Journal of Experimental Marine Biology and Ecology 349 (2007) 131 – 141

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

www.elsevier.com/locate/jembe

Experimental investigation of spatial and temporal variation in estuarine growth of age-0 juvenile red drum (*Sciaenops ocellatus*)

Jason M. Lanier, Frederick S. Scharf *

Department of Biology and Marine Biology, University of North Carolina Wilmington, 601 S. College Rd., Wilmington, NC 28403, United States

Received 14 December 2006; received in revised form 29 March 2007; accepted 10 May 2007

Abstract

Many ecological processes that occur during fish early life history stages are influenced by body size and multiple factors often work synergistically across space and through time to generate variation in body size among individuals. We conducted a replicated field experiment that was designed to quantify the level of spatial and temporal variation in growth of age-0 juvenile red drum during the 2–3 month estuarine recruitment period. The experiment was conducted over 53 consecutive days during fall (Oct–Dec) 2004 in a southeastern North Carolina estuary that has demonstrated consistent annual recruitment of red drum juveniles. After field capture and laboratory acclimatization, fish (30–52 mm TL; 0.19–1.11 g wet weight) were placed in pairs into one of three replicated field cages positioned at six sites along the estuarine salinity gradient. Growth was monitored for five consecutive 10–11 day intervals, with fish replaced between each interval. Time (experimental interval), space (estuary region), and the time × space interaction were evaluated for their effect on juvenile red drum growth. Results demonstrated a significant decrease in growth rates through time and significantly faster growth rates in the central region of the estuary with no significant interaction. The temporal variation in growth appeared to be mostly driven by declining fall water temperatures throughout the estuary. The consistent spatial variation in growth, with fastest growth realized in the central region, regardless of time, may have been partially due to consistent salinity differences among estuary regions. Moderate salinities (15–25 ppt) may enhance osmoregulatory efficiency in juvenile red drum and allow greater scope for growth. The degree of spatial and temporal variability in growth observed in this study implies that the timing of estuarine arrival and initial settlement habitat may have a strong influence on size at age patterns of first year red drum in North Carolina, and thus may impact early juvenile survival and eventual year-class success.

Keywords: Growth rate; Juvenile fish; Caging experiments; Size at age

---

1. Introduction

Many marine fish populations demonstrate considerable variation in abundance from year to year (Rothschild, 1986). The processes that influence growth and survival of early life history stages have long been implicated to play a major role in determining eventual year class success and to contribute to interannual variability (Hjort, 1914; May, 1974; Cushing, 1975). Importantly, Houde (1987) recognized that large fluctuations in the number of successful recruits could result from relatively small variations in mortality and/or growth rates during early life. Furthermore, numerous studies have demonstrated the strong effects of variation

---

* Corresponding author. Tel.: +1 910 962 7796; fax: +1 910 962 4066.

E-mail address: scharff@uncw.edu (F.S. Scharf).

0022-0981/$ - see front matter © 2007 Elsevier B.V. All rights reserved.
doi:10.1016/j.jembe.2007.05.004

in body size among individuals on the survival probability of young fishes (see reviews by Miller et al. (1988) and Sogard (1997)), establishing a mechanistic link between growth and mortality that has been substantiated by several recent investigations focusing on both larval and juvenile life stages. For instance, Rice et al. (1993) modeled individual larval growth and survival through time and found that, in addition to the mean growth rate, the level of growth variation among individual fish within a cohort could contribute substantially to overall cohort survivorship. Similarly, annual cohorts of juvenile cod with fast growth rates during the first year of life realized significantly higher levels of recruitment to later life stages compared to cohorts with slower juvenile growth (Campana, 1996).

For temperate species, the importance of variation in early growth to individual survivorship and eventual cohort strength is believed to vary with latitude (Conover, 1992). At higher latitudes, the growing season is abbreviated and winter conditions are generally more severe. Under these scenarios, early growth rate can have a considerable influence on fish survival throughout the first year of life, which has been demonstrated to be strongly size-dependent due to the allometry of fish energy storage and depletion (Post and Evans, 1989; Shuter and Post, 1990). Many temperate marine fishes utilize estuaries during early juvenile life stages and often overwinter in estuarine or nearshore oceanic waters. Thus, knowledge of the extent and potential causes of growth variability during estuarine residency is essential for understanding the potential influence of size-dependent mortality during the early juvenile period on cohort success and how these effects may vary across the latitudinal range of estuarine-dependent species.

Growth rates have been shown to vary in space and time for many estuarine fishes. Several factors including habitat heterogeneity, water temperature, salinity, and dissolved oxygen concentrations have each been found to significantly affect fish growth rates (Houde, 1989; Peterson et al., 1999; Phelan et al., 2000; Peterson et al., 2004). Often, growth patterns within the estuary demonstrate variation on a landscape or system scale. For example, Sogard (1992) concluded that variability in habitat quality across an estuarine gradient resulted in consistent and significant differences in short-term growth rates for three juvenile fish species. When spatial patterns in growth are observed through time, the response of growth to changing biotic and abiotic conditions becomes complex. Manderson et al. (2002) concluded that simultaneous variability in multiple factors regulating estuarine growth of juvenile winter flounder generated dynamic growth patterns in space and time, with a narrow window of optimum growth.

The red drum, *Scianeops ocellatus*, is an estuarine-dependent fish common in coastal waters of the US south Atlantic and throughout the Gulf of Mexico. Adults have been observed to spawn between mid-August and mid-November in waters adjacent to passes and inlets, with peak spawning generally occurring in September and October (Pearson, 1929; Simmons and Breuer, 1962; Peters and McMichael, 1987; Rooker and Holt, 1997). After tidal transport into estuaries (Holt et al., 1989) and initial settlement in habitats near inlets, juvenile red drum are thought to disperse throughout the estuary, with documented movements into shallow tidal creeks and lower salinity habitats (Pearson, 1929; Peters and McMichael, 1987; Stunz et al., 2002a). Growth rates of age-0 juvenile red drum during the first fall growing season have been estimated between 0.22–0.82 mm day^{-1} (Bass and Avault, 1975; Rooker and Holt, 1997; Scharf, 2000), demonstrating the occurrence of appreciable levels of variation. A detailed analysis of juvenile growth rates in a Texas estuary indicated differential growth among structured habitats and revealed the potential for considerable variation in individual growth rates during the post-settlement period (Stunz et al., 2002b).

Along the US Atlantic coast, spawning and settlement of red drum is restricted to lower latitudes, with North Carolina and southern Virginia representing the current northern extent of the distribution. Significant estuarine recruitment of age-0 juveniles, moreover, has not been demonstrated to occur regularly north of North Carolina. Age-0 red drum in North Carolina experience a shorter growing season prior to their first winter compared with fish inhabiting Gulf of Mexico and other south Atlantic estuaries. Early growth may, therefore, be even more critical to first year survival of North Carolina red drum because of the earlier onset and severity of winter conditions relative to lower latitudes. Juveniles growing at faster rates during fall may experience lower size-dependent predation mortality and should be better able to withstand physiological stresses related to winter conditions. To date, however, studies of the early life history of red drum have been mostly restricted to the Gulf of Mexico (but see Daniel (1988) and Wenner et al. (1990) for data on South Carolina red drum). No detailed evaluation of the magnitude of growth variation or the factors generating variable growth exists for early juvenile red drum at higher latitudes.

Here, we present the results of a field experiment conducted to evaluate the degree of spatial and temporal variability in growth of early juvenile red drum at the northern extent of the range for juvenile recruitment. We examined the growth of caged individuals across a spatial gradient and throughout the fall recruitment period (approximately two consecutive months) to exlore temporal shifts in the spatial variability of growth. Our primary goal was to determine the extent of growth variability among post-settlement juveniles and to identify potentially important environmental factors generating growth variation. Our experimental design enabled us to assess whether the location of high growth nursery habitats shifted during the juvenile recruitment season and the potential effects of recruitment timing on sizes achieved prior to winter.

2. Materials and methods

2.1. Study area and experimental design

The caging experiment was conducted in estuarine waters of the New River estuary, located in southeastern North Carolina. The New River is a relatively enclosed system bordered largely by pine forests and spartina marshes, with direct access to the Atlantic Ocean limited to a single inlet. Large portions of the system are undisturbed as much of the adjacent land is part of the U.S. Marine Corps base Camp Lejeune. The system is mostly shallow throughout, with average depths generally <3–4 m. The New River receives consistent yearly recruitment of age-0 red drum and juveniles have been sampled each fall since 1991 by the North Carolina Division of Marine Fisheries to index juvenile abundance.

For this study, the estuary was broadly stratified based on distance from the mouth of the estuary and salinity profiles. Three strata were designated in the estuary: a polyhaline (>25 ppt) stratum located in the lower estuary closest to the mouth; a mesohaline (15–25 ppt) stratum located in the central region of the estuary; and an oligohaline stratum (5–15 ppt) located furthest upriver from the estuarine mouth. These strata are referred to as northern, central, and southern regions hereafter. There were six experimental sites established, with two sites located within each region (Fig. 1).

During the 2004 fall recruitment period, juvenile age-0 red drum (30–52 mm TL; 0.19–1.11 g wet weight) were collected by seining and transferred to the laboratory for use in growth experiments. Fish were maintained in laboratory aquaria at intermediate salinities (18.6–22.3 ppt) and temperatures (20.8–23.5 °C) that simulated natural temperature ranges experienced by fish during mid-fall. Each day, laboratory held fish were fed thawed, frozen brine shrimp, environmental conditions in the aquaria were measured, and any dead fish were removed. Fish were collected continuously in the field and used in subsequent growth experiments, thus most individuals were retained in the laboratory aquaria for 7–10 days. Food was deprived for 24 h prior to the initiation of each growth experiment to evacuate gut contents and remove the effect of variable stomach fullness on individual fish weights.

Field caging experiments were initiated on Oct 9 and consecutive experiments were conducted every 10–11 days through Nov 30. Prior to the start of each experiment, fish were selected randomly from laboratory populations, measured (TL in mm) and weighed (g), and then placed in groups of two into plastic containers fitted with mesh covers, which were then replaced into the laboratory aquaria overnight. For transport to the field, plastic containers were placed in a large cooler that was filled with seawater and aerated. To remove the effect of variable body size on growth within each experiment, random selection of fish from laboratory aquaria continued until no significant differences in average body size existed among sites (*P*-values for ANOVA's on TL and weight >0.05). Thus, the site and cage for the two individuals within each plastic container were assigned prior to transport to the field using unique numbering for each container.

The experimental design consisted of three replicate cages per site, with a total of six sites positioned along the estuarine gradient. Cage frames were constructed of rolled steel and were approximately 0.75 m × 0.75 m × 0.40 m high. Rigid, nylon mesh bags with 3 mm mesh openings were suspended within each cage frame. Mesh bags were fitted with heavy duty plastic zippers along the top edge for opening and closing. Cage frames were partially embedded in the substrate to allow the bottom of each mesh bag to maintain contact with the bottom, providing caged red drum with access to epibenthic prey resources. At each site, a single cage was fitted with a temperature logger (HOBO Water Temp Pro v2, Onset Computer Corp.) to record hourly temperatures experienced by caged fish.

Once in the field, seawater in the transport cooler was exchanged frequently with estuarine water to acclimate fish to ambient salinities and temperatures in each region. Two fish were placed into each cage and allowed to feed and grow for 10–11 days before fish were retrieved. This time duration was deemed sufficient to allow normal feeding to resume and growth to become indicative of the *in situ* environment. Cages were cleaned in between uses to remove fouling communities and their potential effect on growth. After each 10–

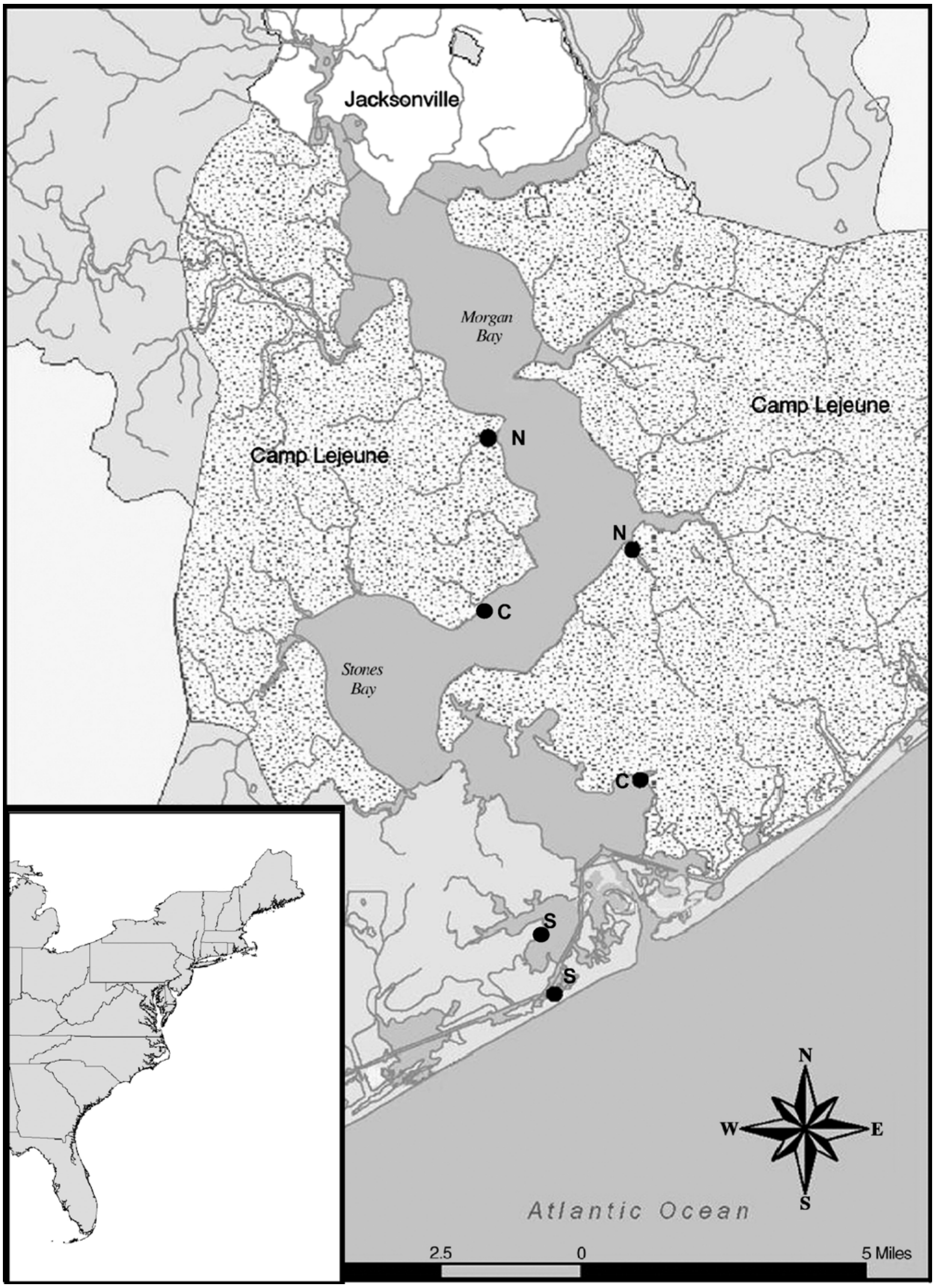

Fig. 1. Map of the New River Estuary, North Carolina. Caging sites are indicated by filled circles. Letters (N, C, or S) adjacent to each site represent the designated estuarine region (northern, central, or southern).

11 day experiment, fish were retrieved from each cage, held on ice, and returned to the laboratory. All but six of 180 fish initially placed into field cages were recovered. Total length (mm) and weight (g) were measured for each fish, and gut contents were examined to evaluate diet and gut fullness of caged individuals.

2.2. Data analysis

For each experimental interval, the average growth rate was calculated for each replicate cage from the two fish present per cage. Absolute growth was calculated as the change in weight (g) or length (TL in mm). Growth comparisons among temporally distinct experiments and spatially distinct regions were made using weight-specific instantaneous growth rates calculated as:

$$W_t = W_0 e^{gt}$$

where W_0 = initial weight (g), W_t = final weight (g), and g = the instantaneous growth coefficient. To further assess variation in habitat quality through space and time, Fulton's condition index (K; Ricker, 1975) was calculated at the start and end of each experiment as:

$$K = 100 * \left(W/L^3\right)$$

where W = weight (g) and L = total length (mm). The differences between starting and ending values of K were calculated for each replicate cage and compared among experiments.

Feeding patterns of caged red drum were compared with diets of free-ranging red drum captured adjacent to caging sites throughout the course of the experiments. Free-ranging red drum were collected weekly by seining as part of a separate study. Stomach contents of caged fish and free-ranging fish captured during the experimental period were identified to the lowest possible taxon. Dietary indices that were calculated for each prey taxon included percent by number (%N) and percent frequency of occurrence (%FO).

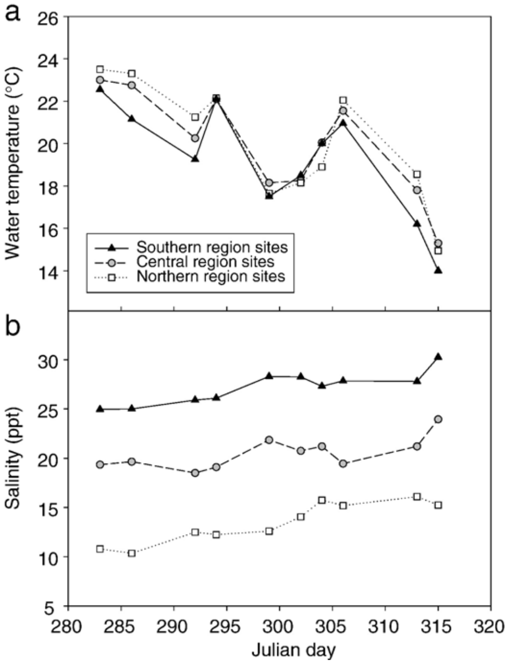

Fig. 2. Patterns of variation in average water temperature (a) and salinity (b) within each estuarine region during the course of the experiment. Results of analyses of temporal and spatial variation are presented in the text. Julian day 283 = October 9.

Table 1
Results of two-factor ANOVA demonstrating the significant main effects of experiment and region on weight-specific (instantaneous) growth of age-0 juvenile red drum during the caging experiment (Oct–Dec 2004)

Source of Variation	DF	Type I SS	Mean square	*F*-value	*P*-value
Model	14	0.02083	0.00149	13.22	<0.0001
Experiment	4	0.01855	0.00464	41.19	<0.0001
Region	2	0.00204	0.00102	9.07	0.0003
Experiment × region	8	0.00022	0.00003	0.25	0.9797
Error	72	0.00810	0.00011		
Total	86	0.02893	0.00034		

Model overall $r^2 = 0.72$.

Statistical analysis of growth was completed using the computer program SAS (SAS software, Inc., 2002). A two-way ANOVA was used to test for the effects of experiment (time), region (space), and their interaction (time × space interaction) on weight-specific growth of juvenile red drum. Similarly, a two-way ANOVA was used to test for the effects of experiment, region, and their interaction on the change in condition index (Fulton's K). Post-hoc contrasts were performed using Tukey's HSD tests with an experimentwise error rate $(\alpha) = 0.05$. Assumptions of normal error distributions and homogeneity of variances for weight-specific growth and differences in condition index among regions and experimental intervals were initially tested using Shapiro–Wilk tests and Bartlett's tests, respectively, with only minor departures from normality detected in a few cases. Prey species richness and evenness were each estimated for diets of caged and free-ranging fish. Species richness was estimated as the total number of prey species found in the diets. Prey evenness was estimated using Hurlbert's PIE (probability of an interspecific encounter) calculated as:

$$\mathrm{PIE} = \left(\frac{N}{N-1}\right)\left(1 - \sum_{i=1}^{s} {p_i}^2\right)$$

where N = the total number of prey eaten; p_i = the proportion of N represented by species i; and s = the total number of prey species eaten. Dietary overlap between caged and free-ranging fish was also assessed, using Schoener's index calculated as:

$$\alpha = 1 - 0.5\left(\sum_{i=1}^{n} |p_{ij} - p_{ik}|\right)$$

where α=dietary overlap, p_{ij}=proportion (normalized frequency of occurrence) of food category i in the diet of caged individuals, and p_{ik}=proportion (normalized frequency of occurrence) of food category i in the diet of free-ranging individuals (e.g., Soto et al., 1998). Values of $\alpha > 0.6$ are considered to represent biologically significant overlap (Wallace, 1981). All dietary comparisons between caged and free-ranging fish were completed using EcoSim null models software (Gotelli and Entsminger, 2001). Multiple linear regression models were used to assess the influence of water temperature, salinity, and dissolved oxygen on growth of caged individuals.

3. Results

3.1. Environmental variability

Among physicochemical attributes, salinity was generally stable temporally and varied across the estuarine space; temperature was spatially stable and varied through time; and dissolved oxygen displayed only slight spatial variation and increased moderately with time. During the course of the experiments, modest increases in salinity that were not statistically significant occurred gradually in all regions (Fig. 2a). The northern, central, and southern estuarine regions exhibited mean salinities of 14.8 ppt, 21.6 ppt, and 27.7 ppt, respectively, that differed significantly (ANOVA $P < 0.001$). The average temperature measured by *in situ* temperature probes across all sites ranged between 13.1–22.3 °C, with minimum and maximum values each occurring in the northern region on Nov 10 and Oct 9, respectively. There was a significant linear effect of day of year on temperature, with each successive day accounting for an average decrease of 0.20 °C (P-values for all three slopes <0.001; Fig. 2b). No differences in the temporal decline of water temperature were observed among regions (ANCOVA: $F_{2,56}=1.438$, $P>0.25$). Dissolved oxygen ranged from 5.12–9.18 mg/L among sites throughout the experimental period and increased modestly as water temperatures fell in late fall. There was no clear spatial pattern of variation in dissolved oxygen. The dissolved oxygen concentration levels observed at our experimental sites were well above the critical level of 2.00 mg/L, estimated for juvenile red drum at water temperatures between 18–24 °C (Neill et al., 2004).

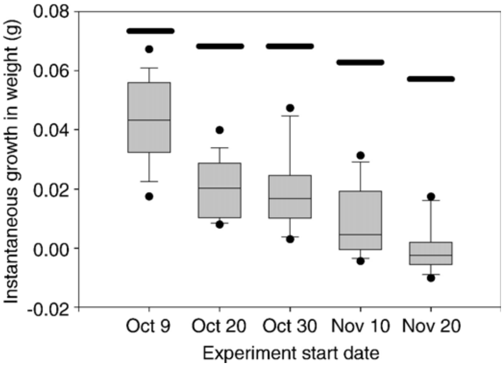

Fig. 3. Weight-specific (instantaneous) growth of caged age-0 red drum pooled across sites for each 10–11 day experimental interval. Horizontal lines of different heights above box plots represent significantly different growth rates (Tukey's HSD tests: $P<0.05$) among experimental intervals. Box plots with horizontal lines of the same height are not statistically different (e.g., Oct 20 and Oct 30).

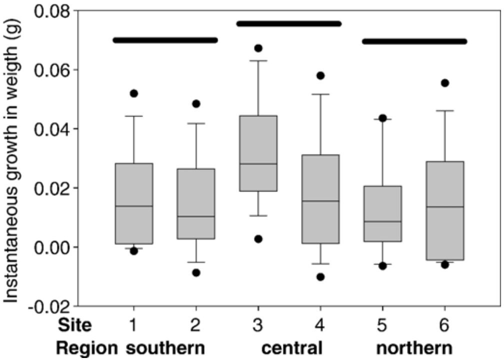

Fig. 4. Weight-specific (instantaneous) growth of caged age-0 red drum at each of six experimental sites for the entire experimental period (53 days). Horizontal lines of different heights above box plots represent significantly different growth rates (Tukey's HSD tests: $P<0.05$) among southern, central, and northern regions. Box plots with horizontal lines of the same height are not statistically different.

3.2. Patterns of growth and condition

Observed weight-specific growth rates of individual fish ranged between −0.01 to 0.07, which translated to absolute growth in weight and length of −0.01 to 0.04 g/day and −0.30 to 0.60 mm/day, respectively. While initial sizes of caged fish were not statistically different within any single experiment, there was a significant increase in size between early and late experiments due to the reduced availability of smaller-sized fish in the field. Therefore, analysis of growth variability was completed using weight-specific rates. Results of analyses using absolute growth measurements were, however, nearly identical. Overall, results from the caging experiment revealed a high level of temporal and spatial variability in growth. Analysis of variance demonstrated significant differences in growth among temporally distinct experiments ($P<0.001$) and estuarine regions ($P<0.001$) with no significant interaction (Table 1).

Growth declined continuously with successive experiments, with a negative mean instantaneous growth rate observed during the last experiment (Fig. 3). Growth differed significantly among all experimental intervals, with the exception of the second and third intervals (Tukey's HSD tests, $P<0.05$; Fig. 3). Across all experiments, caged individuals located in the central estuarine region grew significantly faster compared to fish located in the northern and southern regions (Tukey's HSD tests, $P<0.05$; Fig. 4).

The difference in the condition index (Fulton's K) before and after each caging experiment ranged from −0.229 to 0.275. Similar to the growth response, a significant effect of date ($P<0.001$) and region ($P<0.01$) was detected with no significant interaction (Table 2). However, the temporal and spatial patterns in fish condition were not as clear. A fairly consistent increase in condition was observed during each experimental interval, with the exception of the last, when no increase in condition was evident (Fig. 5). Differences in fish condition were lower during the last experimental interval than all other experimental intervals except the second interval (Tukey's HSD tests, $P<0.05$; Fig. 5). As with growth rate, fish caged in the central region displayed the largest increases in condition (Fig. 6). Post-hoc contrasts indicated that fish in the central region achieved significantly greater increases in condition than fish in the northern region (Tukey's HSD test, $P<0.05$), but condition increases in the central region were not statistically different from the increases in condition observed at southern region sites (Tukey's HSD tests, $P>0.05$).

3.3. Influence of environmental factors on growth

Some of the observed variation in growth could be attributed to variation in environmental variables, including dissolved oxygen, salinity, and water temperature. There was a strong, positive linear relationship between water temperature and instantaneous growth rate (Fig. 7). When several factors were assessed simultaneously using multiple regression, the combination of water temperature, salinity, and dissolved oxygen explained 60% of the variance in observed growth (Table 3). Each of the partial regression coefficients was significant, however, the differences in the standardized beta coefficients indicated that temperature explained the majority of the variability in juvenile red drum growth rates (three times the predictive importance compared to salinity or dissolved oxygen).

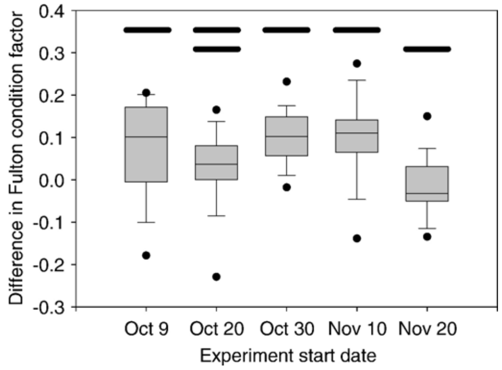

Fig. 5. Difference between initial Fulton condition index and final Fulton condition index after caging for age-0 red drum during fall recruitment 2004 for each of the five experimental intervals. Horizontal lines of different heights above box plots represent significant differences (Tukey's HSD tests: $P<0.05$) among experimental intervals. Box plots with horizontal lines of the same height are not statistically different.

Table 2

Results of two-factor ANOVA demonstrating the significant main effects of experiment and region on the difference (final–initial) in condition index (Fulton's K) of age-0 juvenile red drum between the start and end of each separate caging experiment (Oct–Dec 2004)

Source of Variation	DF	Type I SS	Mean square	F-value	P-value
Model	14	0.28800	0.02057	3.00	0.0012
Experiment	4	0.17624	0.04406	6.43	0.0002
Region	2	0.06976	0.03488	5.09	0.0086
Experiment× region	8	0.03663	0.00458	0.67	0.7181
Error	72	0.49375	0.00686		
Total	86	0.78174	0.00909		

Model overall $r^2=0.37$.

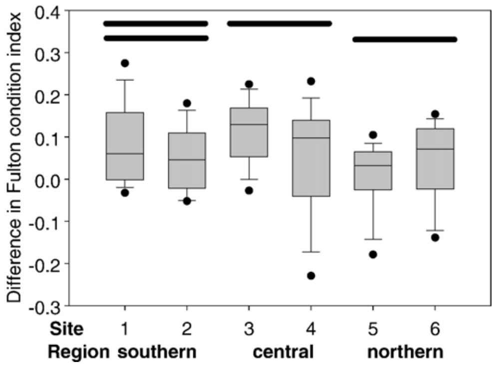

Fig. 6. Difference between initial Fulton condition index and final Fulton condition index after caging for age-0 red drum during fall recruitment 2004 for each of six experimental sites. Horizontal lines of different heights above box plots represent significant differences (Tukey's HSD tests: $P<0.05$) among southern, central, and northern regions. Box plots with horizontal lines of the same height are not statistically different.

3.4. Diets of free-ranging and caged individuals

Diets of caged individuals were examined to identify any changes in food habits across experiments or regions, and, more importantly, to allow comparisons with the diets of free-ranging individuals. Eighty-two percent of caged fish were recovered with food in their guts. Over 97% of individuals recovered after the first caging experiment had food in their stomachs, while 75–82% of individuals recovered after the subsequent experiments were found with food in their stomachs. Over 90% of individuals caged at southern region sites were recovered with food in their guts. In contrast, only 70% of individuals caged at northern sites were recovered with food in their guts. Caged individuals fed primarily on small epibenthic invertebrate taxa including the families Corophiidae (%FO = 11%), Gammaridae (%FO = 11%), Mysidae (%FO = 13%), and Portunidae (%FO = 13%). In addition, pelagic copepods were routinely recovered from the stomachs of caged individuals (%FO = 43%).

The most frequently observed prey taxa in the stomachs of free-ranging age-0 red drum also included copepods (%FO = 23%), as well as the families Gammaridae (%FO = 8%) and Mysidae (%FO = 45%). Fish prey were also recovered occasionally from the stomachs of free-ranging fish (%FO = 8%). Copepods were the most numerous prey in the diet of caged individuals (%*N* = 92%). Copepods were also the numerically dominant prey in the diets of free-ranging individuals (%N = 78%), followed by Mysidae (%*N* = 14%). The species richness (calculated at the family level) of the diets of caged individuals was 15, versus a richness of 11 for free-ranging individuals. Species evenness (Hulbert's PIE index) for the diets of caged and free-ranging red drum was 0.15 and 0.37, respectively, indicating a higher probability of recovering two different prey families from the stomachs of two independent free-ranging red drum compared to caged red drum. Thus, although overall prey species richness was higher for caged individuals, the diet composition of free-ranging fish was spread more evenly among the prey types eaten. The diet overlap calculated using Schoener's index was 0.64, indicating considerable overlap in diet between caged and free-ranging fish.

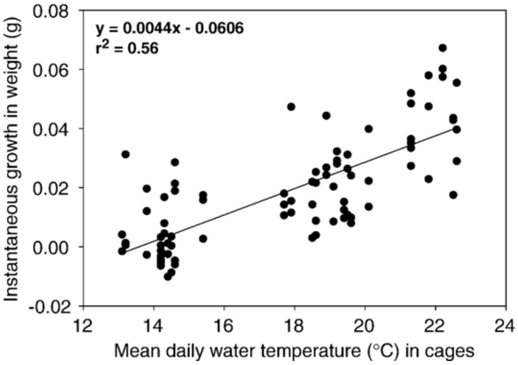

Fig. 7. Bivariate scatterplot of growth rate versus water temperature demonstrating a significant ($P<0.0001$) linear relationship between weight-specific (instantaneous) growth rate for caged individuals and average daily water temperature.

Table 3
Results of multiple regression analysis demonstrating the significant effects of temperature, salinity, and dissolved oxygen concentration on weight-specific (instantaneous) growth of age-0 juvenile red drum throughout the caging experiment (Oct–Dec 2004)

	Coefficient	SE	t	*P*-value	Beta coefficient
Temperature	0.0065	0.0010	6.600	<0.001	1.099
Salinity	0.0010	0.0004	2.807	0.006	0.354
DO	0.0059	0.0028	2.103	0.039	0.368
Constant	−0.1597	0.0425	−3.754	<0.001	

Model $F_{3,83}=41.55$; $r^2=0.60$, $n=87$.

4. Discussion

Water temperature is the primary controlling factor regulating animal metabolic rates in aquatic systems, with available oxygen, salinity, and other factors interacting with temperature to generate variation in the energy budgets of fishes across space and time (Fry, 1947; Neill et al., 2004). The strong temporal variation in growth rate observed in this study appeared to be due mainly to the decline in water temperature with each successive experiment. Water temperatures at the outset of our experiments were 24–26 °C, which was only slightly below the general range found to maximize growth and survival of recently settled juvenile red drum in a Texas estuary (25–27 °C; Rooker et al., 1999). However, temperatures in the New River declined rapidly during October and November and were only 12–15 °C at the end of the experimental period. As water temperatures declined, growth of caged red drum was relatively low during later time periods, with instantaneous growth rates only 25–50% of those achieved during the earliest experiment. During late November, the median growth rate of caged fish was negative. These findings indicate that, in most years in North Carolina estuaries, water temperatures during November will be well below optimal for growth of juvenile red drum and that growth may be negligible during the subsequent winter months.

The strong effects of temperature on growth of caged red drum in this study implicate that variation in recruitment timing among individuals can lead to substantial variability in size at the end of the growing season. Since North Carolina estuaries represent the highest latitudes at which consistent juvenile recruitment is observed for red drum, the growing season is comparatively short and the length of time an individual experiences fast growth conditions may be critical for survival during severe winters. Although moderate growth of red drum juveniles likely occurs during winter months at lower latitudes, growth during the winter period in North Carolina appears to be extremely limited based on our findings. Pre-winter size achieved by first year juvenile fishes has been identified as a potentially critical bottleneck to recruitment in many freshwater species. Specifically, Post and Evans (1989) demonstrated that overwinter mortality was negatively size-dependent in juvenile yellow perch and that variation in growth rates prior to winter could contribute substantially to year class strength. Similarly, in a study of the effect of hatch timing on juvenile largemouth bass survival, Pine et al. (2000) observed that earlier hatched individuals gained exposure to warmer temperatures and a more diverse prey assemblage and thus, realized faster growth and higher survival rates compared to later hatched fish. These studies support the conclusions of Rice et al. (1993), that both the magnitude and the variation in growth rates during fish early life stages may contribute to the strength of selective mortality, and ultimately to year class strength. Severe cold periods have been responsible for episodic mortality events for juvenile red drum in Texas estuaries (Gunter, 1941; McEachron et al., 1995), but variable winter mortality among body sizes has not been investigated. Recruitment timing and size attained prior to winter have been found to significantly affect the probability of survival in other first year fishes that inhabit estuarine waters along the US Atlantic coast (e.g., striped bass, Hurst and Conover, 1998; and Atlantic silverside, Munch et al., 2003). We conclude that these traits may be strongly linked to first year survival in Atlantic coast red drum as well.

Based on the red drum growth rates observed across experiments in our study, size at the onset of winter (e.g., January 1) could be greater by as much as two- to three-fold if estuarine settlement occurred in August versus October. This would result from the combination of an overall shorter growing season prior to the onset of winter and early juveniles being exposed to cold estuarine water temperatures during middle and late fall as opposed to warmer temperatures during late summer and early fall. Hatch date distributions reconstructed from otolith microstructure as part of a separate study (Stewart and Scharf unpublished data) indicate that hatch timing of red drum in North Carolina ranges between late July and late October, with most fish spawned within a two month period (August and September). Thus, sufficient variation in red drum hatch timing exists to generate significant differences in size at the onset of winter, suggesting that variation in the timing of spawning and recruitment events may represent an important process impacting growth and year class strength of North Carolina red drum.

The consistent effect on growth of estuarine region observed in this study may also be related to physicochemical attributes, other than temperature, that vary spatially. Experimental evidence indicates that red drum are efficient osmoregulators, only experiencing a 20–30% decline in growth at extreme salinities of 1 and 45 ppt (Wakeman and Wohlschlag, 1983, Neill et al., 2004). In this study, multiple regression analyses indicated only a moderate effect of salinity on growth, which is in general agreement with previous osmoregulatory evidence. However, the consistent spatial variation observed, with higher growth in the central estuarine region, suggests that differences in salinity may be important for red drum to achieve optimal growth. Salinity in the central region ranged mainly between 17–26 ppt, with a mean of 21.6 ppt, which is well above the isosmotic salinity for red drum of 10–11 ppt (Wakeman and Wohlschlag, 1983). However, high growth at intermediate salinities agrees with the results of Wakeman and Wohlschlag (1983), who found that the standard rate of oxygen consumption of red drum between 150–190 mm standard length was minimal at an intermediate salinity (20 ppt) that was not isosmotic with the blood serum. If North Carolina red drum demonstrate similar physiological traits as those fish from Texas tested by Wakeman and Wohlschlag (1983), then fish caged at intermediate salinities (central region) during our experiments may have realized lower standard metabolic rates, and thus have had more metabolic scope available for growth. A review of the influence of salinity on fish growth concluded that variable growth across a range of salinities is related to the metabolic costs of osmoregulation, which can account for 10 to 50% of the total energy budget of a fish (Boeuf and Payan, 2001). Alternatively, other ecological factors that were not measured directly in this study, including predator densities and prey availability, may also be responsible for the spatial variation in growth that we observed.

Many estuarine fishes are highly mobile. Therefore, even recent growth signatures obtained from the otoliths of free-ranging individuals may not be representative of growth conditions at the site of capture. Field caging experiments, as performed in this study, succeed in ‘anchoring’ individuals to a specific location for a defined time period, ensuring that growth signals directly reflect environmental conditions at that location. However, the growth of caged individuals may be influenced by a number of potential artifacts that are difficult to eliminate or control (Peterson and Black, 1994). For example, the exclusion of predators from the cages could potentially allow for increased time spent foraging by caged individuals compared to free-ranging fish that remain at risk of predation in the same environments. Cages also prevent other similarly-sized fishes from competing directly with the caged individuals for food, allowing the caged individuals to exclusively forage the benthic surface and pelagic volume within the cage. Under these two scenarios, an artificially high growth rate may be observed for caged fish in habitats that might ordinarily generate lower growth rates due to competition and/or threat of predation. Another potential artifact that we examined explicitly in this study was the potential for differences in food habits between caged and free-ranging fish. The dietary overlap between caged and free-ranging red drum during our experiments was relatively high (Schoener's index; $\alpha=0.64$), and we also found similar levels of prey species diversity in the diets. Based on analysis of stomach contents, the greatest difference in food habits was the inclusion of more pelagic crabs in the diets of caged fish, potentially due to the cage attracting settling megalops stages. Since only minor variation between diets was observed, available prey communities were likely similar for caged and free-ranging individuals. Furthermore, caging experiments were sufficiently short in duration (10–11 days) to limit prey depletion within the cages, as the majority (82%) of individuals recovered from cages had food in their stomachs.

5. Conclusions

Significant differences in growth rates of age-0 juvenile red drum emerged among estuarine regions and experimental intervals, indicating that growth varied spatially within the estuary as well as temporally within the recruitment season. Results indicate that the timing of estuarine arrival and the location of initial settlement habitat may each have a strong influence on growth rates realized by early juveniles. Variation in growth rate, and thus size at age, may have important implications for survival during winter periods given that red drum in North Carolina are located at higher latitudes and experience shorter growing seasons and harsher winter conditions relative to more southern populations. Temperature and, to a lesser degree, salinity and dissolved oxygen contributed to temporal and spatial variation in growth, and observed patterns suggest that early estuarine arrival coupled with movement to moderate salinity habitats may promote the highest growth rates for red drum in North Carolina estuaries. Considering the relatively protracted nature of red drum spawning and the potential for size-dependent juvenile mortality, the results of this study reveal that considerable growth variation among first year juvenile red drum may have important implications for survival and eventual year-class success.

Acknowledgements

The authors thank the marine operations staff at the UNCW Center for Marine Science for boat maintenance and construction of cage frames. Thanks also to the Behavioral Ecology Branch at the James J. Howard Marine Sciences Laboratory, NOAA for the loan of the nylon mesh caging enclosures. Troy Alphin helped considerably with the identification of gut contents and Scott Quackenbush provided aquaria space for holding juvenile red drum prior to experiments. The UNCW Fisheries Ecology Lab, especially W. Bradley Tayloe, assisted with all aspects of the study. Tom Lankford and one anonymous reviewer provided valuable comments on earlier drafts of the manuscript. The authors are grateful to North Carolina Sea Grant for providing financial support for this study. **[SS]**

References

Bass, R.J., Avault, J.W., 1975. Food habits, length-weight relationships, condition factor, and growth of juvenile red drum, Sciaenops ocellata, in Louisiana. Trans. Am. Fish. Soc. 104, 35–45.

Boeuf, G., Payan, P., 2001. How should salinity influence fish growth? Comp. Biochem. Physiol., Part C Pharmacol. Toxicol. 130, 411–423.

Campana, S.E., 1996. Year-class strength and growth rate in young Atlantic cod *Gadus morhua*. Mar. Ecol. Prog. Ser. 135, 21–26.

Conover, D.O., 1992. Seasonality and the scheduling of life history at different latitudes. J. Fish Biol. 41, 161–178.

Cushing, D.H., 1975. Marine Ecology and Fisheries. Cambridge University Press, Cambridge.

Daniel, L.B. III, 1988. Aspects of the biology of juvenile red drum, *Sciaenops ocellatus*, and spotted seatrout, *Cynoscion nebulosus*, (Pisces: Sciaenidae) in South Carolina. MS thesis, College of Charleston, pp. 58.

Fry, F.E.J., 1947. Effects of the environment on animal activity. University of Toronto Studies, Biological Series 55. Publication of the Ontario Fisheries Research Laboratory 68, 1–62.

Gotelli, N.J., Entsminger, G.L., 2001. EcoSim: Null Models Software for Ecology. Version 7.0. Acquired Intelligence Inc. & Kesey-Bear.

Gunter, G., 1941. Death of fishes due to cold on the Texas coast, January, 1940. Ecology 22, 203–208.

Hjort, J., 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-V. Reun.-Cons. Int. Explor. Mer. 20, 1–228.

Holt, S.A., Holt, G.J., Arnold, C.R., 1989. Tidal stream transport of larval fishes into non-stratified estuaries. Rapp. P.-V. Reun.-Cons. int. Explor. Mer. 191, 100–104.

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

Houde, E.D., 1989. Comparative growth, mortality, and energetics of marine fish larvae: Temperature and implied latitudinal effects. Fish. Bull. 87, 471–495.

Hurst, T.P., Conover, D.O., 1998. Winter mortality of young-of-the-year Hudson River striped bass (*Morone saxatilis*): size-dependent patterns and effects on recruitment. Can. J. Fish. Aquat. Sci. 55, 1122–1130.

Manderson, J.P., Phelan, B.A., Meise, C., Stehlik, L.L., Bejda, A.J., Pessutti, J., Arlen, L., Draxler, A., Stoner, A.W., 2002. Spatial dynamics of habitat suitability for the growth of newly settled winter flounder *Pseudopleuronectes americanus* in an estuarine nursery. Mar. Ecol. Prog. Ser. 228, 227–239.

May, R.C., 1974. Larval mortality in marine fishes and the critical period concept. In: Blaxter, H.S. (Ed.), The Early Life History of Fish. Springer-Verlag, New York, New York, USA, pp. 3–19.

McEachron, L.W., Matlock, G.C., Bryan, C.E., Unger, P., Cody, T.J., Martin, J.H., 1995. Winter mass mortality of animals in Texas bays. North. Gulf Sci. 13, 121–138.

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

Munch, S.B., Mangel, M., Conover, D.O., 2003. Quantifying natural selection on body size from field data: winter mortality in *Menidia menidia*. Ecology 84, 2168–2177.

Neill, W.H., Brandes, T.S., Burke, B.J., Craig, S.R., Dimichele, L.V., Duchon, K., Edwards, R.E., Fontaine, L.P., Gatlin III, D.M., Hutchins, C., Miller, J.M., Ponwith, B.J., Stahl, C.J., Tomasso, J.R., Vega, R.R., 2004. Ecophys. Fish: a simulation model of fish growth in time-varying environemental regimes. Rev. Fish. Sci. 12, 233–288.

Pearson, J.C., 1929. Natural history and conservation of the redfish and other commercially important sciaenids on the Texas coast. Bull. U.S. Bureau Fish. 44, 129–214.

Peters, K.M., McMichael Jr., R.H., 1987. Early life history of the red drum, *Sciaenops ocellatus* (Pisces: Sciaenidae), in Tampa Bay, Florida. Estuaries 10, 92–107.

Peterson, C.H., Black, R., 1994. An experimentalist's challenge: when artifacts of intervention interact with treatments. Mar. Ecol. Prog. Ser. 111, 289–297.

Peterson, M.S., Comyns, B.H., Rakocinski, C.F., Fulling, G.L., 1999. Does salinity affect growth in juvenile Atlantic croaker, *Micropogonias undulatus* (Linnaeus)? J. Exp. Mar. Biol. Ecol. 238, 199–207.

Peterson, M.S., Comyns, B.H., Rakocinski, C.F., Fulling, G.L., 2004. Defining the fundamental physiology niche of young estuarine fishes and its relationship to understanding distribution, vital metrics, and optimal nursery conditions. Env. Biol. Fish. 71, 143–149.

Phelan, B.A., Goldberg, R., Bejda, A., Pereira, J., Hagan, S., Clark, P., Studholme, A., Calabrese, A., Able, K.W., 2000. Estuarine and habitat-related differences in growth rates of young-of-the-year winter flounder (Pleuronectes americanus) and tautog (Tautoga onitis) in three northeastern U.S. estuaries. J. Exp. Mar. Bio. Ecol. 247, 1–28.

Pine, W.E., Ludsin, S.A., DeVries, D.R., 2000. First summer survival of largemouth bass cohorts: Is early spawning really best? Trans. Am. Fish. Soc. 129, 504–513.

Post, J.R., Evans, D.O., 1989. Size-dependent overwinter mortality of young-of-the-year perch (*Perca flavescens*): laboratory, in-site enclosure, and field experiments. Can. J. Fish. Aquat. Sci. 46, 1958–1968.

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

Ricker, W.E., 1975. Computation and interpretation of biological statistics of fish populations. J. Fish. Res. Bd. Can., 191. 382 p.

Rooker, J.R., 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., Holt, G.J., Fuiman, L.A., 1999. Spatial and temporal variability in growth, mortality and recruitment potential of post-settlement red drum (*Sciaenops ocellatus*) in a subtropical estuary. Fish. Bull. 97, 581–590.

Rothschild, B.J., 1986. Dynamics of Marine Fish Populations. Harvard University Press, Cambridge.

SAS software, Inc., 2002. Version 9.1 of the SAS System for Windows. SAS Institute Inc., Cary, NC, USA.

Scharf, F.S., 2000. Patterns in abundance, growth, and mortality of juvenile red drum across estuaries on the Texas coast and implications for recruitment and stock enhancement. Trans. Am. Fish. Soc. 129, 1207–1222.

Shuter, B.J., Post, J.R., 1990. Climate, population variability, and the zoogeography of temperate fishes. Trans. Am. Fish. Soc. 119, 314–336.

Simmons, E.G., Breuer, J.P., 1962. A study of redfish, *Sciaenops ocellata* Linnaeus and black drum, *Pogonias cromis* Linnaeus. Publications of the Institute of Marine Science, University of Texas, vol. 8, pp. 184–211.

Sogard, S.M., 1992. Variability in growth rates of juvenile fishes in different estuarine habitats. Mar. Ecol. Prog. Ser. 85, 35–53.

Sogard, S.M., 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull. Mar. Sci. 60, 1129–1157.

Soto, M.A., Holt, G.J., Holt, S.A., Rooker, J., 1998. Food habits and dietary overlap of newly settled red drum (*Sciaenops ocellatus*) and Atlantic croaker (*Micropogonias undulatus*) from Texas seagrass meadows. Gulf Res. Rep. 10, 41–55.

Stunz, G.W., Minello, T.J., Levin, P.S., 2002a. A comparison of early juvenile red drum densities among various habitat types in Galveston Bay, Texas. Estuaries 25, 76–85.

Stunz, G.W., Minello, T.J., Levin, P.S., 2002b. Growth of newly settled red drum in different estuarine habitat types. Mar. Ecol. Prog. Ser. 238, 227–236.

Wakeman, J.M., Wohlschlag, D.E., 1983. Time course of osmotic adaptation with respect to blood serum osmolality and oxygen uptake in the euryhaline teleost, *Sciaenops ocellatus* (red drum). Contrib. Mar. Sci. 26, 165–177.

Wallace, J.R.K., 1981. An assessment of diet-overlap indexes. Trans. Am. Fish. Soc. 110, 72–76.

Wenner, C.A., Roumillat, W.A., Moran, J.E., Maddox, M.B., Daniel, L.B., Smith, J.W., 1990. Investigations on the Life History and Population Dynamics of Marine Recreational Fishes in South Carolina, Part I. South Carolina Marine Resources Research Institute, Charleston.