Effects of larval density on the growth and survival of weakfish *Cynoscion regalis* in large-volume enclosures

Janet T. Duffy, Charles E. Epifanio

University of Delaware, Hugh R. Sharp Campus, College of Marine Studies, 700 Pilottown Road, Lewes, Delaware 19958, USA

ABSTRACT: We investigated the effects of 3 different stocking densities on growth and mortality of weakfish *Cynoscion regalis* larvae in large enclosures ($1.4 m^3$) deployed in Delaware Bay, USA. Stocking densities were 50, 500 and 5000 larvae m^{-3}. Larvae in each treatment were fed natural zooplankton prey maintained at 250 prey items l^{-1}; this concentration of prey was based on values measured on the weakfish spawning grounds in Delaware Bay. We conducted separate experiments for early-stage (2 to 9 d post-hatching) and late-stage (9 to 17 d post-hatching) larvae. There was a significant effect of stocking density on growth regardless of larval age. Mean instantaneous growth rates (dry wt) ranged from 0.10 to 0.18 d^{-1} for early-stage larvae and from 0.18 to 0.29 d^{-1} for late-stage larvae. Instantaneous mortality rates were lower than reported field values for weakfish larvae, and there was no significant effect of stocking density. These results indicate that growth of larvae in densely populated patches may be diminished.

KEY WORDS: Weakfish · Larvae · Growth · Mortality · Enclosures

INTRODUCTION

It is widely accepted that the year-class strength of any fish species is largely dependent upon survival through the larval and early juvenile stages (e.g. Houde 1987). Yet many factors act to restrict larval development or cause larval death. Previous studies on growth and mortality have primarily focused on starvation (e.g. Govoni et al. 1983, Frank & Leggett 1986, Leggett 1986) or predation (e.g. Bailey & Batty 1984, Hunter 1984, Hewitt et al. 1985), but other factors may also play a role in natural population fluctuations.

Larval density has recently been recognized as one such factor. Most reported values for larval density are actually underestimates as they fail to account for the patchy distribution of larvae in horizontal space (MacKenzie et al. 1990). However, recent studies have shown that larvae are often distributed in large aggregations (Houde & Lovdal 1985, McGurk 1986). The high density in such patches may lead to intra-specific competition for food and space. If the food resource is limited, this competition may reduce overall growth

(Houde 1977, Taniguchi 1981). In addition, larval density may influence the vulnerability of larvae to predation. McGurk (1986) proposed that the mortality rate of fish eggs and larvae was directly correlated with patch size, and de Lafontaine & Leggett (1989) found that predation rates on yolk-sac larvae of capelin *Mallotus villosus* by jellyfish predators were linearly related to larval density.

Larval density may have indirect effects on predation mortality as well. Houde (1987) suggested that larvae maintained on an inadequate diet or ration exhibited slower growth rates and spent more time in the larval stage. So, for any given predation rate, survival to the juvenile stage would be inversely related to the quality of the diet or the quantity of the ration. However, recent studies indicate that older, larger larvae may be more vulnerable to predation in the plankton than are smaller larvae (Cowan & Houde 1992, Litvak & Legett 1992, Pepin et al. 1992).

Recent studies of growth and mortality in fish larvae have used large-volume enclosures deployed directly in the natural environment. De Lafontaine & Leggett

(1987a) showed that enclosed waters simulate the physical and chemical characteristics of the ambient water column. Moreover, enclosures are large enough that organisms may be stocked at natural densities without severely altering behavioral phenomena (Cowan & Houde 1990, Epifanio et al. 1991, Cowan et al. 1992). Thus, experiments in enclosures may provide more accurate descriptions of growth and mortality rates than do comparable experiments in aquaria. De Lafontaine & Leggett (1987b) demonstrated that the rate of predation by *Aurelia aurita* on larval capelin was lower in large-volume enclosures than in aquaria and was similar to rates occurring *in situ*. Estimates of larval growth in the laboratory may be different from field rates as well. MacKenzie et al. (1990) determined that growth rates in laboratory studies are often lower than *in situ* rates, and Cope (1991) showed that weakfish larvae raised in aquaria exhibited lower growth rates than larvae raised in enclosures at similar prey densities.

In this paper, we describe the effects of stocking density on the growth and survival of weakfish *Cynoscion regalis* larvae in large-volume enclosures. Weakfish (family Sciaenidae) inhabit the U.S. Atlantic coastline from Florida to Massachusetts (Mercer 1983). The weakfish is a commercially important species that winters off of North Carolina and moves into shallow bays and estuaries in the Middle Atlantic Bight to spawn in the spring (Wilk 1976). In Delaware Bay, spawning occurs between May and July, where 2 separate spawning peaks have been observed (Daiber 1957, Villoso 1990, Goshorn & Epifanio 1991a).

MATERIALS AND METHODS

Enclosures. The enclosures were modelled after those of de Lafontaine & Leggett (1987a). Each enclosure was a 1 m diameter, 3 m long cylinder constructed of Dacron sailcloth (25 µm) with a 1 m Nitex conical end (53 µm). Steel rings were lashed to the sides at 1 m intervals for support. The total enclosure volume was 1.4 m^3. A screened, PVC cod-end (53 µm) was secured to the bottom of the enclosure to collect organisms at the conclusion of each experiment. The enclosures were submerged except for 0.5 m which remained emersed to prevent sample loss and wash-over of waves. Enclosures were filled by allowing ambient water to pass through the mesh walls. We suspended a total of 12 enclosures from 2 wooden rafts moored at the southern terminus of Delaware Bay (38° 47′ N, 75° 07′ W) near Cape Henlopen, Delaware, USA (Fig. 1).

Subsurface temperature (1 m) was recorded continuously at the study site for the duration of the experi-

ments (TempMentor-100). In addition, vertical profiles of temperature, salinity, dissolved oxygen, and light intensity were taken hourly over one tidal cycle. Profiles were taken both inside and outside of a randomly selected enclosure.

Weakfish larvae. We investigated the effects of larval density on the growth and mortality rates of early-stage and late-stage weakfish larvae. Ripe adult weakfish were obtained from Delaware Bay in May and June 1992 and were artificially spawned. Eggs were fertilized in the field and returned to the laboratory where they were maintained at 21 °C, 30‰, and 14:10 h light:dark photoperiod. Chloramphenicol (5 mg l^{-1}) was added to enhance egg hatching (Epifanio et al. 1988, Goshorn 1990). Hatching occurred within 48 h. Larvae began feeding exogenously after 52 h and were maintained on a diet of wild zooplankton.

Zooplankton. Zooplankton prey was collected near the study site, returned to the laboratory and sieved
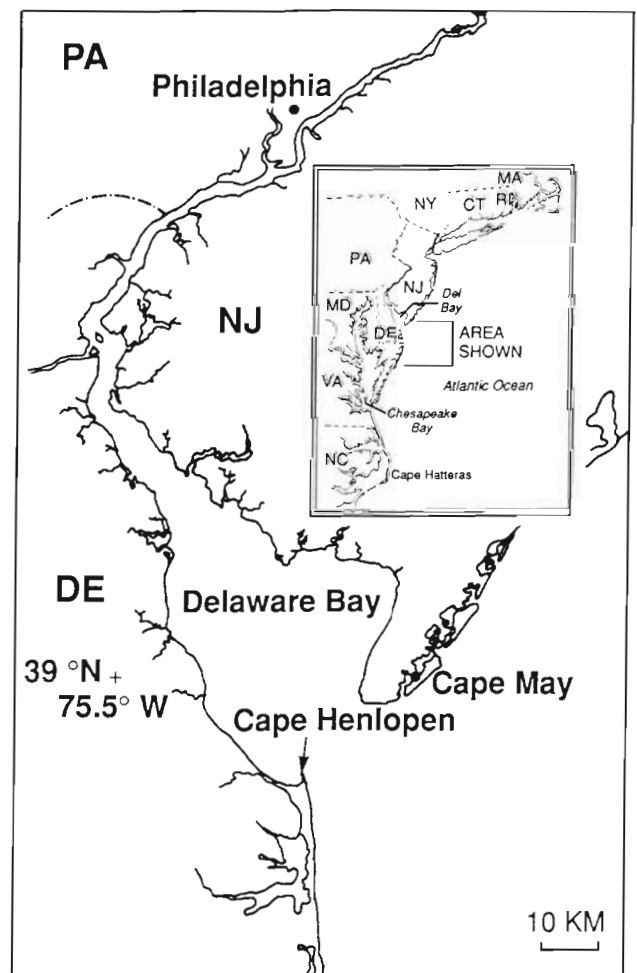

Fig. 1. Study site, Delaware Bay, USA. Arrow: enclosures near Cape Henlopen

through a 253 μm sieve (to exclude potential predators and unsuitable food organisms), then concentrated on a 53 μm sieve. Zooplankton prey was added to the enclosures and the same prey density (250 prey items l^{-1}) was provided for larvae in each treatment. This density was based on concentrations observed on the weakfish spawning grounds in Delaware Bay (Goshorn & Epifanio 1991a). The mesh walls of the enclosures isolated the internal prey assemblage from that in the ambient water column. Microzooplankton (<53 μm) could pass through the walls, but an earlier investigation showed that these organisms are not suitable prey for weakfish larvae (Cope 1991).

We monitored zooplankton concentrations from 2 randomly selected enclosures at 3 depths using a submersible plankton pump. Zooplankton concentrations in all enclosures were adjusted accordingly every 48 h to maintain the desired prey level.

Early-stage experiment. Enclosures were stocked with larvae that were 2 d post-hatching (2 dph). We transported larvae to the enclosure site in 4 l plastic bags filled with temperature-adjusted seawater. The enclosures were stocked at 50, 500 and 5000 larvae m^{-3} (hereafter Low Treatment, Mid Treatment, and High Treatment, respectively), and each treatment was replicated 4 times. These treatments were chosen because they span the densities of weakfish eggs and newly hatched larvae in the Delaware Bay during the spawning season (Feingold 1990, Villoso 1990). We used a formal randomization technique in the assignment of treatments and replicates to the various enclosures. Bags of larvae were allowed to equilibrate in the enclosures for 30 min prior to release.

We harvested all enclosures when the larvae reached 9 dph. Larvae were retrieved by slowly lifting the enclosure and rinsing down the interior with seawater. Experimental organisms were concentrated in the cod-end, and all samples were preserved in 4% formaldehyde and later transferred to 70% EtOH. Larvae were removed from all samples and counted.

Late-stage experiment. After all enclosures had been retrieved from the early-stage experiment, they were immediately re-deployed and stocked with 9 dph larvae that had been reared in the laboratory. In order to allow direct comparisons between the 2 age classes of larvae, it was important to maintain a comparable weight-specific food ration in the 2 experiments. To do this we maintained the same prey concentration for both early-stage and late-stage larvae, and adjusted the stocking density of larvae to assure a metabolically equivalent ration in the 2 experiments. We based this on the allometric relationship between metabolic rate and body weight:

$$\Delta O_2/\Delta t = aW^b$$

where a = metabolic rate of an organism of unit weight; b = a constant; and W = body weight. Values for the constant b vary taxonomically, and for fish a typical value is about 0.8 (Brett & Groves 1988). Therefore, we calculated the appropriate number of 9 dph larvae as:

$$N_{9\,dph} = (W_{2\,dph}/W_{9\,dph})^{0.8}$$

where N = number of 9 dph larvae; W = mean dry wt (μg) of the respective larvae in each age class. We used this equation to calculate stocking densities for the late-stage experiment (23, 238 and 2390 larvae m^{-3}).

We added wild zooplankton to all enclosures (250 prey items l^{-1}), and monitored and adjusted the prey concentration on alternate days. Although older larvae are able to capture and consume larger prey items (Goshorn 1990), the same size range of wild zooplankton was provided as in the early-stage experiment to keep as many factors constant between the 2 experiments as possible. All enclosures were harvested on 17 dph.

Larval recovery. We accounted for the number of larvae lost during enclosure retrieval. In each of 2 preliminary experiments, 6 enclosures were stocked with larvae, allowed to equilibrate for 3 h, and then harvested. The efficiency of larval recovery was high. Results indicated that 85 ± 8.2% of early-stage larvae and 98 ± 2.4% of late-stage larvae were recovered during the retrieval process. All estimates of mortality were corrected for these efficiencies.

Estimation of growth and mortality rates. The notochord length (*NL*) of each larva was measured to the nearest 0.01 mm with the use of a computer-assisted, image-analysis system (Olympus Morphometry, vers. 2.2). *NL* was multiplied by a correction factor of 1.33 to account for shrinkage due to preservation (Goshorn 1990). For samples containing a large number of larvae, 55 were chosen for measurement by inverting the sample vial 3 times and selecting a larva. This method is used in our laboratory and is known to be an adequate method for sampling the larvae. All measured larvae were dried at 60°C for 48 h and weighed individually (Cahn 29 electrobalance). Initial values for dry wt (*W*) and *NL* were obtained from 50 larvae chosen haphazardly at the beginning of each experiment.

Growth in length was calculated for each larva according to:

$$G_L = (L_t - L_s)/t$$

where L_s = mean notochord length (mm) of 50 representative larvae measured at the beginning of the experiment; L_t = notochord length of each larva returned at the end of each experiment; and t = the duration of the experiment in days (Gamble et al. 1985, Cope 1991).

Growth in dry weight was assumed to be exponential (Cope 1991, Goshorn & Epifanio 1991b) and was calculated according to:

$$G_W = (\ln W_t - \ln W_s)/t$$

where W_s = mean dry wt (µg) of 50 representative larvae weighed at the beginning of the experiment; W_t = the dry weight of each larva returned at the end of the experiment; and t = duration of the experiment in days.

Statistical analyses consisted of 1-way, nested ANOVAs where variance among individual larvae was nested within variance among replicate enclosures. Separate analyses were conducted for each of the dependent variables (NL, W, G_L and G_W), and significance was determined at α = 0.05 (Zar 1984). If significant differences were found to exist among treatments, a Tukey Multiple Comparison test was performed to identify the differences between individual treatments.

Mortality was assumed to be exponential (Cope 1991) and was calculated as:

$$Z = (\ln N_s - \ln N_t)/t$$

where N_s = the number of larvae initially stocked; N_t = the number of viable larvae at the conclusion of the experiment; and t = duration of the experiment in days. We performed a 1-way ANOVA to detect significant differences in Z among treatments.

RESULTS

Physical and chemical environment

The subsurface (1 m) temperature at the study site did not fluctuate greatly over the course of the experiments and ranged from a low of 17 °C to a high of 20 °C. Vertical profiles indicated that both temperature and salinity inside the enclosure was similar to the surrounding water column (Fig. 2). Concentrations of dissolved oxygen and levels of light intensity were both lower in the enclosure than in the ambient water column, but were not low enough to affect larval feeding (Breitburg 1990, Pryor & Epifanio 1993).

Zooplankton

In the early-stage experiment, the prey assemblage in the enclosures was dominated by copepod nauplii (56.4%). Rotifers and all life history stages of the calanoid copepod *Acartia tonsa* comprised the majority of the prey assemblage in the late-stage experiment (9.2 and 60.2% respectively). In both experiments the copepods *Oithona* sp., *Paracalanus* sp., and *Pseudocalanus* sp. were also present in high numbers. Although zooplankton densities fluctuated substantially over the course of the experiments, levels were always lower than 250 l^{-1} at sampling, and it was necessary to add zooplankton to enclosures on alternate days to maintain the desired density.

Early-stage experiment

Initial values for NL and W of weakfish larvae were 2.23 mm and 10.48 µg respectively. There was a significant effect of larval density on growth in both parameters (Table 1). Larvae in the High Treatment showed significantly slower growth rates than larvae in either of the other 2 treatments. Mean values for G_L varied with treatment and ranged from 0.08 to 0.21 mm d^{-1}, as did mean G_W (0.10 to 0.18 d^{-1}). Mortality coefficients (Z) also varied among treatments, and although no sig-
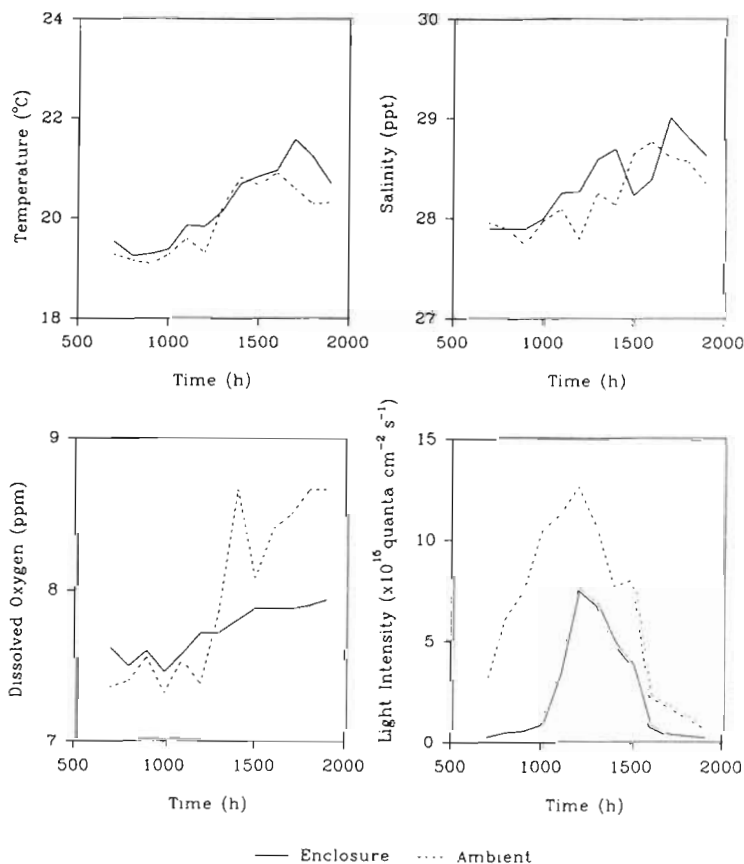

Fig. 2. Depth-averaged profiles of temperature, salinity, dissolved oxygen, and light intensity taken inside and outside of a randomly selected enclosure over 1 tidal cycle

Table 1. *Cynoscion regalis*. Means (± SE) of notochord length (*NL*), dry weight (*W*), growth rate in length (*G_L*), growth in weight (*G_W*), and instantaneous mortality (*Z*) of early-stage (9 dph) and late-stage (17 dph) weakfish larvae stocked at 3 different densities in replicate enclosures (n = 4). Significant differences (α = 0.05) as determined by a Tukey Multiple Comparison test: *p < 0.05; **p < 0.005; ***p < 0.001

Density (larv. m^{-3})	NL (mm)	W (μg)	G_L (mm d^{-1})	G_W (d^{-1})	Z (d^{-1})
9 dph					
50	3.73 (0.06)	36.58 (0.001)	0.21 (0.01)	0.18 (0.003)	0.19 (0.04)
500	3.61 (0.03)	36.50 (0.001)	0.20 (0.004)	0.17 (0.002)	0.16 (0.03)
5000	2.82** (0.03)	23.61* (0.001)	0.08** (0.004)	0.10* (0.004)	0.09 (0.01)
17 dph					
23	6.25*** (0.12)	336.38** (0.02)	0.39*** (0.02)	0.29*** (0.02)	0.16 (0.03)
238	5.02 (0.07)	171.54** (0.01)	0.25 (0.01)	0.20*** (0.01)	0.31 (0.08)
2390	4.79 (0.05)	142.56** (0.01)	0.21 (0.01)	0.18*** (0.004)	0.29 (0.05)

nificant differences were detected, greatest mortality (0.19 d^{-1}) occurred in the Low Treatment.

Late-stage experiment

In the late-stage experiment, initial values for NL and W were 3.14 mm and 29.34 μg, and final values for both parameters varied significantly among treatments (Table 1). G_L was significantly higher in the Low Treatment (0.39 mm d^{-1}) than in the Mid (0.25 mm d^{-1}) or High (0.21 mm d^{-1}) Treatments. G_W again was highest in the Low Treatment, and was significantly different among all 3 treatments. Instantaneous mortality coefficients ranged from 0.16 to 0.31 d^{-1}, and although there were no significant effects of stocking density, larvae in the High Treatment exhibited the highest rate of mortality.

DISCUSSION

These results indicate that larval density has a significant effect on growth, regardless of larval age. Values for G_L and G_W in the Low and Mid Treatments compare well to reported values for other sciaenid larvae raised in enclosures at similar temperatures. Cope (1991) reported G_L values between 0.17 and 0.27 mm d^{-1} and G_W values between 0.14 and 0.21 d^{-1} for weakfish larvae raised at various prey densities, and Cowan

et al. (1992) reported G_W as 0.20 d^{-1} for black drum *Pogonias cromis* larvae. In our experiments, early-stage weakfish larvae in the High Treatment exhibited very low growth rates (G_L = 0.08 mm d^{-1}; G_W = 0.10 d^{-1}), whereas late-stage larvae in the Low Treatment exhibited very high growth rates (G_L = 0.39 mm d^{-1}; G_W = 0.29 d^{-1}).

To investigate the potential cause of the observed lower growth rates, we estimated the overall larval ingestion rate of zooplankton to determine if food limitation played a role. We approximated the proportion of the prey assemblage being consumed by using a model that describes weight-specific ingestion rate for any population of larval fish feeding on wild zooplankton in nature (MacKenzie et al. 1990). We calculated ingestion rate (I, μg food ingested ind.$^{-1}$ d^{-1}) as:

$$\log I = 1.162 \log W + 0.029 T - 1.343$$

where W = dry wt of a larva (μg); and T = temperature (°C). Using the instantaneous growth rates (G_W) from our experiments, we calculated the expected weight of individual larvae on each day in each experimental treatment and then used the above model to calculate the expected daily ingestion rate of the larvae in each treatment. We then used the observed instantaneous mortality rates to determine the expected number of surviving larvae in each treatment and from this calculated the expected quantity of zooplankton being consumed in each treatment during each day of the experiments. Results of this analysis indicated that High Treatment larvae in both experiments may have consumed as much as 50 % of the available ration per day, particularly early in each experiment when the number of surviving larvae was high. However, we replenished the prey every 48 h and the loss to ingestion was somewhat compensated by the reproductive rate of the zooplankton. Nevertheless, there is a real possibility that High Treatment larvae were prey-limited, providing a facile explanation for the reduced growth rates observed in that treatment. However, our calculations showed that larvae in the Low and Mid Treatments were provided with sufficient food for ad libitum feeding for the duration of the experiment. Food limitation is then an unlikely explanation for the significant differences in growth rates between these 2 treatments in the late-stage experiment. Further investigation is necessary before an explanation of these results can be provided.

Food limitation may occur in the field, particularly since both weakfish larvae and their prey appear to occur in patches that are advected along with discrete water parcels in estuarine circulation (Goshorn & Epifano 1991a, P. M. Rowe & C. E. Epifano unpubl.). Unlike sessile organisms that are subject to a continually renewed supply of prey items as tidal currents flow

past them, fish larvae tend to move with a water mass and the quantity of prey in any particular patch is finite. So just as in our enclosures, high densities of weakfish larvae in the field may crop a particular zooplankton patch to levels that affect growth and larval duration. The overall impact of this may be ameliorated by the tidally rhythmic pattern of vertical migration that has been observed for weakfish larvae in Delaware Bay (Rowe & Epifanio unpubl.). While this pattern of migration could result in the exposure of larvae to many different patches of prey during the entire period of larval development, the potential for depleting any particular patch remains.

Daily mortality rates in the enclosures were lower than field estimates for larvae of weakfish and other sciaenids (Peebles & Tolley 1988). This was probably due to the absence of large predators in the enclosures, and the range of mortality values in our experiments was similar to that reported from earlier experiments with weakfish larvae (Cope 1991, Goshorn & Epifanio 1991b) and with other sciaenid species in both the laboratory (Houde & Taniguchi 1981) and in enclosures (Cowan et al. 1992).

We found that instantaneous rates of mortality were not significantly different among treatments in either of these experiments; however obvious trends are present. Counter-intuitively, mortality appears to increase as initial larval density decreases in the early-stage experiment. Cowan & Houde (1990) described a similar phenomenon in their study of bay anchovy. They explained this as a result of bites from mature copepods originally supplied to the larvae as prey in immature stages, and this may have been the case in the present study as well. Carnivorous cycloploid copepods made up a substantial portion of the prey assemblage and may have become predators on the fish larvae as the copepods matured. In the High Treatment, the grazing pressure from so many larvae may have decreased the numbers of these carnivorous zooplankters, resulting in reduced mortality of the larvae. However, the opposite trend was observed with late-stage larvae where the lowest mean mortality was observed in the Low Treatment. It may be that late-stage larvae are sufficiently large to avoid biting zooplankters, and the higher mortality in the High Treatment may have been due to other factors such as competition or crowding.

In our experiments we intentionally excluded large predators. Gelatinous zooplankters such as lobate ctenophores and jellyfish would not only reduce the density of fish larvae in the enclosures, but would also reduce the numbers of microzooplankton. Since gelatinous predators are present in Delaware Bay during the vulnerable larval and early juvenile stages of weakfish development, the inclusion of these predators would

provide a more accurate description of field events and provide additional insight into weakfish recruitment.

We have shown that stocking density directly affects larval growth, but our results suggest that mortality is not directly density-dependent. Larvae in the field are often distributed in dense aggregations, and our results suggest that this may lead to reduced growth. This, in turn, may result in prolonged development and duration of the larval stage, increased exposure to predation, and diminished survival to the juvenile stage.

LITERATURE CITED

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

Breitburg, D. L. (1990). Near-shore hypoxia in the Chesapeake Bay; patterns and relationships among physical factors. Estuar. coast. Shelf Sci. 30(6): 593–609

Brett, J. R., Groves, T. D. D. (1979). Physiological energetics. In: Hoar, W. S., Randall, D. J. (eds.) Fish physiology. VIII: Bioenergetics and growth. Academic Press, New York, p. 261–342

Cope, J. S. (1991). Effects of prey density on growth and survival of larval weakfish (*Cynoscion regalis*) in field-developed enclosures and in laboratory aquaria. M.Sc. thesis, University of Delaware, Lewes

Cowan, J. H., Birdsong, R. S., Houde, E. D., Priest, J. S., Sharp, W. C., Mateja, G. B. (1992). Enclosure experiments on survival and growth of black drum eggs and larvae in lower Chesapeake Bay. Estuaries 15(3): 392–402

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

Daiber, F. C. (1957). The seatrout. Estuar. Bull. 2: 2–6

de Lafontaine, Y., Leggett, W. C. (1987a). Evaluation of *in situ* enclosures for larval fish studies. Can. J. Fish. Aquat. Sci. 44: 54–65

de Lafontaine, Y., Leggett, W. C. (1987b). Effects of container size on estimates of mortality and predation rates in experiments with microzooplankton and larval fish. Can. J. Fish. Aquat. Sci. 44: 1534–1543

de Lafontaine, Y., Leggett, W. C. (1989). Macroinvertebrate predation on larval fish: an *in situ* mesocosm approach. In: Blaxter, J. H. S. (ed.) The early life history of fish. The Third ICES Symposium, Bergen, 3–5 Oct., 1988. International Council for the Exploration of the Sea, Copenhagen, p. 487

Epifanio, C. E., Goshorn, D., Targett, T E. (1988). Induction of spawning in the weakfish, *Cynoscion regalis*. Fish. Bull. U.S. 86: 168–171

Epifanio, C. E., Cope, J. S., Rowe, P. M., Jenkins, F. M. (1991). Comparison of rates of development of Atlantic mud crab larvae in the laboratory and field-deployed enclosures. J. Crustacean Biol. 11(4): 540–545

Feingold, L. E. (1990). Influence of physical parameters on the distribution and survivorship of the early life stages of the weakfish in Delaware Bay. M.Sc. thesis, University of Delaware, Lewes

Frank, K. T., Leggett, W. C. (1986). Effect of prey abundance and size on the growth and survival of larval fish: an experimental study employing large volume enclosures. Mar. Ecol. Prog. Ser. 34: 11–22

Gamble, J. C., MacLachlan, P., Seaton, D. D. (1985). Comparative growth and development of autumn and spring spawned herring larvae reared in large enclosed ecosystems. Mar. Ecol. Prog. Ser. 26: 19–33

Goshorn, D. M. (1990). Distribution of larval weakfish (Cynoscion regalis) in The Delaware Bay and the relationship of field prey concentration to laboratory determined growth and mortality rates. Ph.D. dissertation. University of Delaware, Lewes

Goshorn, D. M., Epifanio, C. E. (1991a). The diet and prey abundance of weakfish larvae in Delaware Bay. Trans. Am. Fish. Soc. 120: 684–692

Goshorn, D. M., Epifanio, C. E. (1991b). Development, survival, and growth of larval weakfish (Cynoscion regalis) at different prey concentrations. Trans. Am. Fish. Soc. 120: 693–700

Govoni, J. J., Hoss, D. E., Chester, A. J. (1983). Comparative feeding of three species of larval fishes in the Northern Gulf of Mexico: Brevoortia patronus, Lieostomus xanthurus, and Micropogonias undulatus. Mar. Ecol. Prog. Ser. 13: 189–199

Hewitt, R. P., Theilacker, G. H., Lo, N. C. H. (1985). Causes of mortality in young jack mackerel. Mar. Ecol. Prog. Ser. 26: 1–10

Houde, E. D. (1977). Food concentration and stocking density effects on laboratory-reared larvae of bay anchovy, Anchoa mitchilli and the lined sole, Achirus lineatus. Mar. Biol. 43: 333–341

Houde, E. D. (1987). Fish early life dynamics and recruitment variability. Am. Fish. Soc. Symp. 2: 17–29

Houde, E. D., Lovdal, J. D. A. (1985). Patterns of variability in ichthyoplankton occurrence and abundance in Biscayne Bay, Florida. Estuar. coast. Shelf Sci. 20: 79–103

Houde, E. D., Taniguchi, A. K. (1981). Marine fish larvae growth and survival: effects of density-dependent factors: spotted seatrout (Cynoscion nebulosus) and lined sole (Achirus lineatus). EPA 600/3-18-052, Narragansett, RI

Hunter, J. R. (1984). Inferences regarding predators on the early life stages of cod and other fishes. In: Dahl, E., Danielssen, D. S., Moksness, E., Solemdal, P. (eds.) The propagation of cod: Gadus morhua (L.). Flødevigen rapportser., Arendal, 1: 533–562

Leggett, W. C. (1986). The dependence of fish survival on food and predator densities. In: Skreslet, S. (ed.) The role of freshwater outflow in coastal marine ecosystems. NATO ASI Ser Vol. G7, p. 118–137

Litvak, M. K., 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

MacKenzie, B. R., Leggett, W. C., Peters, R. H. (1990). Estimating larval fish ingestion rates: can laboratory derived values be reliably extrapolated to the wild? Mar. Ecol. Prog. Ser. 67: 209–225

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

Mercer, L. P. (1983). A biological fisheries profile of weakfish, Cynoscion regalis. Special Scientific Report No. 39. State-Federal Fisheries Management Program, Project SF-13, U.S. Dept of Commerce, National Marine Fisheries Service, Morehead City, NC

Peebles, E. B., Tolley, S. G. (1988). Distribution, growth, and mortality of larval spotted seatrout Cynoscion nebulosus: a comparison between two adjacent estuarine areas of southwest Florida. Bull. mar. Sci. 42: 397–410

Pepin, P., Shears, T H., de Lafontaine, Y (1992). Significance of body size to the interaction between larval fish (Mallotus villosus) and a vertebrate predator (Gasterosteus aculeatus). Mar. Ecol. Prog. Ser. 81: 1–12

Pryor, V., Epifanio, C. E. (1993). Prey selection by larval weakfish (Cynoscion regalis): effects of size, speed, and abundance. Mar. Biol. 116: 31–37

Taniguchi, A. K. (1981). Survival and growth of larval spotted seatrout (Cynoscion nebulosus) in relation to temperature, prey abundance, and stocking densities. In: Lasker, R., Sherman, K. (eds.) The early life history of fish: recent studies. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178: 507–508

Villoso, E. P. (1990). Reproductive biology and environmental control of spawning cycle of weakfish, Cynoscion regalis (Bloch and Schneider), in the Delaware Bay. Ph.D. dissertation, University of Delaware, Lewes

Wilk, S. J. (1976). The weakfish – a wide ranging species. Marine resources of the Atlantic Coast, Fisheries Leaflet No. 18. Atlantic States Marine Fisheries Commission, Highlands, NJ

Zar, J. H. (1984). Biostatistical analysis. Prentice-Hall, Englewood Cliffs

This article was submitted to the editor