Seasonal variability in antipredator performance of red drum larvae

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ABSTRACT: Variability in environmental conditions during early life-history stages can have important consequences for recruitment and population success. The red drum *Sciaenops ocellatus* spawns between September and November, a period of seasonal temperature decline overlain by quick and rather unpredictable change brought by frequent meteorological fronts. During 3 consecutive spawning seasons (2005 to 2007), we assessed behavioral performance of wild-caught red drum larvae in response to simulated predator attacks. Responsiveness and reactive distance of postsettlement red drum larvae decreased towards the end of the season. Several factors could explain the observed seasonal trends in escape performance, including variability in egg quality, changes in the intensity of predation, and declining temperatures (which may act on performance through a developmental mechanism). Our data suggest that long-term thermal experience (10 to 14 d) is more important than short-term thermal acclimation in determining escape performance. These results imply that late season larvae are less likely to survive to the juvenile stage and recruit to the fishery.

KEY WORDS: Escape responses · Fish larvae · Responsiveness · *Sciaenops ocellatus* · Seagrass · Survival skills

INTRODUCTION

Life-history trade-offs and reproductive strategies are thought to be adaptations to maximize survival of offspring in the face of changing environmental conditions (Stearns 1992, Zera & Harshman 2001). These adaptations to environmental uncertainty (e.g. blooms of food organisms, Cushing 1990, Beaugrand et al. 2003) are particularly relevant in species that produce offspring several times during a season. Batch spawning, a widespread strategy in teleosts, has been interpreted as a mechanism to cope with unpredictability of the conditions that early life-history stages will face (Trippel et al. 1997). Since females have a finite amount of energy to invest in reproduction per season, parameters such as propagule size sometimes decrease towards the end of the spawning season (Chambers & Waiwood 1996, Kjesbu et al. 1996), possibly affecting offspring fitness.

The reproductive season of the red drum *Sciaenops ocellatus* (Osteichthyes, Sciaenidae) in the western Gulf of Mexico starts by late August or early September, when water temperature is around 30°C (Perez-Dominguez et al. 2006). Along the Texas coast, spawning is widespread nearshore (Holt 2008), and tidal currents transport the eggs and early larvae through inlets toward juvenile habitats in the bays and estuaries. After 2 to 3 wk, planktonic larvae settle in nursery habitats such as seagrass meadows or marsh edges (Rooker & Holt 1997, Stunz et al. 2002). Successive cohorts arrive at these habitats until early November, by which time water temperatures have dropped to about 20°C (Perez-Dominguez et al. 2006). Significant unpredictability is superimposed upon this predictable seasonal change in temperature when sporadic low pressure meteorological fronts bring rapid drops in air temperature followed by gradual warming. Temperature has well-known effects on developmental and growth rates of larval fishes (Blaxter 1992). Therefore, size and age at hatching and settlement, pelagic stage duration, and size structure in nursery habitats, change markedly as the season progresses. Along with temperature and day length (from 13 h in late August to 11 h in early November), several other environmen-

tal factors are likely to change during the season, including abundances of prey, predators, and competitors, and the density of seagrasses (Orth et al. 1984). Indeed, Rooker et al. (1999) reported different mortality rates of red drum larvae in seagrass beds at different times of the season.

In a recent study, Fuiman et al. (2005) found high variability in survival skills of red drum larvae from different batches produced by captive broodstock. Larvae from early and late batches showed poorer escape performance in response to simulated predator attacks than larvae from mid-season batches. Since the adults and larvae were maintained in the laboratory under constant conditions, these results suggested that the variability in larval performance could be a consequence of seasonal differences in the quality of eggs produced by females. Our goal was to determine whether seasonal variability in larval escape performance occurs in nature. Therefore, we measured escape performance of wild-caught red drum larvae over 3 spawning seasons. This also gave us the opportunity to explore natural variability in antipredator performance during a period of predictable and unpredictable change in environmental conditions.

MATERIALS AND METHODS

Experimental larvae. Red drum larvae were collected in seagrass meadows near Lydia Ann Channel in Aransas Bay, South Texas, USA (27° 54.5' N, 97° 2.4' W) during the spawning seasons of 2005, 2006, and 2007. Sampling started in mid-September before the first recruits arrived to the nursery habitats and was intended to continue weekly until all red drum larvae or juveniles left the seagrass beds by the end of November. However, the active hurricane season of 2005 and a bloom of the harmful alga *Karenia brevis* in 2006 reduced the number of sampling dates in those years. Over the 3 years, we collected larvae from 23 September to 29 November for a total of 19 separate sampling dates. Mean (±SD) total length (TL) of the 393 larvae captured was 13.6 ± 2.9 mm, ranging from 8.3 to 22.9 mm. We defined larvae as individuals shorter than 25 mm TL (the size at complete squamation) following the ontogenetic criteria of Fuiman et al. (1998).

Larvae were collected during the central hours of the day between 11:00 and 15:00 h by towing an epibenthic sled (1 m width, 25 cm height, and 1 mm mesh size) on shallow banks where seagrasses were abundant. Tows were intentionally short (less than 20 m) to avoid damaging the larvae. On average, 25 larvae were transported to the laboratory in buckets with aerated sea water within 1 h of capture. Once in the laboratory, larvae were kept for ca. 40 h in fiberglass tanks filled with

filtered and aerated sea water (27°C, 27‰) with a patch of artificial seagrass to provide shelter and reduce stress, and received an ad libitum diet of *Artemia* nauplii. Photoperiod was set at 12 h light:12 h dark.

Escape response experiments. Experiments to measure escape responses to a visual stimulus followed established protocols (see for example Fuiman & Cowan 2003). On the second day after capture, 22 (or all available) larvae were transferred to individual glass containers (20 cm in diameter, 6 cm deep) filled with 1 l of seawater. The containers and fish were kept overnight in a temperature-controlled room. Water temperature the previous night and during the behavioral tests was the same for all samples (average ± SD: 22.6 ± 1.2°C). On the day of the experiments, one larva at a time was gently transferred to a transparent glass chamber (75 × 70 × 25 mm) containing 50 ml of seawater. The chambers were deliberately shallow to limit the vertical component of escape responses. Larvae were allowed to recover from handling for at least 30 min before the chamber was placed into position for the visual startle assay and left undisturbed for at least another 3 min.

The visual stimulus was a vertically oriented black oval (15 × 10 mm) on a white card (10 × 15 cm) at the end of a pendulum (115 cm in length). The pendulum was held by an electromagnet connected to a switch so its release could be triggered from an adjacent room to avoid human disturbance of the fish. The pendulum was released when the larva was near the front of the chamber and facing toward the side where the stimulus would be presented. Once released, the pendulum accelerated toward the experimental fish, but a tether kept the pendulum from making contact with the container holding the fish. The approaching pendulum elicited responses of the type used by fish larvae to escape predators (e.g. Fuiman 1994). Responses were recorded by a high-speed video camera (250 frames s^{-1}) synchronized with the pendulum release and located 50 cm below the chamber to obtain a view perpendicular to the horizontal plane. Recordings of the escape responses were digitalized and stored in a computer for subsequent motion analysis. Larvae that showed abnormal behavior during the acclimation period were not tested. All larvae were humanely killed immediately after the experiments. Digital pictures of each larva were taken under a dissecting microscope to measure TL using image analysis software (Image J 1.33, http://rsb.info.nih.gov/ij).

Data analysis. Time of the season was computed as the number of days since 21 September, which was the earliest date in any of the years of the study on which red drum larvae were found in the seagrass meadows. The latest date on which larvae were captured during the study was 27 November (i.e. 68 d after 21 September) in 2007, which was also the year with the earliest

appearance of settled larvae. Water temperature data were obtained from instruments installed at the University of Texas Marine Science Institute pier, located on the Aransas Pass Ship Channel (27° 50.3′ N, 97° 3.1′ W). This pass is the main access to the bay for eggs and larvae, and the closest (less than 7 km) to the field sites where the experimental fish were collected. Data from a prior study at the same site (Perez-Dominguez et al. 2006) show very strong correlations (r = 0.97) between daily mean temperatures at the pass and those registered in the seagrass beds where our larvae were collected.

Because temperature can have both short- and long-term effects on fish performance (Blaxter 1992), we converted hourly temperature records to daily mean temperatures and used these to calculate mean temperatures for different time periods prior to fish capture. Mean temperature on the day of capture (T_c) reflects the most recent thermal experience of the larvae. Mean temperature over the previous 10 d (T_{10}) reflects the conditions to which the fish were acclimatized. Finally, since red drum larvae reach settlement size in about 3 wk (Herzka et al. 2001), the 20 d mean (T_{20}) approximates lifetime thermal experience. Seasonal changes in antipredator performance were analyzed with respect to T_c, T_{10}, and T_{20} to gain a better understanding of the nature of thermal effects.

Frame-by-frame motion analysis was performed on the high speed video recordings using WINanalyze (version 1.9 2D, Mikromak). Two behavioral variables were obtained: responsiveness (binary variable, indicating whether or not the larva responded to the stimulus) and reactive distance (distance in mm between the pendulum and the chamber when the fish initiated the escape response). Using the same experimental protocol, Fuiman et al. (2006) demonstrated that these 2 variables affected the likelihood of red drum larvae evading attack by an actual piscine predator.

We used principal components analysis to construct composite variables to test for effects of seasonality on antipredator performance using time of season, T_c, T_{10}, T_{20}, and TL as measures of seasonal change. The scores for each fish on the first 2 principal components were used as predictive variables in subsequent analyses. The effect of time of the season and fish size on responsiveness was tested using a probit generalized linear model with year as a factor. Reactive distance was log-transformed to normalize the distribution which was skewed to the right. A general linear model was used to assess the effects of year, season, and size on reactive distance. These multivariate models were refined using the Akaike information criterion (AIC, Burnham & Anderson 2002) to reduce the number of parameters. All the analyses were performed using SPSS 16.0 for Windows.

RESULTS

A total of 323 larvae was tested for escape responses. One-third (102) of them did not respond to the visual stimulus. Considering data from all years, responsiveness was highly variable during the first half of the season and decreased sharply from more than 80% in mid-October to less than 30% in November (Fig. 1). Time of the season explained 45.6% ($F_{2, 320} = 133.9$, p < 0.001) of the variability in responsiveness through a quadratic regression weighted by the number of fish tested for each date. For those fish that responded to the stimulus, mean reactive distance was also highly variable, and the relationship with time of the season, weighted by the number of fish responding, was negative although not very strong ($r^2 = 0.049$, $F_{1,208} = 10.8$, p = 0.001). Mean reactive distance was positively correlated with responsiveness (Pearson correlation weighted by number of fish responding, R = 0.635, p = 0.004, Fig. 2).

T_c, T_{10}, and T_{20} decreased significantly as the season progressed (Fig. 3a). Mean TL increased toward the end of the season (Fig. 3b) because only recently arrived larvae were present in the seagrass beds at the beginning of the season, and the supply of new recruits (small larvae) stopped at the end of the season. Combining all seasonally changing variables, the first 2 principal components explained more than 93% of the total variance. The first factor was defined by high loadings for the 3 temperature averages (T_c, T_{10}, and
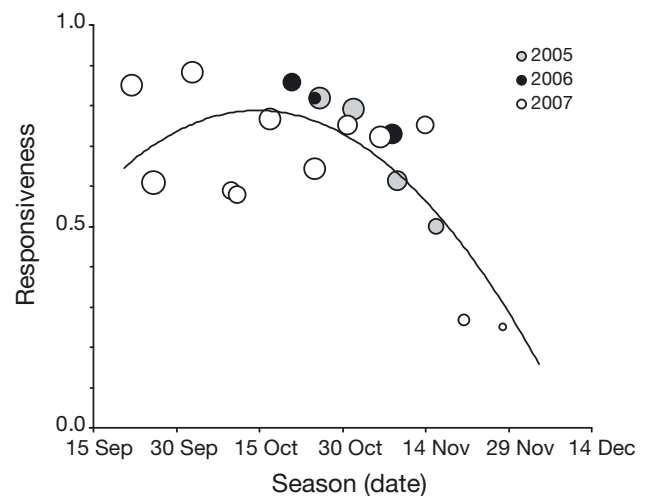

Fig. 1. *Sciaenops ocellatus*. Responsiveness, expressed as proportion of fish responding to the visual stimulus, observed at different times of the reproductive season for the 3 years of the study. Size of the symbols is proportional to the number of individuals tested for each sampling date (n = 8 to 28). Line represents a quadratic regression obtained for all 3 years combined, taking into account the number of fish tested on each date
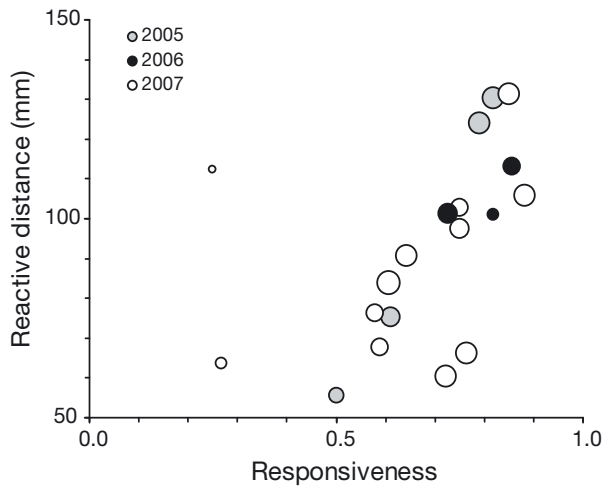
Fig. 2. *Sciaenops ocellatus*. Relationship between larval reactive distance and responsiveness averaged per sampling date in 3 different years. Symbol size is proportional to the number of individuals tested
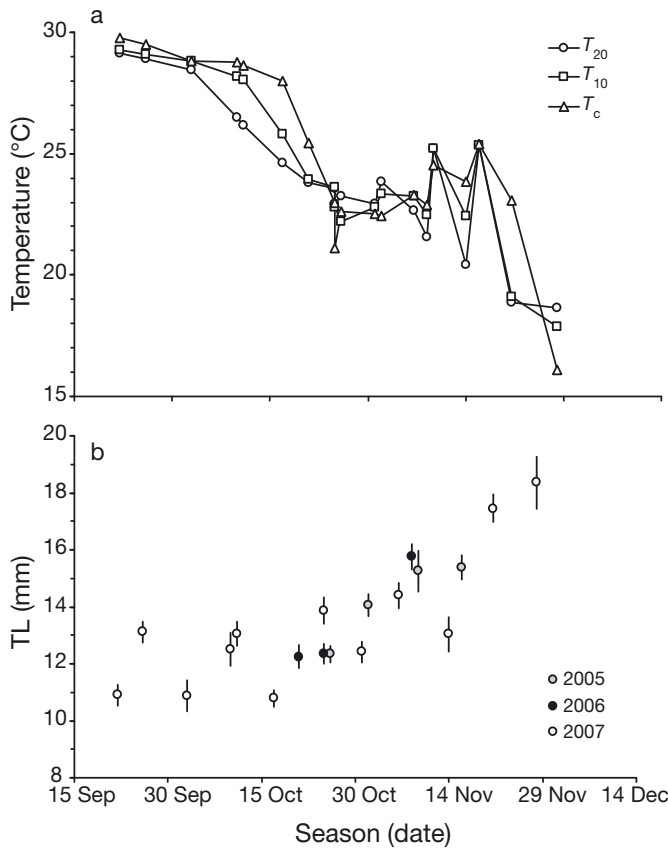

Fig. 3. *Sciaenops ocellatus*. (a) Seasonal variability of the thermal averages of the day of capture (T_c) and the 10 and 20 d before capture (T_{10} and T_{20}). (b) Increase in mean (±SE) total length (TL) of fish captured as the season progresses in 3 sample years

Table 1. Principal components loadings for seasonally changing variables. Temperature averages of the day of capture (T_c); T_{10} and T_{20}: 10 and 20 d before capture; TL: total length

Seasonally changing variable	Factor 1	Factor 2
T_c	0.935	0.175
T_{10}	0.968	0.179
T_{20}	0.951	0.160
Time of season	–0.936	0.010
TL	–0.604	0.794
Percent of total variance explained	79.1	14.4

T_{20}) and time of the season. The second factor was defined primarily by TL. Therefore, we interpret Factor 1 as an axis of primarily season and Factor 2 as fish size (Table 1).

We used a generalized linear model (GLM) with responsiveness as a binary dependent variable, year as a categorical variable and season (Factor 1) and fish size (Factor 2) as covariates. This model was statistically significant overall (likelihood ratio χ^2 = 56.4, p < 0.001) but showed no significant interactions (Wald χ^2 < 1.4, p > 0.50) nor significant effects of year, season or size (Wald χ^2 < 2.6, p > 0.10). We simplified the model by removing year, which resulted in a substantial reduction of the AIC from 370.4 to 366.6. The new model showed no significant interaction between season and fish size (Wald χ^2 = 2.5, p > 0.112) but significant decreases in responsiveness with both season (Wald χ^2 = 4.5, p = 0.034, Fig. 4a) and fish size (Wald χ^2 = 30.3, p < 0.001, Fig. 4b). The effect of fish size on responsiveness was much greater than the effect of season.

Reactive distance of the individuals that responded to the stimulus was highly variable, ranging from 1.7 to 297.8 mm. However, no significant portion of this variability was explained by year (GLM: $F_{2,191}$ = 1.11, p = 0.331), season or fish size ($F_{1,191}$ < 0.61, p > 0.438), and neither the 2-way or 3-way interactions were significant. Nevertheless, when we excluded year as categorical variable, season, size, and their interaction all became significant (GLM: season, $F_{1,198}$ = 7.09, p = 0.008; size, $F_{1,198}$ = 16.65, p < 0.001; Season × Size, $F_{1,198}$ = 8.15, p = 0.005).

DISCUSSION

Antipredator performance of postsettlement red drum larvae was lower during the second half of the season. This temporal trend is partially consistent with the pattern suggested by data previously obtained from larvae reared from captive-spawned adult red drum (Fuiman et al. 2005). Both Fuiman et
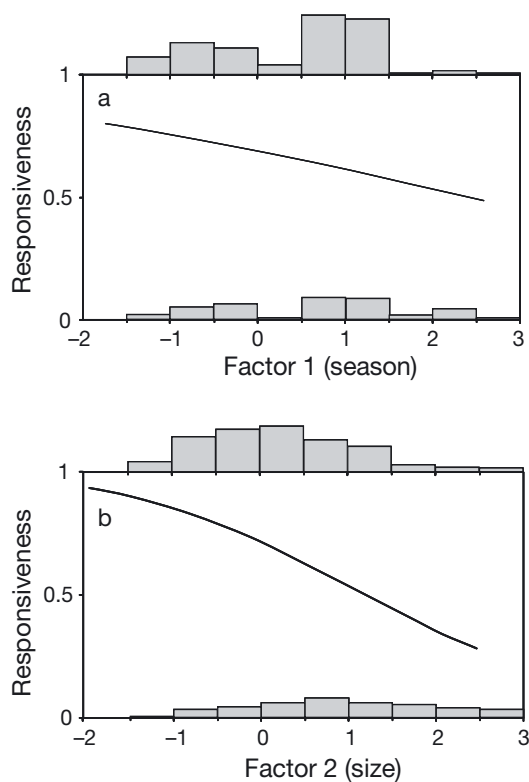
Fig. 4. *Sciaenops ocellatus*. Relationships (probit regression lines) between probability of the fish responding to the visual stimulus and (a) time of the season (Factor 1, see 'Materials and methods') or (b) fish size (Factor 2) combining all fish from the 3 study years. Histograms show the relative frequency distributions for (a) responsive and (b) non-responsive individuals

al. 2005 and the present studies showed high performance at mid-season and reduced performance late in the season. Our results, however, show high, but variable performance early in the spawning season. The 2 measures of performance used in our study, responsiveness and reactive distance, are important to survival during encounters with predators. Responsiveness accounted for 86% of the variation in escape potential of red drum larvae in experiments with real piscivores (Fuiman et al. 2006). Reactive distance was 1 of 3 performance variables that predicted escape potential for individual larvae attacked by a longnose killifish (Fuiman et al. 2006). In our data set, size of the larvae and time of the season were inextricably linked, and therefore, we cannot conclude which variable is responsible for the decrease in performance. It is important to note that laboratory experiments on larvae from the same population showed that responsiveness was positively correlated with TL (Fuiman et al. 1999). Nonetheless, responses of wild fish did not show a clear pattern (Smith & Fuiman 1994), partly because of the large

variability of the very large size class. The apparent contradiction between the 3 studies could mean that the seasonal trend is actually stronger than our analyses suggest.

Several biotic and abiotic factors could explain the observed changes in escape performance during a time of the year in which ecological conditions vary rapidly. The seasonal decline in escape performance of wild-caught red drum may have been due to changes in their interactions with predators and habitats. For instance, those individuals that do not respond to less imminent threats and instead trust crypsis may avoid false alarms that could attract attention from predators, leading to higher survival chances (Fuiman 1993). In this case, we would expect selective mortality that would favor larvae with reduced responsiveness and reactive distance, like those observed at the end of the season. Seagrass beds contain different fish (predator) assemblages depending on the structure, density and morphology of the plants (Orth et al. 1984, Baelde 1990). Since growth and production of seagrasses fluctuate as environmental conditions change during the fall (Herzka & Dunton 1997), a change in predation pressure can also be expected (Orth et al. 1984). For example, at the end of the fall the dense seagrass meadows become sparser therefore providing a less complex habitat and a likely increase in predation pressure.

Alternatively, the seasonal change in antipredator performance could be caused by maternal effects, such as egg quality or timing of spawning (Mousseau & Fox 1998, Green 2008). Our results are compatible with the hypothesis of seasonal variation in egg quality suggested by Fuiman et al. (2005) to explain the variability in survival skills they observed among captive-spawned red drum larvae. Firstly, it is possible that females of different quality spawn at different times of the season, such as bigger, older females spawning early and producing higher quality eggs than smaller, younger females that spawn later (e.g. Schultz 1993, Cargnelli & Gross 1996). Alternatively, individual females may spawn over a prolonged period, producing eggs that vary in quality over time. Since many marine fishes produce eggs from energy reserves ('capital breeding' sensu Stephens et al. 2009), egg quality typically decreases toward the end of the season as females deplete their resources (e.g. Chambers & Waiwood 1996, Kjesbu et al. 1996). Unlike many other fractional spawners, however, red drum females continue to eat during the spawning period ('income breeding') so that their eggs are provisioned with nutrients from the diet instead of body reserves, and captive females are able to produce egg batches of relatively constant quality over several months (authors' unpubl. data).
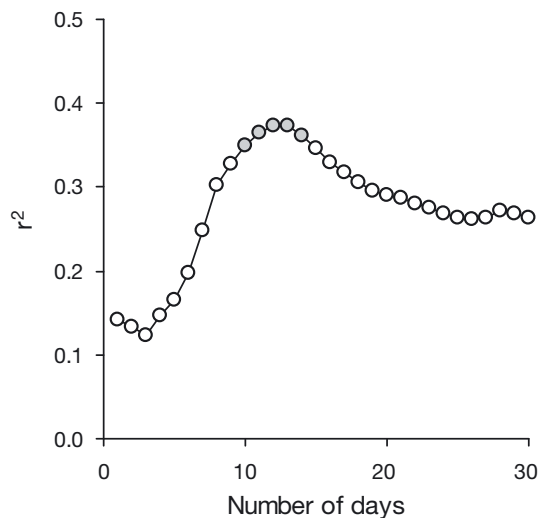
Fig. 5. Coefficients of determination (r^2) for quadratic relationships between responsiveness (weighted by sample size) and mean thermal experience plotted against the number of days for which mean thermal experience was calculated. ○: range of number of days for which the proportion of variability explained by thermal experience is maximal

Timing of spawning is one of the obvious ways females can influence which environmental conditions the offspring will experience (Mousseau & Fox 1998). This is particularly relevant for a species such as red drum whose reproductive season happens over a period when temperatures drop more than 10°C (our Fig. 3a, Perez-Dominguez et al. 2006). This temperature decrease is usually not entirely gradual because of unpredictable weather events that occur in the latter half of the season. In some years, temperatures stay close to late summer levels until November, while in other years temperatures drop early and subsequently rise. Temperature has well-known immediate physiological effects on almost every aspect of fish performance (Blaxter 1992). To avoid this confounding effect, we tested all fish at the same temperature. Our results are compatible with an acclimation effect and with developmental plasticity, i.e. thermal conditions experienced during early developmental stages could produce different phenotypes (Atkinson 1996) that vary in performance.

Our formal analysis considered larval thermal experience measured over 3 different time frames to provide insight into the mechanism of seasonal effects on escape performance. To expand that approach, we also computed thermal experience for each fish for all possible spans of days and related each measure to responsiveness through a quadratic equation. The proportion of variability explained (r^2) by thermal experience reached a maximum at 10 to 14 d $(r^2 = 0.374,$ Fig. 5), suggesting that long-term thermal experience

(acclimatization, Wilson & Franklin 2002) is more important than short-term thermal experience in determining escape performance in these larvae.

In summary, given the decline in 2 measures of performance that are important to surviving attacks, we would expect the probabilities of individual larvae surviving predator attacks to decrease as the season progresses. This seasonal variability in escape potential during a stage when predation mortality is high (Rooker et al. 1999, Stewart & Scharf 2008) could have previously unexplored consequences for population success. For example, it suggests that egg batches produced at the end of the season would contribute fewer recruits to the population. In any case, time of the season, temperature and size distribution of red drum larvae in the seagrass meadows are all highly interrelated in our study making the mechanism of the observed variability in escape behavior unclear. Disentangling these effects will require an experimental approach.

LITERATURE CITED

Atkinson D (1996) Ectotherm life-history responses to developmental temperature. In: Johnston IA, Bennett AF (eds) Animals and temperature: phenotypic and evolutionary adaptation. Cambridge University Press, Cambridge, p 183–204

Baelde P (1990) Differences in the structures of fish assemblages in *Thalassia testudinum* beds in Guadeloupe, French West Indies, and their ecological significance. Mar Biol 105:163–173

Beaugrand G, Brander KM, Lindley A, Souissi S, Reid PC (2003) Plankton effect on cod recruitment in the North Sea. Nature 426:661–664

Blaxter JHS (1992) The effect of temperature on larval fishes. Neth J Zool 42:336–357

Burnham KP, Anderson DR (2002) Model selection and multi-model inference: a practical information-theoretic approach. Springer, New York, NY

Cargnelli LM, Gross MR (1996) The temporal dimension in fish recruitment: birth date, body size, and size-dependent survival in a sunfish (bluegill: *Lepomis macrochirus*). Can J Fish Aquat Sci 53:360–367

Chambers RC, Waiwood KG (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

Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv Mar Biol 26:249–292

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

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

Fuiman LA, Cowan JHJ (2003) Behavior and recruitment success in fish larvae: repeatability and covariation of survival skills. Ecology 84:53–67

Fuiman LA, Poling KR, Higgs DM (1998) Quantifying developmental progress for comparative studies of larval fishes. Copeia 1998:602–611

Fuiman LA, Smith ME, Malley VN (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

Fuiman LA, Cowan JH Jr, Smith ME, O'Neal JP (2005) Behavior and recruitment success in fish larvae: variation with growth rate and the batch effect. Can J Fish Aquat Sci 62:1337–1349

Fuiman LA, Rose KA, Cowan JH Jr, Smith EP (2006) Survival skills required for predator evasion by fish larvae and their relation to laboratory measures of performance. Anim Behav 71:1389–1399

Green BS (2008) Maternal effects in fish populations. Adv Mar Biol 54:1–105

Herzka SZ, Dunton KH (1997) Seasonal photosynthetic patterns of the seagrass *Thalassia testudinum* in the western Gulf of Mexico. Mar Ecol Prog Ser 152:103–117

Herzka SZ, Holt SA, Holt GJ (2001) Documenting the settlement history of individual fish larvae using stable isotope ratios: model development and validation. J Exp Mar Biol Ecol 265:49–74

Holt SA (2008) Distribution of red drum spawning sites identified by a towed hydrophone array. Trans Am Fish Soc 137:551–561

Kjesbu OS, Solemdal P, Bratland P, Fonn M (1996) Variation in annual egg production in individual captive Atlantic cod (*Gadus morhua*). Can J Fish Aquat Sci 53:610–620

Mousseau TA, Fox CW (1998) The adaptive significance of maternal effects. Trends Ecol Evol 13:403–407

Orth RJ, Heck KL, van Montfrans J (1984) Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuar Coasts 7:339–350

Perez-Dominguez R, Holt SA, Holt GJ (2006) Environmental variability in seagrass meadows: effects of nursery environment cycles on growth and survival in larval red drum *Sciaenops ocellatus.* Mar Ecol Prog Ser 321: 41–53

Rooker JR, Holt SA (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 JR, Holt SA, Holt GJ, Fuiman LA (1999) Spatial and temporal variability in growth, mortality, and recruitment potential of postsettlement red drum, *Sciaenops ocellatus*, in a subtropical estuary. Fish Bull 97:581–590

Schultz ET (1993) The effect of birth date on fitness of female dwarf perch, *Micrometrus minimus* (Perciformes: Embiotocidae). Evolution 47:520–539

Smith ME, Fuiman LA (2004) Behavioral performance of wild-caught and laboratory-reared red drum *Sciaenops ocellatus* (Linnaeus) larvae. J Exp Mar Biol Ecol 302:17–33

Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford

Stephens PA, Boyd IL, McNamara JM, Houston AI (2009) Capital breeding and income breeding: their meaning, measurement, and worth. Ecology 90:2057–2067

Stewart CB, Scharf FS (2008) Estuarine recruitment, growth, and first-year survival of juvenile red drum in North Carolina. Trans Am Fish Soc 137:1089–1103

Stunz GW, Minello TJ, Levin PS (2002) A comparison of early juvenile red drum densities among various habitat types in Galveston Bay, Texas. Estuaries 25:76–85

Trippel EA, Kjesbu OS, Solemdal P (1997) Effects of adult age and size structure on reproductive output in marine fishes. In: Chambers RC, Trippel EA (eds) Early life history and recruitment in fish populations. Chapman & Hall, London, p 31–62

Wilson RS, Franklin CE (2002) Testing the beneficial acclimation hypothesis. Trends Ecol Evol 17:66–70

Zera AJ, Harshman LG (2001) The physiology of life history trade-offs in animals. Annu Rev Ecol Syst 32:95–126