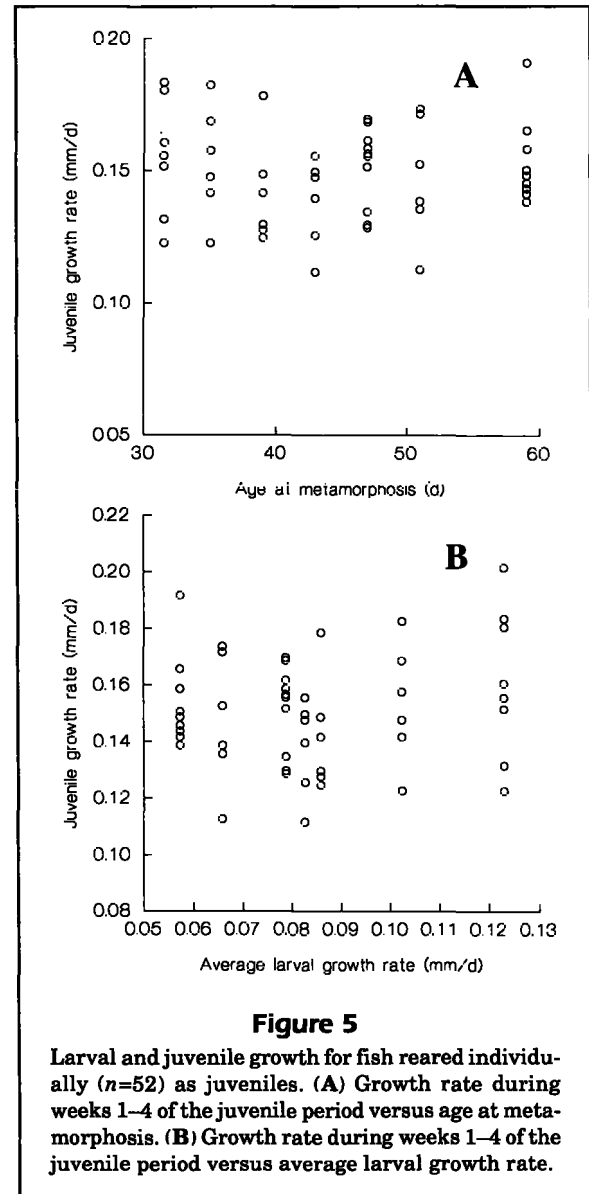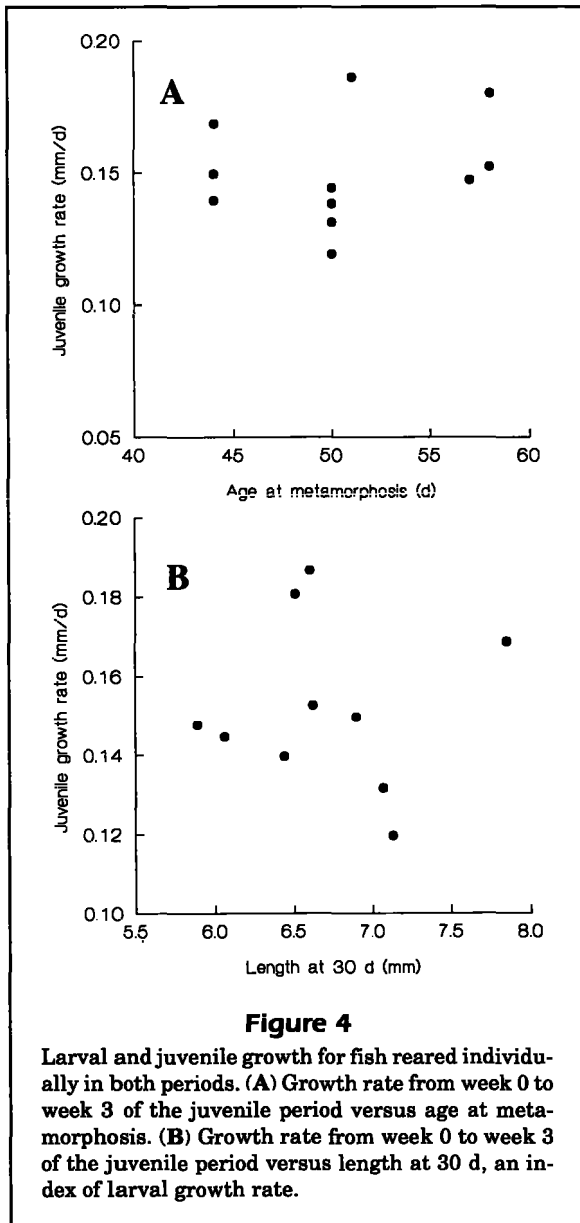
Figure 2

(A) Age at metamorphosis versus length at 30 d. (B) The relationship between average larval growth rate and length at 30 d.

Figure 3

(A) Age at maximum larval length (untransformed) versus length at 30 d. (B) Latency period (untransformed) versus the age at maximum larval length.

phosis ($r=0.22$, $n=11$, $P=0.52$; Fig. 4A). Similarly, juvenile growth rate showed no relationship to length at 30 d ($r=-0.001$, $n=10$, $P=0.99$, Fig. 4B). For comparative purposes, juvenile growth rate was also regressed against the measure of larval growth rate used by Bertram et al. (1993). The slope of the relationship, -0.18 mm/d, although not significantly different from 0, was identical to that reported by Bertram et al. (1993).

Group-reared larvae

Length at metamorphosis was independent of age at metamorphosis among members of family 3 ($r=-0.09$, $n=205$, $P=0.23$) reared in groups as larvae and individually as juveniles. (Note that 175 of these larvae came from a single rearing aquarium and that the

remainder were also from a single tank.) Length at metamorphosis ranged from 5.6 mm to 7.36 mm (6.6 ±0.3 mm). Age at metamorphosis ranged from 32 d to 59 d (42.6 [(±6.7] d). Individual growth rates during weeks 1–4 of the juvenile period were unrelated to age at metamorphosis ($r=0.055$, $n=52$, $P=0.71$; Fig. 5A). Juvenile growth rates were unrelated to larval growth rates ($r=0.14$, $n=52$, $P=0.322$; Fig 5B). Because juvenile growth rates were equivalent, we pooled cohorts that metamorphosed at different times on the basis of the number of days after metamorphosis. Coefficients of variation for size-at-d postmetamorphosis were unrelated to postmetamorphic age (weeks 1–4) and never exceeded 0.08.

Individual juveniles exhibited significantly faster growth rates during weeks 1–4 than during weeks 5–7 ($t=9.45$, df=17, $P<0.0001$).

Figure 4

Larval and juvenile growth for fish reared individually in both periods. (A) Growth rate from week 0 to week 3 of the juvenile period versus age at metamorphosis. (B) Growth rate from week 0 to week 3 of the juvenile period versus length at 30 d, an index of larval growth rate.

Figure 5

Larval and juvenile growth for fish reared individually (n=52) as juveniles. (A) Growth rate during weeks 1–4 of the juvenile period versus age at metamorphosis. (B) Growth rate during weeks 1–4 of the juvenile period versus average larval growth rate.

Discussion

Our data on growth dynamics of larval fishes show that size at age is highly variable during the larval period. Patterns in CV's for size at age demonstrate that most of the variation upon which selection can act is found during the early to mid phase of the larval period. Chambers et al. (1988), who analyzed average growth rates of larvae reared in groups, also found that CV's for size at age increased from hatching to a peak of 0.135 at 28 d and subsequently declined as metamorphosis approached. In this study, most larval growth occurred during the first 30 d. Individual larvae that grew most rapidly and reached

the largest size at about day 30, midway through the larval period, metamorphosed at the youngest ages. Travis (1981), who reared anuran larvae individually, also reported that age at metamorphosis was inversely related to size midway through the larval period. Despite the nonlinear growth observed, the length at 30 d and the average larval growth rate were positively correlated. Thus, the general conclusion (derived from those studies where average larval growth was used and larval growth was assumed to be linear) that rapid growth reduces the duration of the larval period is supported (Chambers and Leggett, 1987; Chambers et al., 1988; Bertram et al., 1993).

The relationship between larval growth rate and larval-period duration, however, may not be straight-forward. Although larval growth rate is the primary factor influencing larval-period duration, its effects appear to be modified by the duration of the latency period. Larvae that grow rapidly tend to reach maximum larval length at an early age. However, individuals that reach maximum larval length at an early age have a longer latency period than those larvae that reach maximum length late in the larval period. This finding suggests that rapid growth is associated with a long latency period. Slower-growing larvae, in comparison, may reach metamorphosis at a later age but have a considerably shorter latency period. Moreover, this suggests that metamorphosis may require a minimum duration, independent of size. These findings are consistent with Ricklefs' (1973, 1979) hypothesized tradeoff between growth rate and the acquisition of mature tissue function in birds. In this connection, it is noteworthy that a tradeoff between growth rate and the rate of protein turnover has been documented for the mussel *Mytilus edulis* (Hawkins et al., 1986). Our findings are also consistent with Balon's (1990) suggestion that through epigenetic interactions, individuals within a clutch may form distinct developmental groups—some being more altricial and others more precocial.

Growth rate estimates will be biased if mortality is size dependent. Biased growth-rate estimates will, in turn, reduce estimates of variation in growth rate. However, the extent of variability in larval growth rates reported here are not due to size-dependent mortality. Our analysis could not detect size-dependent mortality, and there was no reduced variability in growth until the end of week 4. Survival to metamorphosis was relatively high (26 out of 53 [49%] from family 1) for individuals replaced on day 22. High survival from day 1 to metamorphosis (175 out of 400 [44%]) was also observed for group-reared larvae in one of the rearing aquaria for family 3. Importantly, the CV for size and age at metamorphosis was similar for the individual and group-reared larvae. The CV for age at metamorphosis was 0.14 and 0.17 for individually reared and group reared larvae (n =175), respectively. The CV for size at metamorphosis was 0.045 and 0.046 for individually reared and group-reared larvae (n=175), respectively. (Note that the CV's for age and size at metamorphosis for the full data set of group reared larvae [n=205] were indistinguishable from those reported above for the reduced data set [n=175]). The similarity of CV's for age and size at metamorphosis implies similar scope for variation in growth rate despite differences in the rearing protocol.

We used a small number of female broodstock. This small number of fish, however, did not preclude in-

sight into the potential for variation in larval growth and development at the population and species level. Previous research on early life history traits in winter flounder has shown that most of the total variation in metamorphic traits (age and size at metamorphosis) occurred within rather than among maternal families (Chambers and Leggett, 1992). Differences between families in the relationship between size and age at metamorphosis (Chambers and Leggett, 1987; see below) and length at metamorphosis (Chambers and Leggett, 1992, Bertram et al., 1993), although detectable, appear small in comparison with the similarities between families for variation in age at metamorphosis. Indeed, Chambers and Leggett (1992) reported that most variation in age at metamorphosis resided within each rearing aquarium. The CV's for age and size at metamorphosis reported here are similar to those reported by Chambers and Leggett (1987) despite differences in rearing temperatures and origins of broodstock employed in the two studies. Chambers and Leggett (1992) developed several qualitative expectations for parental influences on larval flatfishes. They suggested that parentage is likely to influence larval traits but that its contribution to the total phenotypic variation in larvae is expected to diminish during the larval period. In addition, the degree of parental influence is likely to be trait-specific. The absence of parental effects on important traits such as larval-period duration (age at metamorphosis) supports the potential generality of our results on early life history traits based on few parents. Moreover, in the absence of field data, laboratory-based research such as this represents the only basis for characterizing and predicting the dynamics of patterns of individual larval growth and development.

The survival consequences of individual variation in larval growth and development reported here are presently unknown. We do not know whether individuals that grow rapidly and metamorphose at an early age have a survival advantage over those that grow more slowly and metamorphose at an older age. Despite the limited supporting evidence, there has been widespread acceptance of the hypothesis that rapid larval growth conveys a survival advantage because those individuals are large at age and often have a reduced larval-period duration (Bertram, 1993; Leggett and Deblois, 1994). D'Amours (1992) tested directly the hypothesis that rapid larval growth increases survival by using wild 0-group (17–47 d) Atlantic mackerel, *Scomber scombrus*. Comparing the otolith microstructure of larvae from one cohort captured at two different intervals in time, he found no evidence of higher survivorship among faster-growing larvae. In addition, two studies have

found that larvae that are small at age may, under certain circumstances, be less vulnerable to predation than are large members of a cohort (Litvak and Leggett, 1992; Pepin et al., 1992; Bertram, 1996). In flatfishes and in other fishes that switch habitats at metamorphosis, the time of transition is likely to be associated with high mortality. In recent laboratory experiments, Whiting and Able (1995) demonstrated that mortality from shrimp (*Crangon septemspinosa*) predation on settled winter flounder (10.1–14.5 mm) was twice that of presettled individuals (≤11 mm). Bertram and Leggett (1994), however, could detect no difference in shrimp-induced mortality for winter flounder that differed in either length or age at metamorphosis. In the present study, there was a positive relation between length and age at metamorphosis for individually reared winter flounder, but this trend was not evident from the larger sample of group-reared fish (see also Bertram et al., 1993). However, the results may not be strictly comparable because different families were used for the individual and group rearing. Chambers and Leggett (1987) reported a positive relation between length and age at metamorphosis for 8 of 18 families of laboratory-reared winter flounder from Newfoundland. The appropriate experiments have not been conducted to determine whether both large size and old age at metamorphosis reduce mortality due to predation. Therefore, to date, there is no firm basis for interpreting the survival consequences of the individual variation in larval growth and development patterns reported here.

The results of this study are consistent with Bertram et al.'s (1993) finding that size at age does not diverge continuously during the larval and juvenile periods. Overall, the results show that juvenile growth rates are parallel, despite differences in larval growth rates and age at metamorphosis. The parallel nature of juvenile growth rates shows that slow-growing larvae partially compensated for their small size at age by increasing their juvenile growth rates to a greater degree than did fish that grew rapidly as larvae. However, the compensatory growth among slow-growing larvae was not sufficient to cause convergence in juvenile size at age. If these growth rates are maintained, differences in size at age of juveniles that metamorphosed early and late would remain.

Previous work has shown that growth rates of group-reared fish were maintained from weeks 1–7 of the juvenile period (Bertram et al., 1993). In the present study, however, the growth rate of individually reared juveniles was slower in weeks 5–7 than during weeks 1–4. There is reason to believe that food availability was a factor in this difference. Ju-

veniles reared in groups in 7-L containers were exposed to concentrations of 292 prey/d per fish. Juveniles reared individually in 0.4-L containers received 100 prey/d because rations were 0.25 *Artemia* nauplii/(mL·d) for both container sizes. Consequently, food availability may have limited the growth rate of individually-reared juveniles during weeks 5–7 when fish were relatively large and food requirements were maximal.

An important conclusion from this study is that the insight into the dynamics of larval growth and development was gained only because the data were presented as individual-based observations. Although the CV's of size at age would have been available if the weekly length measures of individuals had been pooled, the underlying growth dynamics and individual variability would have been concealed. Moreover, a single "growth" curve fit to such size-at-age data would not accurately reflect the growth patterns of individual larvae. In this connection, we point out that a recent description of winter flounder larval "growth," based upon reconstructions of size at age from otolith microstructure (Jearld et al., 1993), bears little resemblance to the individual growth trajectories shown here.

Darwin (1859) wrote: "No one supposes that all individuals of the same species are cast in the very same mould"; but it is only recently that fishery scientists have begun to investigate the potential population consequences of phenotypic variability in early life history stages. Because mechanisms controlling survival and recruitment of fishes operate at the level of the individual (Crowder et al., 1992), baseline estimates on phenotypic variability are required. This study clearly shows that rearing marine fish larvae individually in the laboratory can provide such estimates. We have shown that there is considerable variability in the dynamics of individual larval growth and development. Studies that examine the survival consequences of such variability represent a logical next step in research programs designed to provide a mechanistic understanding of the factors that affect survival during fish early life history.

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