Behavior and recruitment success in fish larvae: variation with growth rate and the batch effect

Lee A. Fuiman, James H. Cowan, Jr., Michael E. Smith, and Jonathan P. O'Neal

Abstract: Predation-mortality risk for red drum (*Sciaenops ocellatus*) larvae does not appear to be related to their growth rate, but important differences in behavioral performance occur between batches of larvae. This conclusion is based upon field-enclosure and laboratory experiments that assessed the degree to which predation-mortality rates and behavioral survival skills vary with growth rate. In field enclosures, populations composed of 15 fast-growing larvae and 15 slow-growing larvae of a comparable size were exposed to a predatory fish. Growth rate did not affect predation rate. In the laboratory we measured 11 survival skills on 100 larvae of a common size from 10 batches of eggs. For each batch, behavioral performance of fast-growing larvae was compared with that of slow-growing larvae. Growth rate did not affect performance in 10 of the 11 survival skills, but behavioral performance varied among treatment groups (growth rate × batch), with higher performance in most survival skills for some treatment groups and consistently poorer performance for other groups. This coordinated pattern of behavioral performance forecasts differential survival among batches. The variation among batches may be related to timing of spawning within the reproductive season of this serially spawning species.

Résumé : Le risque de mortalité dû à la prédation chez le tambour rouge (*Sciaenops ocellatus*) ne semble pas relié au taux de croissance, mais il existe d'importantes différences de performance comportementale chez les divers groupes de larves. Cette conclusion se base sur des expériences en laboratoire et en enclos en nature qui ont évalué à quel point les taux de la mortalité due à la prédation et les habiletés comportementales de survie varient en fonction du taux de croissance. Dans les enclos de terrain, nous avons exposé à la prédation par des poissons des populations de 15 larves à croissance rapide et 15 larves à croissance lente de même taille. Le taux de croissance n'affecte pas le taux de prédation. En laboratoire, nous avons évalué 11 habiletés de survie chez 100 larves de même taille provenant de 10 masses d'oeufs. Pour chaque masse d'oeufs, nous avons comparé la performance comportementale des larves à croissance rapide à celle des larves à croissance lente. Le taux de croissance n'affecte pas la performance de 10 de 11 habiletés de survie, mais la performance comportementale varie d'un traitement à l'autre (taux de croissance × masse d'oeufs); les meilleures performances dans la majorité des habiletés de survie se retrouvent dans certains groupes et les pires performances sont régulièrement dans d'autres groupes. Ce pattern coordonné de performances comportementales laisse présager une différence de survie chez les différents groupes. Les causes de la variation chez les différents groupes peuvent être reliées au moment de la ponte au cours de la période de reproduction chez cette espèce qui pond de façon répétée.

[Traduit par la Rédaction]

Introduction

Fluctuations in population sizes of many highly fecund marine organisms occur because of variability in the level of recruitment (Caley et al. 1996; Todd 1998). For fishes, recruitment variability is largely attributable to variable mortality of larval stages (Cushing 1975; Sissenwine 1984; Houde 1987). With the exception of catastrophic environmental events, factors affecting survival of larval and juvenile fishes are believed to be related by what Cushing (1975) called the "single process": as the length of time that larvae spend in a stage vulnerable to high mortality increases, the time over which the mortality operates also increases, thereby increasing cumulative mortality (Dahlberg 1979; McGurk 1986; Houde 1987). Moreover, it is clear that small changes in growth and mortality rates of larvae can generate order-of-magnitude or greater differences in annual recruitments (Shepherd and Cushing 1980; Davis et al.

Received 29 March 2004. Accepted 31 December 2004. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 25 June 2005.
J18053

L.A. Fuiman[1] and M.E. Smith.[2] Department of Marine Science, University of Texas at Austin, 750 Channel View Drive, Port Aransas, TX 78373, USA.
J.H. Cowan, Jr.,[3] and J.P. O'Neal.[4] Department of Marine Sciences, University of South Alabama, Mobile, AL 36688, USA.

[1]Corresponding author (e-mail: lee@utmsi.utexas.edu).
[2]Present address: Department of Biology, Western Kentucky University, Bowling Green, KY 42101, USA.
[3]Present address: Coastal Fisheries Institute, Louisiana State University, Baton Rouge, LA 70803-7503, USA.
[4]Present address: Barry A. Vittor and Associates Inc., Mobile, AL 36695, USA.

 doi: 10.1139/F05-053

1991; Houde 2002), and that relationships among larval traits — size, growth rate, and behavioral processes such as foraging and predator defense — are critical for determining survival (Bailey and Houde 1989). Although causes of in-situ mortality are rarely known explicitly (Sissenwine 1984; Houde 1987), it is clear that the factors that control predation rates ultimately can affect recruitment success.

A general paradigm has emerged from intuition that larger individuals are usually less vulnerable to predation and thus more likely to survive than smaller individuals (Anderson 1988; Miller et al. 1988; Rice et al. 1993*a*). This parsimonious and simple view places great emphasis on larval size as a factor in predation vulnerability and on growth rate as a controller of cumulative size-dependent predation mortality. Within virtually every cohort of fish there is appreciable variation in the growth rate of individuals. Evidence of this variability is commonly seen in the laboratory in the form of a size hierarchy or growth depensation, where the range of sizes of individuals increases with age (Blaxter 1988). For example, the coefficient of variation (standard deviation (SD) divided by the mean) for total length (TL) of red drum (*Sciaenops ocellatus*) larvae may increase from 5% to 15% during the second week posthatching (Smith and Fuiman 2003). Such variability has been attributed to elevated competition in dense cultures of larvae (Blaxter 1976), but the presence of two- to three-fold variation in growth rates within cohorts in large enclosures stocked at near-natural densities of larvae and zooplankton prey (Cowan and Houde 1990; Secor and Dean 1992; Folkvord et al. 1994), and considerable variation in size at age in field-collected fish (Fitzhugh et al. 1996; Rooker and Holt 1997) and larvae raised in isolation (Smith and Fuiman 2003), suggest that high variability in growth rate might be a natural phenomenon.

An obvious and important advantage of fast growth is the reduction in predation mortality by shortening the time that larvae spend in a stage vulnerable to high mortality (Cushing 1975; Houde 1987). Simulations using individual-based models have verified this contribution of growth rate to cumulative predation risk and the composition of the surviving population (e.g., Cowan et al. 1996; Letcher et al. 1996; Heath and Gallego 1997). However, experiments conducted in mesocosm enclosures indicate that under some circumstances, larger or faster growing larvae are more vulnerable to predators than smaller larvae (e.g., Fuiman 1989; Cowan and Houde 1992; Litvak and Leggett 1992). In addition, a recent field study showed an inverse relationship between growth rate and predation vulnerability that was independent of both size and time (Takasuka et al. 2003).

Thus, predation mortality is not determined solely by a size-based "window of vulnerability". The predation process ultimately decomposes into discrete events involving individuals and taking place over very short periods of time. The immediate outcome depends upon the behavior of predator and prey. In particular, the routine behavior of a larva will influence its likelihood of encountering a predator and, when it is challenged by a predator, evasive skills (including sensory and locomotor performance) are its ultimate hope for survival. Therefore, individuals will enjoy the lowest immediate predation risk if their behavior minimizes encounters with predators, their sensory capabilities allow them to perceive a threat and initiate a response, and their evasive performance maximizes the effectiveness of the response. The question arises, is predation mortality little more than the accumulation of deaths of individuals that were unfortunate enough to have encountered a predator during their vulnerable stage? Or is there a subset of individuals that have a suite of behavioral or physiological characteristics that confer greater fitness in predator–prey interactions, leaving less fit individuals to succumb to predators?

It has been suggested that the survivors of a larval year class are exceptional individuals (Crowder et al. 1992; Rice et al. 1993*b*; Heath and Gallego 1997), and field studies provide growing evidence of differential survival among individuals or cohorts of larvae (e.g., Rice et al. 1987; Meekan and Fortier 1996; Hare and Cowen 1997). Individuals and cohorts may benefit (or suffer) from spatial or temporal heterogeneity in extrinsic factors, such as food, predators, nursery habitat, and contaminants. But there may also be intrinsic variability in offspring viability that arises from variations in maternal investment in egg quality (e.g., Kjørsvik 1994; Chambers and Waiwood 1996). Such variations in investment may occur within a spawn or among spawns; the latter variation is referred to as a batch effect.

Here we investigate the possibility that exceptional individuals are those that combine fast growth with optimal antipredator behavior. Such a combination of attributes could be favored by natural selection, although recent studies of juvenile Atlantic silverside (*Menidia menidia*) showed that swimming performance was inversely related to growth rate, implying a trade-off between these traits (Billerbeck et al. 2001; Lankford et al. 2001). Nevertheless, there is also a mechanistic basis for a positive relationship. Growth rate and the sensory and locomotor capabilities that mediate all behaviors are fundamentally the products of physiological processes. The variation in growth rate observed within a cohort may be only the most obvious manifestation of more pervasive physiological variability among individuals. Such variability may affect all physiological processes, including survival skills that rely on sensory and locomotor performance.

We investigated the relationships between growth rate, behavioral survival skills, and predation mortality of red drum larvae in laboratory and field-enclosure experiments. Our objectives were to determine whether relative (within batches) or absolute differences in growth rate are associated with differences in behavioral performance and predation-mortality rate. We found no relationship between growth rate and either predation mortality or behavioral performance, but we did find significant differences in performance between batches of larvae (spawns). Closer examination of this batch effect suggested that behavioral performance might be related to variations in egg quality during the reproductive season of this serially spawning species.

Methods

The red drum has a reproductive strategy typical of many marine fishes. It is a generalized perciform fish that has high fecundity and spawns multiple times annually between mid-August and late November. It has planktonic eggs and estuary-dependent larvae that settle out of the water column

at 4–6 mm TL to take up residence in seagrass beds (Rooker et al. 1998). We compared predation-mortality rates for fast- and slow-growing larvae in a field-enclosure experiment and compared the performance of behavioral survival skills by fast- and slow-growing larvae in a laboratory experiment. The larvae used in the laboratory experiment were those analyzed by Fuiman and Cowan (2003) but applied here to resolving different questions. Procedures for animal care and the laboratory experiment are summarized here; details were provided by Fuiman and Cowan (2003).

We obtained larvae with different growth rates without restricting diets or altering temperature, by taking advantage of growth-rate variability that is common in cultures of fish larvae (Smith and Fuiman 2003). In the laboratory, fast-growing larvae were selected for experiments when the first individuals in a tank reached the target length (7.5 mm TL; 63% of complete development based on the ontogenetic index (O_L) using complete squamation at 25 mm TL to define metamorphosis; Fuiman et al. 1998). Later, when the slowest growing individuals in the same tank reached the same target size, slow-growing larvae were removed for experiments. This provided a near-maximum range of growth rates and allowed comparisons of different batches of larvae, without artifacts from inducing growth-rate variability experimentally. In the mesocosm experiment, test populations were composed of larvae of similar sizes but different ages selected from cohorts of larvae being reared contemporaneously.

Animal care

Eggs were obtained from captive broodstock maintained at the Fisheries and Mariculture Laboratory of the University of Texas Marine Science Institute and the Coastal Conservation Association / Central Power and Light Marine Development Center hatchery (Corpus Christi, Texas) between July 1997 and May 1998 for the laboratory experiment and between June and July 1999 for the field-enclosure experiment. Broodstock were induced to spawn by manipulation of temperature and photoperiod; no hormonal injections were given. Each of four broodstock tanks contained 2 or 3 males and 2 or 3 females that spawned voluntarily. For each spawn (batch), 5000 eggs were incubated in a bucket. They hatched within 24 h of fertilization and were then placed in a 150-L conical rearing tank with aeration and a recirculating biological filter. Water temperature and salinity were maintained at 26.4 ± 0.7 °C (mean ± SD) and 30.1 ± 1.7 ppt, respectively. Larvae were maintained on a 12 h light : 12 h dark cycle with overhead fluorescent lighting providing illumination at 10 $\mu E \cdot m^{-2} \cdot s^{-1}$. Larvae were fed a mixture of rotifers (*Brachionus* sp.) and planktonic algae (*Isochrysis galbana* or *Nannochloropsis oculata*) once daily until 13 days posthatching. The larvae were fed newly hatched brine shrimp (*Artemia salina*) once per day from 10 days posthatching onward.

Field-enclosure experiment

Seven predation trials were conducted on 24 July and 4 August 1999 in cylindrical mesocosm enclosures, with three trials (enclosures) on the earlier date and four trials on the later date. Larvae were taken from three separate batches such that on each date fast growers from one batch were combined with slow growers of the same size from another batch. Each enclosure was 1 m in diameter by 3 m deep (volume 2.4 m^3) and suspended from a raft in waters adjacent to the University of Texas Marine Science Institute. Enclosure walls were constructed from 2-oz. blue Dacron sailcloth and the flat bottom panel was 53-μm nylon mesh (Nitex) with a 10 cm diameter hole at its center (plugged during deployment). Four external stainless-steel rings attached at 1-m intervals along the enclosures maintained each enclosure's shape during deployment. When deployed, approximately 0.5 m of each enclosure (not including the submerged 3 m) remained above the water surface to prevent loss of contents from enclosures or contamination from the surrounding water.

Prior to experimentation, otoliths of either fast- or slow-growing red drum larvae in one of the test populations were chemically labeled for subsequent identification. Larvae were removed from a rearing tank and placed in 4 L of alizarin complexone dihydrate (ALC) solution (50 $mg \cdot L^{-1}$) at a temperature of 27 °C. After 5 h of immersion, larvae were "rinsed" by siphoning as much of the ALC solution as possible and replacing it with clean, filtered seawater (~27 °C, 27 ppt). This rinsing process was repeated until the water had no visible traces of ALC. The larvae were then transferred to a 2-L mesh-sided (153 μm) holding chamber floating in their rearing tank. This procedure provided labeled larvae with the same water conditions as all other larvae, while separating them from the others prior to experimental trials. The group of larvae that was labeled alternated from trial to trial (i.e., slow growers in one trial, fast growers in the next), to eliminate any bias due to marking.

An assemblage of natural zooplankton (between 250 μm and 1 mm in size) was added to each enclosure at a concentration of approximately 90–100 $zooplankters \cdot L^{-1}$ (i.e., ~180 000 per enclosure). This zooplankton served as a food source for the larvae, as well as alternative prey for the predator. About 1 h after the alternative prey were added, 30 red drum larvae were introduced (15 fast growers from one batch and 15 slow growers from another batch) into each enclosure. Larvae were allowed to acclimate and disperse for ~12 h before a single predator (a pinfish, *Lagodon rhomboides*, 40–50 mm TL) was added to each enclosure. Pinfish are voracious predators of fish larvae and are common in the habitats occupied by red drum larvae (Fuiman 1994). In addition to the seven predation enclosures, eight enclosures were used as controls to establish the recovery rate for these trials. Control enclosures contained the same concentrations of larvae and zooplankton as the predation enclosures but without a predator.

Trials lasted approximately 6 h after introduction of the predators. After a trial, the contents of each enclosure were collected by removing the plug from the drain hole and lifting the enclosure from the water so that the water drained through the mesh bottom. As each enclosure was lifted, its sides were washed to free larvae that may have adhered. Predators were removed as soon as possible (within 5 min) to prevent additional predation on larvae as they became concentrated at the bottom during the recovery process. When each enclosure was removed from the water, its contents were placed in a 19-L bucket and returned to the laboratory, where the remaining larvae were removed, counted,

and stored in 40% isopropyl alcohol until their otoliths could be examined for an ALC mark.

The numbers of fast- and slow-growing larvae recovered from an enclosure were used to compute instantaneous hourly mortality rates, after correcting for losses of larvae from control enclosures:

$$Z_r = -\{[\ln(N^{P}_{t,r}/N_0) - \ln(N^{C}_{t,r}/N_0)]/t\}$$

where Z_r is the corrected instantaneous hourly mortality rate for larvae of relative growth rate r (r = fast or slow), t is the duration of the trial in hours, N_0 is the number of larvae initially stocked, $N^{P}_{t,r}$ is the number of larvae of growth rate r recovered from an enclosure that contained a predator, and $N^{C}_{t,r}$ is the number of larvae recovered from a control enclosure (Fuiman and Gamble 1988).

Laboratory experiment

Three laboratory assays of behavioral performance were conducted on five fast-growing larvae and five slow-growing larvae from each of 10 replicate batches of larvae (100 larvae). The assays were routine swimming, acoustic startle stimulation, and visual startle stimulation, which yielded 11 variables (survival skills): routine swimming speed and, for each of the two types of startle stimuli, responsiveness, response latency, response distance, response duration, and response speed. Routine swimming speed is a measure of unstimulated movement and pertains to rates of encounter with predators and food items. The other performance variables are attributes of an evasive response that would be used when a predator attacks.

Each assay was repeated 5 times for each larva. Analyses of variability within individuals demonstrated that all variables were repeatable (Fuiman and Cowan 2003). Therefore, the data set for this study comprised the mean of each variable for each larva (n = 100 larvae). These means were based upon five trials for routine swimming speed, acoustic responsiveness, and visual responsiveness. The number of values contributing to the means for the remaining variables was the number of times (out of 5) a larva responded to the acoustic or visual stimulus.

Routine swimming was measured by placing a larva in a glass watch bowl with 1 L of seawater and recording its behavior for 2.5 min on videotape. The acoustic startle stimulus was a 500-Hz tone played at 5 dB above background through a loudspeaker (20 cm diameter) for a period of about 0.5 s. The visual startle stimulus was a black oval on a white card attached to a pendulum (after Batty 1989). When the pendulum was released from its resting position 17° from the bottom of its path, it accelerated toward an acrylic chamber containing a larva. A video camera recorded the larva's behavior in all assays.

Each set of experiments was conducted over a 2-day period. The routine swimming assay was conducted first, followed by the acoustic startle assay. Larvae were exposed to the acoustic stimulus once and then set aside in a sound-dampening box until the remaining four larvae were tested. This sequence was repeated until each larva was tested 5 times. Afterward, larvae were fed a small ration of brine shrimp and left undisturbed until the following day, when the visual startle assay was conducted. Each larva in turn was presented with the visual stimulus, until all larvae were tested 5 times. We examined the performance of individual larvae over the course of the five trials and found no evidence for habituation to either stimulus.

Analysis of video recordings included computer-assisted measurement of distances traveled by the larvae. Spatial resolution of these measurements was 0.4 mm per pixel for the routine swimming and acoustic startle assays and 0.2 mm per pixel for the visual startle assay. Durations of responses and latency of acoustic responses were measured by counting video fields (0.0167 s each). Latency of visual responses was determined from the electronic timer on the video display.

Statistical analysis

Growth rate of an individual was expressed in two ways: relative and absolute. Relative growth rate was a binary categorical variable (fast, slow) that identified whether an individual was selected as one of the fast-growing members of its batch or one of the slow-growing members. Absolute growth rate was a continuous variable that was independent of batch membership. It was calculated as a larva's TL (millimetres to the nearest 0.1 mm) minus length at hatching (2.77 ± 0.10 (mean ± SD; n = 40), divided by its age (days posthatching).

Field-enclosure experiment

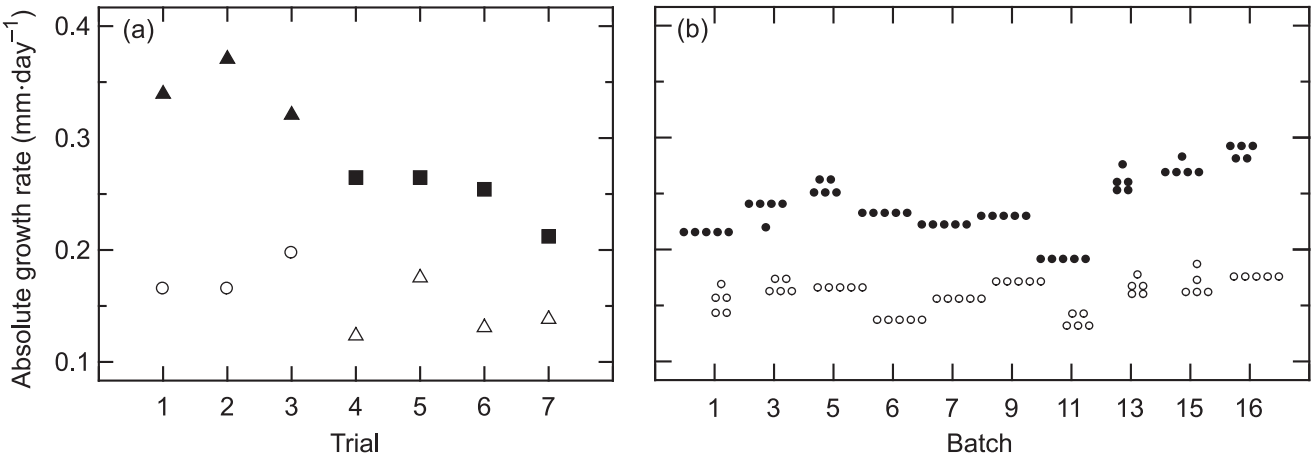
The enclosure experiment directly examined the relationship between growth rate and predation mortality but without the behavioral information of the laboratory experiment. Results were analyzed as a single-factor (relative growth rate) paired-treatment experiment in which the mortality rate for fast-growing larvae in a particular enclosure was compared with the mortality rate of the slow-growing larvae in the same enclosure ($Z_f - Z_s$). This comparison was made with the nonparametric Wilcoxon's signed rank test and Student's t test for paired samples.

Laboratory experiment

Probability plots and skewness coefficients were examined to determine whether each of the 11 survival skills was normally distributed. Routine swimming speed, acoustic-response latency, and acoustic-response duration were strongly positively skewed, so a log-transformation was applied before statistical analysis. Acoustic and visual responsiveness were calculated as proportions of five trials in which each larva responded to each of the stimuli. Therefore, an angular (arcsine) transformation was applied to the square root of each value before statistical analysis to normalize the distributions, with corrections for a mean of 0% or 100% (Snedecor and Cochran 1967).

Effects of relative growth rate on the 11 performance measures were assessed by multivariate analysis of variance (ANOVA) and univariate ANOVA of the 100 larvae, using a mixed-effects model in a randomized-block design in which relative growth rate was a fixed effect and batch was a random blocking factor. This design allowed testing for differences in relative growth rate within batches and for differences among batches. Effects of absolute growth rate and batch on behavioral performance were assessed by analyses of covariance. The first stage of the analysis of covariance tested for a significant interaction term (difference in slopes among batches). When the interaction was not sig-

Fig. 1. Distribution of growth rates of populations of red drum (*Sciaenops ocellatus*) larvae used in field-enclosure experiments (*a*) and individual larvae used in laboratory experiments (*b*). The absolute growth rate is the difference between total length (TL) on the test date and length at hatching (2.77 mm TL) divided by age on the test date (days post hatching). Solid symbols denote larvae with fast relative growth rates; open symbols denote larvae with slow relative growth rates. The symbols in *a* identify batches. In *b*, batches are numbered consecutively; gaps in numbering are due to incomplete experiments, mass mortalities, or unhealthy batches of eggs or larvae.



nificant (equal slopes), the model was recomputed without the interaction term and the main effects (absolute growth rate, batch) were tested. The statistical power for tests of a growth-rate effect on predation-mortality rate and behavioral performance was computed to detect the null hypothesis that $\mu_1 = \mu_2$, using SAS® (version 8.2; SAS Institute Inc. 2001). All other statistical analyses were performed with SYSTAT® (version 10.2; Systat Software, Inc. 2002).

We explored patterns in behavioral performance among relative growth rates and batches of larvae with hierarchical cluster analysis. The data set for cluster analysis was summarized for each of the 11 performance variables by computing the means for each of the 20 treatment combinations of relative growth rate and batch. Each performance variable was standardized to a zero mean and unit variance to prevent the scale of any variable from biasing the analysis. Clusters were derived by applying hierarchical clustering to a similarity matrix of Euclidean distances for the 11 standardized variables. Three linkage methods were applied (complete, average, Ward) to examine the stability of the resulting clusters.

Results

Field-enclosure experiment

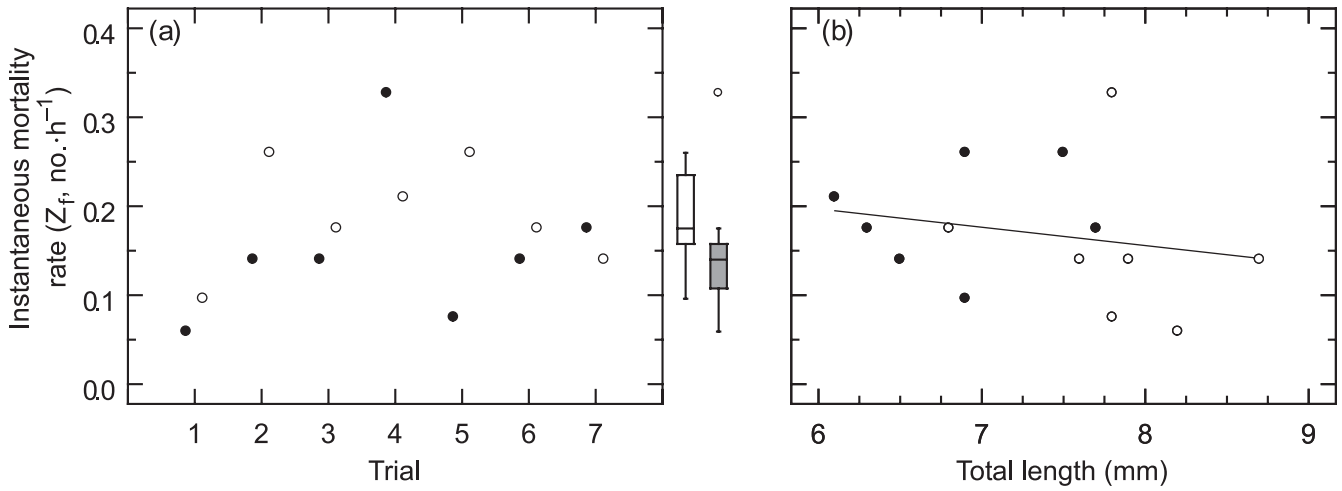
Fast-growing larvae came from two batches and were 16 or 19 days old with mean absolute growth rates of 0.34 and 0.25 mm·day^{-1}, respectively (Fig. 1*a*). Slow-growing larvae came from two batches (one in common with fast-growing larvae) and were 25 or 27 days old with mean absolute growth rates of 0.18 and 0.14 mm·day^{-1}, respectively. Larvae were 7.3 ± 0.76 mm TL (mean ± SD) overall, but despite efforts to use larvae of similar sizes, the mean length of fast-growing larvae was always slightly greater than that of slow-growing larvae in the same trial. Differences in mean TL between fast- and slow-growing larvae within a trial were 1.0 ± 0.70 mm (mean ± SD).

Larval recovery rates in the eight control enclosures ranged from 90% to 100% (mean recovery = 95%). At the end of a predation trial between 6 and 18 (mean = 11.1) of the 30 larvae were recovered from each enclosure. Taking control recovery data into account, instantaneous mortality rates for fast-growing larvae (Z_f) ranged from 0.06 to 0.33·h^{-1} and entirely included the range of mortality rates for slow-growing larvae (Z_s = 0.10–0.26·h^{-1}) (Fig. 2*a*). Mortality rates were greater for slow-growing larvae than for fast-growing larvae in five of the seven trials. Differences in mortality rate ($Z_f - Z_s$) within a trial averaged –0.04·h^{-1}, ranging from –0.19 to +0.12·h^{-1}. Disregarding the differences in TL, there was no difference in Z due to growth rate (Wilcoxon's test, $P = 0.23$; paired Student's t test, $P = 0.35$). To account for the potential effect on Z of the slight differences in size between fast- and slow-growing larvae, we computed residuals from a regression of Z against TL (Fig. 2*b*). Residuals for fast- and slow-growing larvae were not significantly different (Wilcoxon's test, $P = 0.50$; paired Student's t test, $P = 0.68$), from which we conclude that there was no difference in mortality rate due to growth rate even after we corrected for differences in size. The statistical power of the paired t tests, using the observed differences in Z between fast- and slow-growing larvae, was 0.14 (raw data) and 0.07 (TL residuals), owing to the very small differences between means and high variability within growth-rate groups.

Laboratory experiment

The 100 larvae tested were 7.7 ± 0.19 mm TL (mean ± SD), ranging from 7.1 to 8.2 mm TL. Mean absolute growth rates of larvae used in the laboratory experiment were similar to those of larvae used in the field-enclosure experiment (Fig. 1*b*). Growth of larvae within batches varied so much that the ages and absolute growth rates of fast- and slow-growing larvae did not overlap across the 10 batches. Fast growers ranged from 18 to 27 days old and had grown 0.19–0.29 mm·day^{-1}, whereas slow growers were 29–37 days old and had grown 0.13–0.19 mm·day^{-1}. Mean differences in age and growth rate within batches were 10.2 days and 0.08 mm·day^{-1}, respectively. One batch (No. 11) grew especially slowly, so the fast growers had a mean absolute

Fig. 2. (*a*) Instantaneous hourly predation-mortality rates for seven experimental groups of red drum larvae. Each group comprised 15 fast-growing larvae (●) and 15 slow-growing larvae (○). Experiments were conducted in field enclosures with a single predatory fish. Box diagrams on the right-hand margin of *a* summarize data for fast-growing (shaded rectangle) and slow-growing (open rectangle) larvae as the interquartile range (rectangle), median (horizontal line within the rectangle), range of values within 1.5 times the interquartile range from the median (vertical line), and unusually small or large values (circle). (*b*) Relationship between instantaneous hourly predation-mortality rates (Z) and mean TL of larvae for the same experimental groups. The regression equation (line) is $Z = 0.320 - 0.021$ TL ($P = 0.47$). Experiments were conducted in field enclosures with a single predatory fish.



growth rate only slightly greater than the slow growers of other batches (Fig. 1*b*).

Relative growth rate

Multivariate ANOVA indicated that relative growth rate had no significant effect on survival skills ($P = 0.159$). The statistical power of the multivariate ANOVA test for the observed effect of relative growth rate on all survival skills was 0.09. When survival skills were examined individually (univariate ANOVA), only visual-response duration demonstrated a significant effect of relative growth rate ($P = 0.015$; Fig. 3). Even though visual-response duration for fast growers (0.11 ± 0.02 s (mean ± SD)) was greater than for slow growers (0.09 ± 0.02 s), the difference within a batch was small (0.01 s ± 0.03; mean ± SD). Power calculations for individual survival skills (univariate ANOVA) were mixed, with some tests exhibiting acceptable power (0.89 and 0.96 for acoustic- and visual-response speed, respectively), moderate power (0.43) for acoustic responsiveness, and low power for the other variables (<0.18). The statistical power was low because observed differences between fast- and slow-growing larvae were very small (generally <8% of the overall mean value of a variable). We consider this magnitude of difference in behavior, and in the predation-mortality rate (see the field-enclosure experiment), to be biologically insignificant, especially over the extremes of growth rate we observed.

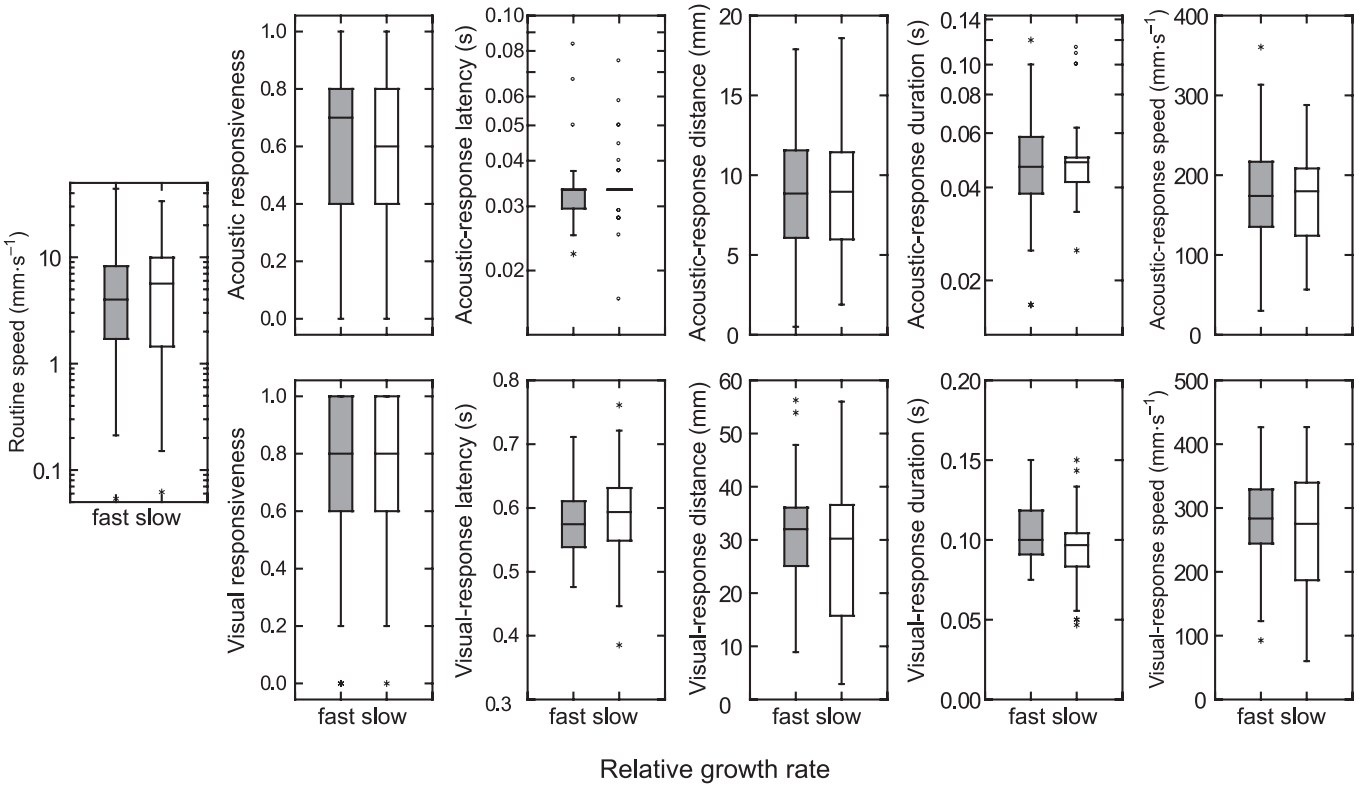
In contrast to the lack of a growth-rate effect, there were significant differences in survival-skill performance among batches of larvae (multivariate ANOVA, $P < 0.0005$). Univariate F statistics showed that the growth-rate effect was significant ($P < 0.05$) for 6 of the 11 survival skills and marginal ($0.05 \le P \le 0.08$) for 3 others (Fig. 4). Only visual-response distance and visual-response duration were clearly not different between batches ($P = 0.248$ and $P = 0.511$, respectively). For many of the nine variables in which the batch effect was significant, one or two batches displayed extreme values relative to the other batches. For example, mean acoustic responsiveness was 57.4% overall, but batch 1 had a much higher mean (84.0%), whereas batches 15 and 16 had a much lower mean (30.0% and 32.0%, respectively; Fig. 4). Mean acoustic-response latency for batch 15 (0.05 s) was higher than the overall mean (0.03 s), owing to three larvae with very late responses. Acoustic-response distance averaged 9.2 mm overall, but batch 1 averaged 13.0 mm, which was 2.5 times the mean for individuals from batch 13 (5.3 mm). Overall responsiveness to the visual stimulus averaged 75.0%, but several batches had distinctly lower averages (34.0%, 54.0%, and 58.0% for batches 15, 16, and 13, respectively). Visual-response latency averaged 0.58 s overall, with a high mean value of 0.64 s for batch 16 and a relatively low value of 0.53 s for batch 9.

Absolute growth rate

Treating growth rate as a continuous random variable and analyzing effects with analyses of covariance produced only a few differences from the results for relative growth rate. The same single variable, visual-response duration, was significantly related to absolute growth rate ($P = 0.014$) but it lacked a batch effect ($P = 0.152$). However, simple linear regression of visual-response duration on absolute growth rate (batch effect omitted) showed that the relationship was not significant ($P = 0.097$, $R^2 = 0.029$).

Four of the 11 performance variables — routine swimming speed and acoustic-response distance, duration, and speed — displayed a significant interaction between absolute growth rate and batch, indicating that slopes of the relationships varied among batches. More specifically, most, but not all, batches showed no significant relationship between a survival skill and growth rate. Batches 1 and 13 displayed a significant negative relationship between routine swimming speed and absolute growth rate ($P \le 0.021$, $R^2 \ge 0.508$). For batch 13, acoustic-response distance was negatively related to absolute growth rate, but the relationship was positive for

Fig. 3. Comparisons of behavioral performance of red drum larvae with fast and slow relative growth rates. Only visual-response duration varied with growth rate. Sample sizes are 50 larvae for routine speed and acoustic and visual responsiveness and 46–50 larvae for other variables, depending on responsiveness. Box diagrams summarize the data for fast-growing (shaded rectangle) and slow-growing (open rectangle) larvae as the interquartile range (rectangle), median (horizontal line within the rectangle), range of values within 1.5 times the interquartile range from the median (vertical line), and unusually small or large values (asterisk and circle).



batch 16 ($P \leq 0.038$, $R^2 \geq 0.436$). Acoustic-response duration was positively related to growth rate in batches 3 and 16 ($P \leq 0.045$, $R^2 \geq 0.512$). Both batches 9 and 16 showed a positive relationship between acoustic-response speed and growth rate, whereas batch 13 showed a negative relationship ($P \leq 0.044$, $R^2 \geq 0.416$).

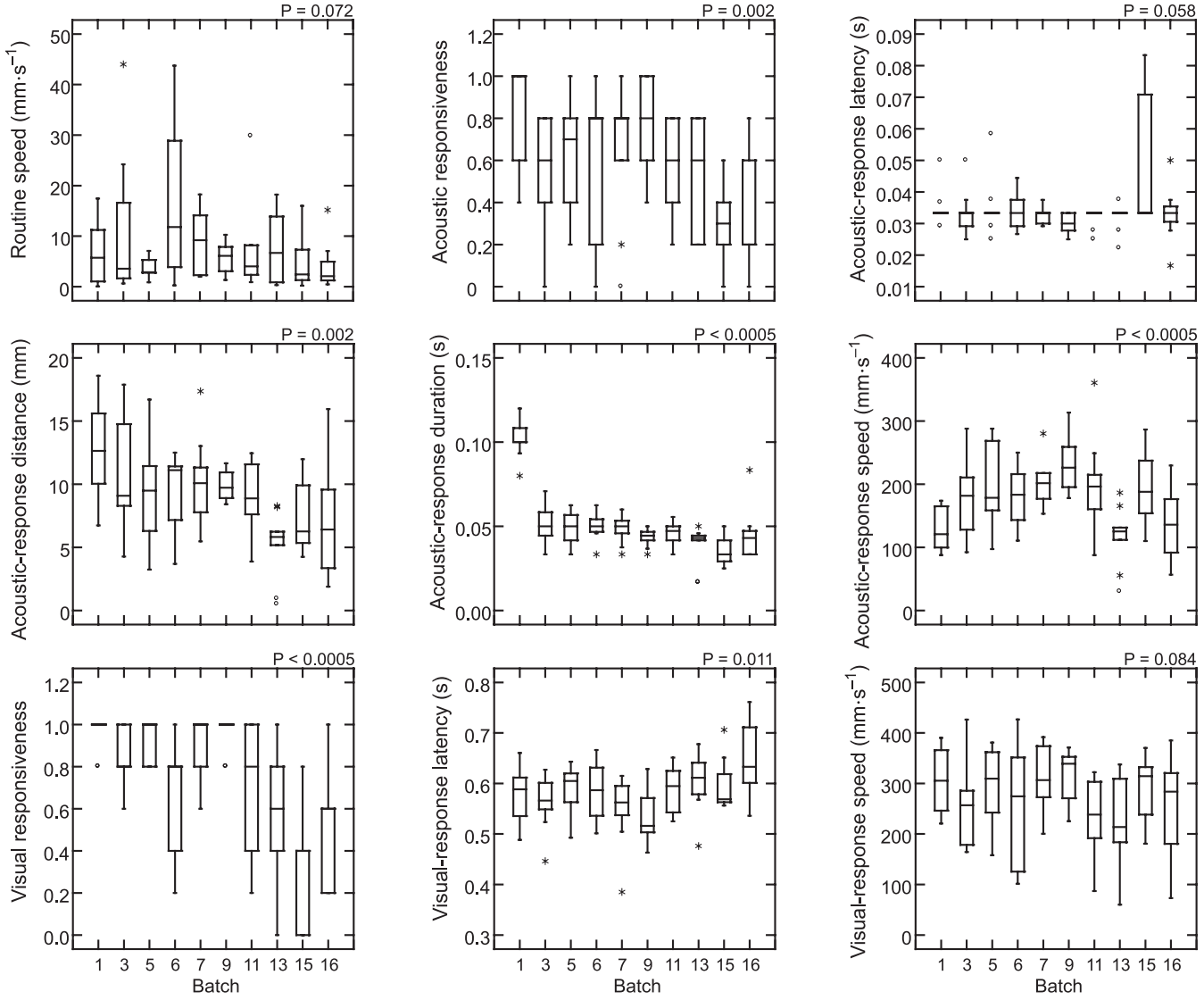
Four variables that lacked a significant interaction term had a significant batch effect ($P \leq 0.011$), indicating that there were differences among batches in mean level of the behavioral performance variable. These variables were acoustic responsiveness, acoustic-response latency, visual responsiveness, and visual-response latency. Neither absolute growth rate nor the interaction term made a significant contribution to variation in these performance measures. Unlike the analyses of relative growth rate, the batch effects on the relationships between absolute growth rate and acoustic-response distance, duration, and speed were not significant. Differences in elevation for responsiveness and latency of acoustic and visual responses were attributable to a few batches. Batches 15 and 16 had relatively low acoustic responsiveness and batch 1 had high acoustic responsiveness. Batch 15 also had high acoustic latency. For visual responsiveness, four batches (11, 13, 15, 16) had low values compared with other batches. Batch 16 had relatively high visual-response latencies. Inasmuch as absolute growth rate did not have a significant effect on these performance variables, these differences mirrored those described for relative growth rate (Fig. 4).

Patterns in behavioral performance

The numerous significant differences in behavioral performance attributable to batches in both analyses, including significant interaction terms in the analysis of absolute growth rate, prompted a closer examination of the pattern of variability in behavior among the batches. Cluster analysis was performed on the 20 treatment groups (2 relative growth rates × 10 batches) rather than the 10 batches because of the significant interactions and because experiments were conducted on all members of a treatment group (but not all members of a batch) together. Two of the cluster linkage methods (complete, average) produced entirely concordant membership of two primary clusters (initial branching in Figs. 5*a* and 5*b*), although details of the relationships within each of these clusters differed. The third method (Ward linkage) assigned 15 of the 20 treatment groups to the same two clusters (Fig. 5*c*). The remaining five treatment groups, which formed a discrete subgroup in all three analyses, were placed in a different primary cluster by the Ward linkage method. Given the instability in the assignment of these five treatment groups, we regarded these intermediate treatment groups separately (cluster I in Fig. 5).

Inspection of mean values for survival skills of treatment groups revealed that the stable primary clusters (A, B) were quite distinct (Fig. 6). They were separated not on the basis of a few variables but rather according to differences in almost all survival skills. Means for each variable were always greater for cluster A than for cluster B. Formal comparison

Fig. 4. Comparisons of behavioral performance of different batches of red drum larvae (growth rates are combined within each batch). Only survival skills for which there was a significant ($P < 0.05$) or marginally significant ($0.05 \leq P \leq 0.08$) batch effect are shown. Sample sizes are 10 larvae for routine speed and acoustic and visual responsiveness and 7–10 larvae for other variables, depending on responsiveness. Box diagrams summarize the data for fast-growing (shaded rectangle) and slow-growing (open rectangle) larvae as the interquartile range (rectangle), median (horizontal line within the rectangle), range of values within 1.5 times the interquartile range from the median (vertical line), and unusually small or large values (asterisk and circle).



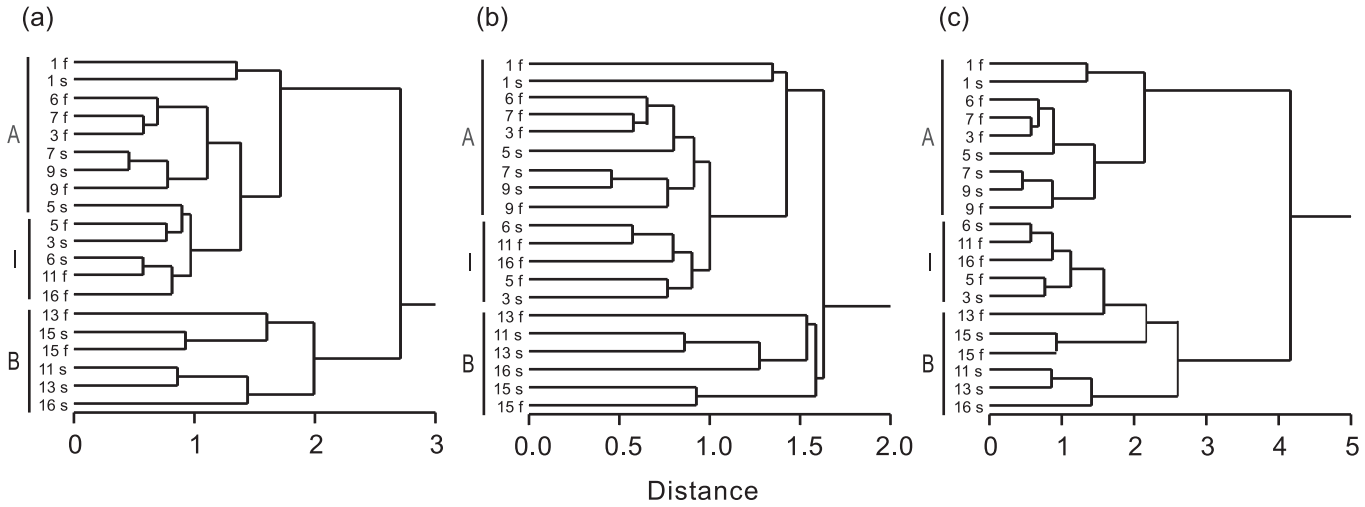
of these clusters (two-sample Student's t test, $n = 9, 6$) revealed significant differences ($P \leq 0.044$) in 8 of the 11 variables. Only routine swimming speed, acoustic-response latency, and acoustic-response speed were not significantly different ($P \geq 0.113$). The most trenchant differences ($P \leq 0.008$) between clusters A and B were for visual responsiveness (averaging 89.8% and 53.0%, respectively), visual-response distance (32.6 and 22.9 mm), acoustic responsiveness (74.2% and 42.7%), acoustic-response distance (11.1 and 6.3 mm), and acoustic-response duration (0.057 and 0.037 s) (Fig. 6).

Subgroup I, which was variously assigned to cluster A or cluster B, displayed intermediate levels of behavioral performance. Mean values for visual responsiveness (73.5%) and acoustic-response distance (8.9 mm) and duration (0.047 s) were midway between the corresponding values for clusters A and B (Fig. 6). However, this intermediate subgroup was more similar to cluster A in terms of visual-response distance, duration, and speed, but more similar to cluster B in terms of acoustic responsiveness and visual-response latency.

Discussion

A direct link between larval growth rate and predation vulnerability has been the subject of some debate (Bailey and Houde 1989; Leggett and Deblois 1994; Takasuka et al. 2003). Our experiments demonstrate that growth rate and predation vulnerability are not related, positively or negatively, in red drum larvae at this stage of development. This conclusion is based upon separate comparisons of predation-

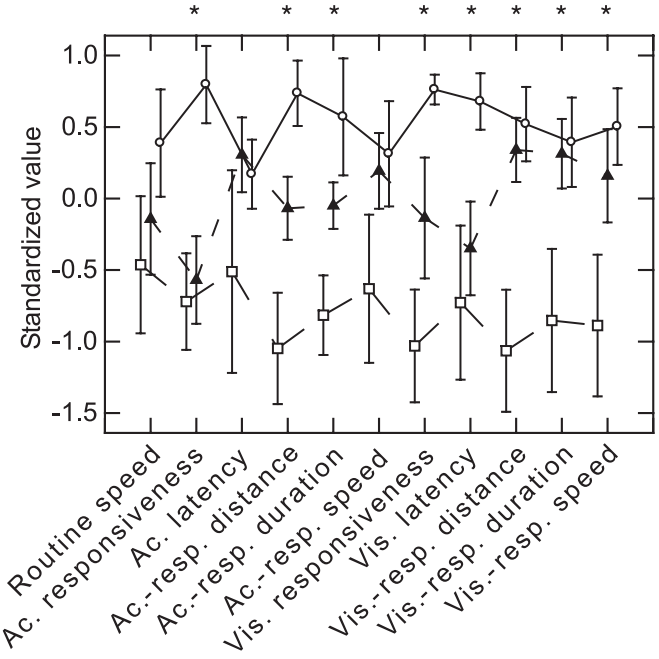
Fig. 5. Relationships among 20 treatment groups of red drum larvae (2 growth rates × 10 batches) based on the similarity of their behavioral performance (11 variables) derived from hierarchical cluster analysis (complete linkage (*a*), average linkage (*b*), and Ward linkage (*c*) methods). Cluster analyses identified two stable clusters (A, B) and one intermediate cluster (I). Codes at ends of branches identify batch number and relative growth rate (fast (f) or slow (s)).



mortality rates and behavioral mechanics of predator evasion. Our conclusion is supported by the study by Bertram and Leggett (1994), who conducted experiments in 7-L laboratory containers to compare predation mortality of winter flounder (*Pseudopleuronectes americanus*) larvae that varied in age at metamorphosis but not in length at metamorphosis. Using a shrimp (*Crangon septemspinosa*) as the predator, they too were unable to establish any difference in instantaneous predation mortality for larvae of different ages (i.e., mean growth rate histories). We concur with Bertram and Leggett (1994) that any differences in instantaneous predation vulnerability between same-sized larvae of different growth-rate histories are "subtle and potentially ecologically inconsequential", provided the slower growing larvae are not malnourished. But this differs from the field observations of Takasuka et al. (2003) and their proposed "growth-selective predation" hypothesis.

In previous research studies in which a relationship between larval growth rate and predation vulnerability was discussed, larval size (independent of larval nutritional condition) was often a confounding factor. For example, in studies suggesting that predation vulnerability decreases with larval growth rate (Miller et al. 1988; Bailey and Houde 1989), larval size, rather than growth rate, probably had the greater effect on mortality. Many studies have shown that larger individual larvae tend to be less vulnerable to predation (Anderson 1988; Miller et al. 1988; Fuiman 1994) because of a decrease in the number of potential predators and an increase in escape ability as larvae become larger. Yet in-situ enclosure experiments (Fuiman 1989; Litvak and Leggett 1992; Cowan and Houde 1992) and modeling simulations (Cowan et al. 1996; Letcher et al. 1996; Paradis et al. 1996) have indicated that under some circumstances, larger larvae are more vulnerable to predators than smaller larvae. This result is believed to be due, in part, to increased encounter rates attributable to higher swimming speeds of larger larvae, and increased larval pigmentation and movement that may make larvae more conspicuous to predators

Fig. 6. Mean performance for clusters identified in Fig. 5. Lines connect standardized (mean = 0, standard deviation = 1) mean values for each performance variable of cluster A (○, n = 45 larvae), cluster B (□, n = 30 larvae), and cluster I (▲, n = 25 larvae). Vertical lines through means represent ±1 standard error. An asterisk indicates a significant difference ($P < 0.05$) between cluster A and cluster B. The sign for the standardized value of acoustic- and visual-response latencies was reversed for better comparison with other variables. Ac., acoustic; vis., visual; resp., response.



(Bailey and Houde 1989; Fuiman and Magurran 1994). Larger larvae also may be at a disadvantage when encountering predators that preferentially attack larger prey (Litvak and Leggett 1992), or nonvisual predators, such as jellyfish,

because of increased prey target size (Bailey and Batty 1984; Litvak and Leggett 1992). Simple and parsimonious conceptual models that relate larval size to predation vulnerability as a monotonic function are therefore difficult to defend (Cowan et al. 1997). The importance of size to the staging and outcome of a predator–prey interaction (immediate mortality) does not, however, diminish the importance of larval growth rate as a regulator of cumulative cohort-specific mortality rate. Growth rate determines the span of time during which predation-mortality risk is especially high and, in this way, determines cumulative mortality, as has been well demonstrated by both conceptual arguments (Cushing 1975; Houde 1989) and modeling studies (Cowan et al. 1996, 1997; O'Neal 2002).

Our finding of no difference in predation-mortality rates between fast- and slow-growing larvae in field enclosures must be considered in light of the fact that survival-skill performance in the laboratory experiment varied among batches of larvae. It was not possible to determine whether there was a batch effect in the enclosure experiment because fast and slow growers of the same size could not be placed in the same enclosure on the same day.

The batch effect on behavioral performance was pervasive, in contrast to the absence of a growth-rate effect. We did not expect such strong differences between the replicates (batches) and so this batch effect merits closer scrutiny in future experiments. The batch effect was present directly (main effect) or indirectly (interaction) for 8 of 11 survival skills. A pattern of variation in the broad array of survival skills emerged, in which treatment groups (relative growth rate × batch, the individual elements of the interaction term) were characterized by a common level of performance for most survival skills, rather than proficiency in one or a small set of skills. The 20 treatment groups fell into three classes, two of which represented distinctive extremes of behavioral performance (clusters A and B in this study).

Differences between clusters A and B were many and the magnitudes of these differences were ecologically meaningful. The difference in responsiveness to the visual stimulus paralleled the difference in responsiveness to the acoustic stimulus, a pattern we previously observed at the level of individual larvae (Fuiman and Cowan 2003). Initiating a response to a threatening stimulus is the first and most critical stage in predator evasion because only after a response begins do aspects of its timing, magnitude, and direction come into play. If our measures are relevant to the natural predation scenario, the difference of 32–37 percentage points in responsiveness could translate into a substantial difference in mortality between batches. For example, laboratory experiments showed that pinfish (14–15 cm TL) caught 98% of non-responding red drum larvae of the size studied here, whereas they caught 57% of responding larvae (Fuiman 1994). These percentages, when applied to mean visual- and acoustic-responsiveness values observed in the current study, predict that larvae from treatment groups in cluster A would survive 32%–39% of attacks, but that larvae from treatment groups in cluster B would survive 19%–24% of attacks.

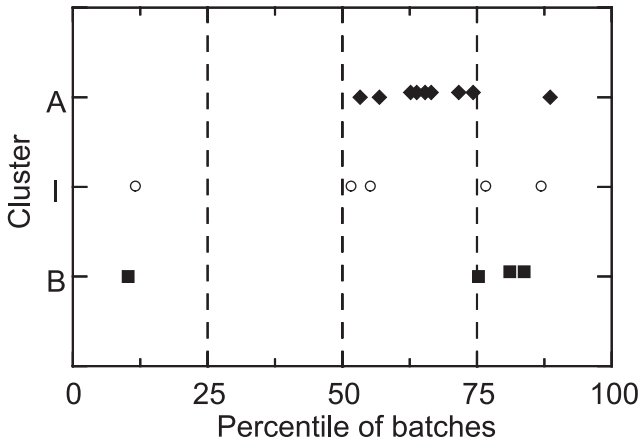
These calculations, however, do not take into account the coordinated differences in other survival skills that coincide with differences in responsiveness to further enhance the survival of cluster A larvae relative to cluster B larvae. Cluster A larvae traveled 5–10 mm farther during a response, and approximately 40–60 $mm \cdot s^{-1}$ faster, although their responses lasted only 0.02 s longer (i.e., faster acceleration). The optimal strategy for predator evasion by a fish larva attacked by a larger fish is rapid acceleration that takes the larva out of the predator's path in the final moments of the attack (Blaxter and Fuiman 1990; Fuiman and Magurran 1994). Cluster A larvae also had a 0.05 s shorter latency in their response to the visual stimulus. This earlier response corresponded to a mean reactive distance of 21.9 cm from the accelerating stimulus, compared with 16.5 cm for cluster B larvae. This left larvae with an average of 0.22 and 0.17 s (clusters A and B, respectively) before the "predator" would have made contact had the larva not responded. Therefore, the opposite sign of the difference in response latency between clusters A and B is fully concordant with the other variables: a negative difference or earlier response signifies better performance (a greater distance between predator and larva and more time to escape). The benefit of ever earlier responses does not increase indefinitely, however. Very early responses are detrimental because they allow the predator sufficient time to correct its attack path to intercept the moving prey (Fuiman 1993; Fuiman and Magurran 1994). Overall, the earlier response and seemingly small advantage in response distance for cluster A larvae amplify the effect of their heightened responsiveness on the probability of surviving a predatory attack.

An obvious and important question, given the presence of a batch effect on larval performance and its likely importance to predation-mortality risk, is, What is the cause of the batch effect? Our experimental design did not allow us to draw definitive conclusions, but we can comment on the most obvious possibilities: variations in rearing conditions or in egg quality. It is unlikely that rearing conditions varied enough to generate differences in behavior. We maintained reasonably constant conditions of temperature, salinity, and photoperiod, and used consistent rearing procedures (initial stocking density, feeding regime). However, all batches assigned to cluster B occurred after the end of October 1997. It is possible that an obscure or undocumented but detrimental change in rearing conditions or procedures took place at this time, but we are unable to determine what this might have been.

Variation in parental or egg quality is a possible explanation for the variation in behavior among batches. We obtained eggs for our laboratory experiment from four separate broodstock tanks, each containing 2 or 3 females and 2 or 3 males. Therefore, each batch was produced by an unknown number of parents, and different batches obtained from the same tank may have been produced by the same or different parents. Therefore, it is impossible to assess the role of genetics in the behavioral differences we observed or to make inferences about changes in an individual female's egg quality over time. Nevertheless, we do have evidence that reproductive seasonality may have had an effect on batch variability, and we discuss this possibility in order to identify an important topic for future research.

Our broodstock spawned voluntarily over a protracted reproductive season (5–9 months for any particular broodstock

Fig. 7. Possible relationship between behavioral performance of batches of red drum larvae and timing of batch production within the spawning season. Relative timing is expressed as the ordinal rank of a batch divided by the number of batches produced by a tank of broodstock in a season. Fast- and slow-growing larvae within each batch are plotted separately. Batches in cluster A (◆) had better behavioral performance than batches in cluster B (■). Batches labeled I (○) had intermediate behavioral performance. Data shown are for nine batches; spawning data were not available for one batch.



tank) that was often out of phase with their natural spawning period (locally September and October, according to hatching dates of wild-caught larvae; Rooker and Holt 1997). Generally, spawning in a tank would begin at some point in the year and its frequency would increase over the next 3–5 months, then decrease before ceasing completely. Batches having poorly performing larvae (cluster B) were produced during the early and late stages of this reproductive period (that is, in the first and last quartiles of spawns). All but one of the batches in cluster A were produced during the third quartile of the spawns from a tank (Fig. 7). The lone exception was fast-growing larvae from batch 6, which were spawned at the end of the season (87th percentile of spawns). This apparent association between relative timing of a batch within the spawning period and behavioral performance of offspring may be the product of poorer maternal or egg quality at the start and end of the reproductive period. Several studies have shown that egg quality (e.g., diameter, dry weight, and energy, yolk, fatty acid, amino acid, or hormone content) can vary among batches with a peak at midseason (e.g., Kamler and Stachowiak 1992; Kjørsvik 1994; Chambers and Waiwood 1996), but links between egg quality and larval behavior have not been established. Browman et al. (2003) found no connection between maternal nutritional condition and routine swimming behavior of offspring in Atlantic cod (*Gadus morhua*), at least under non-extreme conditions.

In summary, we found that growth rates of red drum larvae were not related, positively or negatively, to predation-mortality rate or to performance of various survival skills. There were significant and coordinated differences among batches of larvae in the behavioral skills larvae could use to evade predators. Specifically, elevated responsiveness to threatening stimuli and improved timing and heightened magnitude of escape responses produced compounding benefits to the survival potential of some batches over others. The underlying causes of the variability among batches are not known, but seasonality of maternal or egg quality is a possible source of variation in larval behavioral performance. Understanding the causes of variation in larval antipredator behavior and their implications for larval-stage mortality and subsequent recruitment success is a critical area for further research.

Acknowledgements

We thank Connie R. Arnold, formerly of the University of Texas Marine Science Institute, and Robert Vega of the Texas Parks and Wildlife Department for maintaining broodstock and generously providing red drum eggs and spawning records. Several students, including Adrienne Berg, Cynthia Faulk, Vanessa Malley, Daniel Sabath, Etai Timna, and Jeremy Walther, cared for larvae and helped with experiments. Our analyses benefited from discussions with Ken Rose and Eric Smith. Thanks are also extended to Ewa Kamler and Elin Kjørsvik for help with literature. Experiments were conducted in accordance with the regulations of the University of Texas at Austin Institutional Animal Care and Use Committee. This material is based upon work supported by the National Science Foundation under grant Nos. 9521240 (to L.A.F.) and 9529207 (to J.H.C.), and is contribution No. 1339 of the University of Texas Marine Science Institute.

References

Anderson, J.T. 1988. A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. J. Northwest Atl. Fish. Sci. **8**: 55–66.

Bailey, K.M., and Batty, R.S. 1984. Laboratory study of predation by *Aurelia aurita* on larvae of cod, flounder, plaice and herring: development and vulnerability to capture. Mar. Biol. (Berl.), **83**: 287–291.

Bailey, K.M., and Houde, E.D. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. Adv. Mar. Biol. **25**: 1–83.

Batty, R.S. 1989. Escape responses of herring larvae to visual stimuli. J. Mar. Biol. Assoc. U.K. **69**: 647–654.

Bertram, D.F., and Leggett, W.C. 1994. Predation risk during the early life history periods of fishes: separating the effects of size and age. Mar. Ecol. Prog. Ser. **109**: 105–114.

Billerbeck, J.M., Lankford, T.E., and Conover, D.O. 2001. Evolution of intrinsic growth and energy acquisition rates. I. Trade-offs with swimming performance in *Menidia menidia.* Evolution, **55**: 1863–1872.

Blaxter, J.H.S. 1976. Reared and wild fish — how do they compare? *In* Proceedings of the Tenth European Symposium on Marine Biology, 7 July 1975, Brussels, Belgium. Vol. 1. *Edited by* G. Persoone and E. Jaspers. Institute for Marine Scientific Research, Bredene, Belgium. pp. 11–26.

Blaxter, J.H.S. 1988. Pattern and variety in development. *In* Fish physiology. Vol. 11. *Edited by* W.S. Hoar and D.J. Randall. Academic Press, San Diego, Calif. pp. 1–58.

Blaxter, J.H.S., and Fuiman, L.A. 1990. The role of the sensory systems of herring larvae in evading predatory fishes. J. Mar. Biol. Assoc. U.K. **70**: 413–427.

Browman, H.I., St.-Pierre, J.-F., Skiftesvik, A.B., and Racca, R.G. 2003. Behaviour of Atlantic cod (*Gadus morhua*) larvae: an attempt to link maternal condition with larval quality. *In* The Big Fish Bang: Proceedings of the 26th Annual Larval Fish Conference, 22–26 July 2002, Oslow, Norway. *Edited by* H.I. Browman and A.B. Skiftesvik. Institute of Marine Research, Bergen, Norway. pp. 71–95.

Caley, M.J, Carr, M.H., Hixon, M.A., Hughes, T.P., Jones, G.P., and Menge, B.A. 1996. Recruitment and the local dynamics of open marine populations. Annu. Rev. Ecol. Syst. **27**: 477–500.

Chambers, R.C., and Waiwood, K.G. 1996. Maternal and seasonal differences in egg sizes and spawning characteristics of captive Atlantic cod, *Gadus morhua*. Can. J. Fish. Aquat. Sci. **53**: 1986–2003.

Cowan, J.H., Jr., and Houde, E.D. 1990. Growth and survival of bay anchovy *Anchoa mitchilli* larvae in mesocosm enclosures. Mar. Ecol. Prog. Ser. **68**: 47–57.

Cowan, J.H., Jr., and Houde, E.D. 1992. Size-dependent predation on marine fish larvae by ctenophores, scyphomedusae, and planktivorous fish. Fish. Oceanogr. **1**: 113–126.

Cowan, J.H., Jr., Houde, E.D., and Rose, K.A. 1996. Size-dependent vulnerability of marine fish larvae to predation: an individual-based numerical experiment. ICES J. Mar. Sci. **53**: 23–37.

Cowan, J.H., Jr., Rose, K.A., and Houde, E.D. 1997. Size-based foraging success and models of larval fish populations. *In* Early life history and recruitment in fish populations. *Edited by* R.C. Chambers and E.A. Trippel. Chapman and Hall, London. pp. 357–386.

Crowder, L.W., Rice, J.A., Miller, T.J., and Marschall, E.A. 1992. Empirical and theoretical approaches to size-based interactions and recrutiment variability in fishes. *In* Individual-based models and approaches in ecology. *Edited by* D.L. DeAngelis and L.J. Gross. Chapman and Hall, New York. pp. 237–255.

Cushing, D.H. 1975. Marine ecology and fisheries. Cambridge University Press, Cambridge.

Dahlberg, M.D. 1979. A review of survival rates of fish eggs and larvae in relation to impact assessments. Mar. Fish. Rev. **41**(3): 1–12.

Davis, C.S., Flieri., G.R., Wiebe, P.H., and Franks, F.J.S. 1991. Micropatchiness, turbulence and recruitment in plankton. J. Mar. Res. **49**: 109–151.

Fitzhugh, G.R., Crowder, L.B., and Monaghan, J.P., Jr. 1996. Mechanism contributing to variable growth in juvenile southern flounder (*Paralichthys lethostigma*). Can. J. Fish. Aquat. Sci. **53**: 1964–1973.

Folkvord, A., Øiestad, V., and Kvenseth, P.G. 1994. Growth patterns of three cohorts of Atlantic cod larvae (*Gadus morhua* L.) studies in a macrocosm. ICES J. Mar. Sci. **51**: 325–336.

Fuiman, L.A. 1989. Vulnerability of Atlantic herring larvae to predation by yearling herring. Mar. Ecol. Prog. Ser. **51**: 291–299.

Fuiman, L.A. 1993. Development of predator evasion in Atlantic herring, *Clupea harengus* L. Anim. Behav. **45**: 1101–1116.

Fuiman, L.A. 1994. The interplay of ontogeny and scaling in the interactions of fish larvae and their predators. J. Fish Biol. **45**(Suppl. A): 55–79.

Fuiman, L.A., and Cowan, J.H., Jr. 2003. Behavior and recruitment success in fish larvae: repeatability and covariation of survival skills. Ecology, **84**: 53–67.

Fuiman, L.A., and Gamble, J.C. 1988. Predation by Atlantic herring, sprat, and sandeels on herring larvae in large enclosures. Mar. Ecol. Prog. Ser. **44**: 1–6.

Fuiman, L.A., and Magurran, A.E. 1994. Development of predator defences in fishes. Rev. Fish Biol. Fish. **4**: 145–183.

Fuiman, L.A., Poling, K.R., and Higgs, D.M. 1998. Quantifying developmental progress for comparative studies of larval fishes. Copeia, 1998: 602–611.

Fuiman, L.A., Smith, M.E., and Malley, V.N. 1999. Ontogeny of routine swimming speed and startle responses in red drum, with a comparison of responses to acoustic and visual stimuli. J. Fish Biol. **55**: 215–226.

Hare, J.A., and Cowen, R.K. 1997. Size, growth, development, and survival of the planktonic larvae of *Pomatomus saltatrix* (Pisces: Pomatomidae). Ecology, **78**: 2415–2431.

Heath, M., and Gallego, A. 1997. From the biology of the individual to the dynamics of the population: bridging the gap in fish early life studies. J. Fish Biol. **51** (Suppl. A): 1–29.

Houde, E.D. 1987. Fish early life dynamics and recruitment variability. Am. Fish. Soc. Symp. No. 2. pp. 17–29.

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

Houde, E.D. 2002. Mortality. *In* Fishery science: the unique contributions of early life stages. *Edited by* L.A. Fuiman and R.W. Werner. Blackwell Science, Oxford. pp. 64–87.

Kamler, E., and Stachowiak, J. 1992. Egg size and reproductive effort in tench (*Tinca tinca* (L.)) females from heated waters. Pol. Arch. Hydrobiol. **39**: 101–107.

Kjørsvik, E. 1994. Egg quality in wild and broodstock cod *Gadus morhua* L. J. World Aquacult. Soc. **25**: 22–29.

Lankford, T.E., Billerbeck, J.M., and Conover, D.O. 2001. Evolution of intrinsic growth and energy acquisition rates. II. Trade-offs with vulnerability to predation in *Menidia menidia*. Evolution, **55**: 1873–1881.

Leggett, W.C., and DeBlois, E. 1994. Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? Neth. J. Sea Res. **32**: 119–134.

Letcher, B.H., Rice, J.A., Crowder, L.B., and Rose, K.A. 1996. Variability in survival of larval fish: disentangling components with a generalized individual-based model. Can. J. Fish. Aquat. Sci. **53**: 787–801.

Litvak, M.K., and Leggett, W.C. 1992. Age- and size-selective predation on larval fishes: the bigger-is-better hypothesis revisited. Mar. Ecol. Prog. Ser. **81**: 13–24.

McGurk, M.P. 1986. Natural mortality of marine pelagic fish eggs and larvae: role of spatial patchiness. Mar. Ecol. Prog. Ser. **34**: 227–242.

Meekan, M., and Fortier, L. 1996. Selection for fast growth during the larval life of Atlantic cod *Gadus morhua* on the Scotian Shelf. Mar. Ecol. Prog. Ser. **137**: 25–37.

Miller, T.J., Crowder, L.B., Rice, J.A., and Marschall, E.A. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Can. J. Fish. Aquat. Sci. **45**: 1657–1670.

O'Neal, J.P. 2002. The relationship between growth rate and predation mortality in larval fishes: an assessment using mesocosm enclosures and individual based modeling. M.S. thesis, University of South Alabama, Mobile.

Paradis, A.R., Pepin, P., and Brown, J.A. 1996. Vulnerability of fish eggs and larvae to predation: review of the influence of the relative size of prey and predator. Can. J. Fish. Aquat. Sci. **53**: 1226–1235.

Rice, J.A., Crowder, L.B., and Holey, M.E. 1987. Exploration of mechanisms regulating larval survival in Lake Michigan bloater: a recruitment analysis based on characteristics of individual larvae. Trans. Am. Fish. Soc. **116**: 703–718.

Rice, J.A., Crowder, L.B., and Rose, K.A. 1993*a*. Interactions between size-structured predator and prey populations: experimental test and model comparisons. Trans. Am. Fish. Soc. **122**: 481–491.

Rice, J.A., Miller, T.J., Rose, K.A., Crowder, L.B., Marschall, E.A., Trebitz, A.S., and DeAngelis, D.L. 1993*b*. Growth-rate variation and larval survival — inferences from an individual-based size-dependent predation model. Can. J. Fish. Aquat. Sci. **50**: 133–142.

Rooker, J.R., and Holt, S.A. 1997. Utilization of subtropical seagrass meadows by newly settled red drum (*Sciaenops ocellatus*): patterns of distribution and growth. Mar. Ecol. Prog. Ser. **158**: 139–149.

Rooker, J.R., Holt, S.A., Soto, M.A., and Holt, G.J. 1998. Postsettlement patterns of habitat use by sciaenid fishes in subtropical seagrass meadows. Estuaries, **21**: 318–327.

SAS Institute Inc. 2001. SAS®. Version 8.2 [computer program]. SAS Institute Inc., Cary, N.C.

Secor, D.H., and Dean, J.M. 1992. Comparison of otolith-based back-calculation methods to determine individual growth histories of larval striped bass, *Morone saxatilis*. Can. J. Fish. Aquat. Sci. **49**: 1439–1454.

Shepherd, J.G., and Cushing, D.H. 1980. A mechanism for density-dependent survival of larval fish as the basis of a stock–recruitment relationship. J. Cons. Cons. Int. Explor. Mer, **39**: 160–167.

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

Smith, M.E., and Fuiman, L.A. 2003. Causes of growth depensation in red drum, *Sciaenops ocellatus*, larvae. Environ. Biol. Fishes, **66**: 49–60.

Snedecor, G.W., and Cochran, W.G. 1967. Statistical methods. Iowa State University Press, Ames.

Systat Software, Inc. 2002. SYSTAT®. Version 10.2 [computer program]. Systat Software, Inc., Point Richmond, Calif.

Takasuka, A., Aoki, I., and Mitani, I. 2003. Evidence of growth-selective predation on larval Japanese anchovy *Engraulis japonicus* in Sagami Bay. Mar. Ecol. Prog. Ser. **252**: 223–238.

Todd, C.D. 1998. Larval supply and recruitment of benthic invertebrates: Do larvae always disperse as much as we believe? Hydrobiologia, **376**: 1–21.