

Defining the fundamental physiological niche of young estuarine fishes and its relationship to understanding distribution, vital metrics, and optimal nursery conditions

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Synopsis

Because estuarine nekton are ‘integrators of the environment’ abiotic and biotic factors can influence or constrain the relative value of estuarine nursery zones. Recent laboratory experiments on young spot, *Leiostomus xanthurus*, indicate that both water temperature and salinity significantly affect somatic growth. These experimental data contrast with previous work on young Atlantic croaker, *Micropogonias undulatus*, white trout, *Cynoscion arenarius*, and mullet, *Mugil* sp. Together these results suggest that quantifying vital metrics of nekton, such as survival and growth, along realistic environmental gradients through critical laboratory experiments, allows a more accurate definition of constraints on habitat use. Our studies of factors influencing recruitment success in both winter- and spring/summer-spawning fishes illustrate seasonal as well as intrafamilial differences in growth. Effective management of coastal ecosystems must take into account both variability in abiotic conditions and the nested habitat component, both of which can be modified by coastal development, which could lead to reduced productivity and sustainability of these estuarine landscapes.

Introduction

Environmental variability and linkages between adjacent subsystems are characteristics of coastal ecosystems, and, in fact, may be defining features of these interface landscapes. Large- and small-scale patterns of variability influence the well-adapted biota that use coastal interface ecosystems. For example, Malloy & Targett (1994) documented that scope for growth in juvenile summer flounder, *Paralichthys dentatus*, collected in North Carolina was more influenced by colder water temperatures than for those fish collected in Delaware. Understanding the effects of large-scale patterns in abiotic conditions (natural and anthropogenic) is necessary for a more complete understanding of recruitment variability, fisheries

dynamics, and effective management (Rose 2000). Estuarine ecosystems are ideal for studying such variability because these ecosystems are affected by large fluctuations in abiotic conditions, they are strongly influenced by anthropogenic activities, and they support large populations of nekton.

Estuaries are productive ecosystems that are comprised of a mosaic of spatially and temporally variable environments (Miller & Dunn 1980, Peterson & Ross 1991, Peterson 2003), which are used by a myriad of nekton during all or part of their life histories. Fluctuations in estuarine hydrographic conditions comprise a dome-shaped gradient of variability with an intermediate zone of relatively high variability and tails composed of relatively stable up-estuary and down-estuary zones (Peterson & Meador 1994, Miller et al. 2000). The resulting

environmental heterogeneity consequently engenders a mosaic of rate-determining environments (Demers et al. 2000) that have both direct and indirect effects on the ecological and physiological processes that regulate nekton growth and survival (Malloy & Targett 1991, Neill et al. 1994, Lankford & Targett 1994, Peterson et al. 2000, Secor et al. 2000). Because estuarine nekton are 'integrators of the environment', these background conditions influence or constrain the relative value of estuarine nurseries (Miller et al. 2000, Ross 2003). For example, variability in water temperature, salinity, and dissolved oxygen related better to early growth of juvenile sciaenids than did variability in diet and habitat structure across a coastal Louisiana landscape (Baltz et al. 1998). Meng & Matern (2001) suggested that habitat suitability is controlled by temperature and interannual variations in freshwater flow (and thus salinity structure) for larvae of native and introduced fishes in California. In contrast, Craig & Crowder (2000) noted that while significant correlations often occur between abiotic factors and habitat selection by marsh fishes, it is still questionable whether they are simply correlates of other processes or whether factors other than abiotic conditions are important.

Overlap of physico-chemical and prey availability gradients contribute to nursery ground suitability and strongly influence the relative nursery value of specific locations in terms of recruitment success and production. Controlled laboratory experiments coupled with detailed field studies addressing causality and the relative importance of processes such as survival, growth, and reproduction are required to develop a more accurate understanding of constraints on aquatic habitat use. Delineating a species' fundamental physiological niche (Spotila et al. 1989) is prerequisite for evaluating any other aspect of habitat quality in estuaries. In fact, in a recent study of community assembly rules, Belyea & Lancaster (1999) argue that environmental constraints restrict species establishment and mediate interactions among successive recruits; changes in these constraints, either exogenous or endogenous, may drive community change.

We estimated laboratory growth and survival of juvenile spot, *Leiostomus xanthurus*, exposed to various abiotic regimes as defined by 12 tempera-

ture and salinity combinations, and compared these results with our published data on other winter and spring-summer spawning estuarine-dependent species. The use of a laboratory approach will lead to a better understanding of the importance of abiotic conditions for defining the fundamental physiological niche and thus the distribution and abundance of estuarine-dependent species along estuarine landscapes.

Materials and methods

Field collection procedures

We collected spot for the laboratory experiments with a 3.05 m bag seine constructed of 3.2 mm mesh in February 1999 from shallow marsh areas of Davis Bayou, Mississippi. Conditions at the time of collection were 8.5 psu and 19.0°C.

Laboratory procedures

We slowly acclimated these spot (15–20 mm TL) over 48 h to $24 \pm 1^\circ\text{C}$, 13 psu, and a 10:14 light-dark cycle centered at 13:00 h under flow-through conditions (total volume exchange every 6 h) and then maintained them in two fiberglass aquaria (~216 and 330 l) for 9 days. We then randomly assigned five fish per replicate ($n = 9$) into their experimental aquaria under the same conditions noted above. Over a 6 day period, we slowly changed experimental conditions from $24 \pm 1^\circ\text{C}$ and 13 psu to treatment conditions (see below). We replaced fish that died during this acclimation period. Once the experiment began, we did not replace dead fish. We removed fish from each replicate aquarium at the start of the experiment, weighed them (wet mass, WM to 0.001 g) in groups of five (Ohaus Balance) in ambient water, and returned them to the aquarium. During maintenance and experimental periods, we fed fish thawed and rinsed brine shrimp, *Artemia salina*, *ad libitum* twice daily for 10 min, and then we removed all remaining food. We did not feed fish on the days they were weighed. The experiment ended after 30 days and we then obtained live weights of fish from each replicate and preserved fish in 95% ethanol.

We randomized and interspersed experimental aquaria containing young juvenile spot representing nine replicates of the various treatment com-

binations in a 3×4 factorial design (12, 17 and 22°C and 3, 10, 17 and 24 psu) (5 fish per replicate; total of 45 fish per temperature–salinity treatment) over a 30 day period. Water temperature and salinity ranges bracketed conditions experienced by spot during the recruitment period. For each experimental temperature (12, 17 and 22°C, $n = 9$ baths), we maintained water temperature in three connected water baths arranged in a vertical stack. Thermostatically controlled 1-kW submersible heaters and a Frigid-Unit water cooler maintained water temperature in the air-conditioned laboratory.

Each replicate consisted of a 21 l glass aquarium supplied with saline water pumped from floor-vaults containing the appropriate salinity (40 Fathoms sea salts). Water exchanged completely in each experimental aquarium every 24 h and water level equilibrated in each unit with a standpipe. A small aeration stone located at the opposite end of the aquarium aerated and circulated water in each experimental unit. Every day, we recorded the water temperature of each bath, and every other day we recorded salinity from each replicate tank during acclimation and experimentation.

Processing otoliths

We removed the left sagittae from experimental fish, rinsed, and embedded them in epoxy resin molds. We viewed otoliths (Olympus dissecting microscope at 50× magnification), and measured them in the sagittal plane. Although daily growth increments have been validated in spot and other young sciaenids (reviewed in Paperno et al. 1997), otoliths from field-caught and lab-grown spot were strikingly different in appearance. The lab-reared outer portion of otolith growth was relatively translucent, compared to the opaque inner portion of the otolith, which formed under natural conditions in the field. Otoliths of field-caught fish did not have this outer translucent portion. Because we could not accurately read daily growth increments from laboratory fish, we estimated lab growth by the relative width of the translucent outer portion of the otolith.

Data analysis

Since individual growth could not be followed within each replicate, we calculated the mean relative increase in body mass (Ricker 1975) as

$$G = \left(\frac{(\text{FWMM} - \text{IWMM})}{\text{IWMM}} \right) \times 100$$

where FWMM = mean final WM and IWMM = mean initial WM.

We were also interested in determining if somatic and otolith growth were coupled. Thus, we similarly estimated lab growth using changes in relative otolith diameter (OD), which was measured along the longest axis. We expressed the relative increase in OD as

$$\text{OD} = \left(\frac{(\text{WDIAM} - \text{IDIAM})}{\text{IDIAM}} \right) \times 100$$

where WDIAM is the mean whole diameter (field and lab growth) and IDIAM is the mean inner diameter (field growth). These two growth estimates each served as response variables in a two-way Analysis of Variance (ANOVA). If a significant F -value ($p < 0.05$) resulted, we used a Sidak pairwise comparison test to distinguish treatment means. At the end of the experiment, we compared both G and OD for a random subset of spot ($n = 12$; representing all treatments) with the Pearson's Correlation statistic to assess whether body and otolith growth were coupled. We conducted all tests with SPSS (Windows Version 11.5) statistical software (SPSS, Inc., Chicago, III).

Results

Initial mean wet mass (IWMM) of spot ranged from 0.567 g (12°C, 24 psu) to 0.688 g (22°C, 10 psu). There was no interaction in IWMM between temperature and salinity ($F_{6,11} = 0.882$, $p = 0.511$), nor the main effects of temperature ($F_{2,11} = 0.416$, $p = 0.661$) or salinity ($F_{3,11} = 0.488$, $p = 0.691$) across treatments. Only 2.9% of 540 total fish died during the 30 day experiment with most fish dying in the coldest (i.e., 12°C) treatment (Figure 1).

Significant temperature ($F_{2,107} = 194.30$, $p < 0.001$) and salinity ($F_{3,107} = 5.134$, $p = 0.002$) effects on somatic growth occurred, with no apparent interaction ($F_{6,107} = 1.583$, $p = 0.160$). Maximum growth of juvenile spot occurred at 22°C (Sidak, $12 < 17 < 22^\circ\text{C}$), and growth peaked at salinities above 10 psu (Sidak, $3 < 10$,

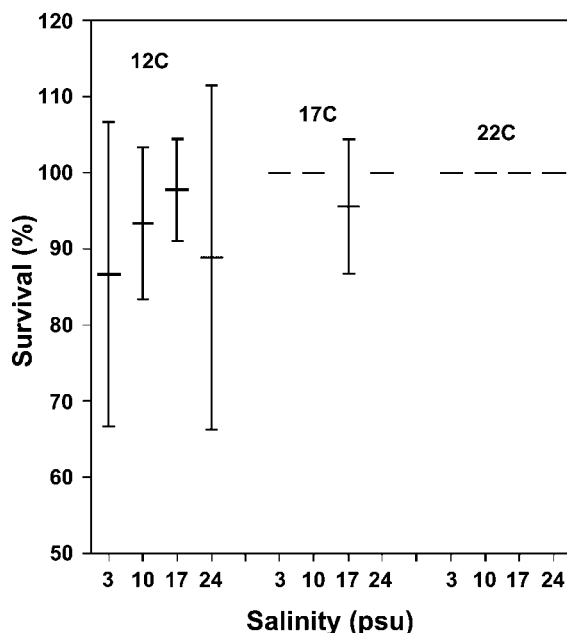


Figure 1. Percentage (mean \pm 1 SD) survival of young spot exposed to 12 combinations of water temperature (12, 17, 22°C) and salinity (3, 10, 17, 24 psu). SD = standard deviation.

17 and 24 psu; 10 = 17 and 24 psu; and 17 = 24 psu) (Figure 2a). Relative somatic growth was significantly lower in the 12°C treatment than in other treatments and growth increased slightly with increasing salinity in the 12°C treatment (Figure 2a). Compared to the 12°C treatment, somatic growth was significantly higher in the 17 and 22°C treatments, and varied only slightly with salinity (Figure 2a). There was a significant temperature ($F_{2,59} = 20.65$, $p < 0.001$) effect on OD in lab-reared spot, but no salinity effect ($F_{3,59} = 1.24$, $p = 0.307$) nor an interaction ($F_{6,59} = 0.525$, $p = 0.786$) (Figure 2b). Thus, otolith growth of juvenile spot clearly increased as an increasing function of temperature (Sidak, $12 < 17 < 22^\circ\text{C}$). There was a significant correlation between G and OD for a random subset of spot (representing all 12 treatments; $r = 0.884$, $p < 0.001$, $n = 12$).

Discussion

Our studies of factors that may influence recruitment success in both winter- and spring/summer-

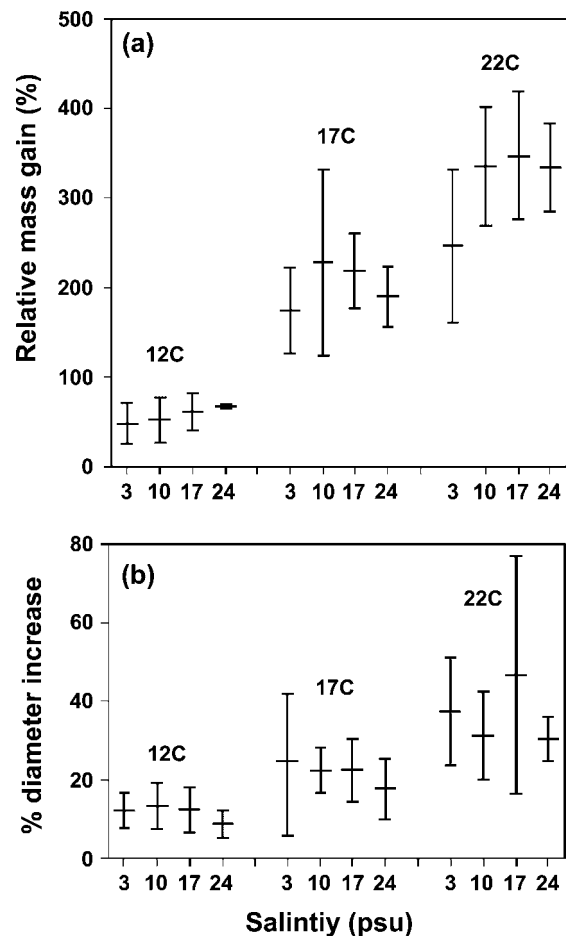


Figure 2. (a) Plot of mean (\pm 1 SD) relative WM gain ($G = ((\text{FWMM} - \text{IWMM}) / \text{IWMM}) \times 100$, where FWMM = mean final WM and IWMM = mean initial WM) and (b) mean (\pm 1 SD) percent diameter increase ($\text{OD} = ((\text{WDIAM} - \text{IDIAM}) / \text{IDIAM}) \times 100$, where WDIAM = mean whole diameter (field and lab growth) and IDIAM = mean inner diameter (field growth) of young spot exposed to 12 combinations of water temperature (12, 17, 22°C) and salinity (3, 10, 17, 24 psu). SD = standard deviation.

spawning estuarine-dependent fishes show both seasonal and intrafamilial differences in growth. Survival and growth can vary based on the spatially and temporally explicit environmental conditions into which young recruits initially settle, and can be species-specific. For example, earlier laboratory experiments on young Atlantic croaker, *Micropogonias undulatus*, involving a fixed water temperature (25°C) and variable salinity (Peterson et al. 1999) indicated that young fish

grew faster in 5 psu compared to 20 psu salinity and grew at intermediate rates when salinity decreased from 20 to 5 psu. In contrast, our present laboratory results using young spot exposed to the 22°C treatment indicated that growth of this species is less influenced by salinity than Atlantic croaker. OD increased significantly with temperature but not salinity, although both G and OD were highly correlated. Furthermore, whereas juvenile spot exhibited significantly slower growth in 3 psu compared to 10, 17 or 24 psu at 22°C, somatic growth was not influenced across intermediate salinity treatments. In contrast, young Atlantic croaker exposed to gradually decreasing salinity conditions, including 10 and 17 psu, showed intermediate somatic growth. Previous studies on the same winter spawners (Perez 1969, Moser & Gerry 1989) also suggest that energetic costs of salinity adaptation may be higher for Atlantic croaker than spot, with Atlantic croaker being more sensitive to salinity fluctuation. Spot also adapt more quickly to increasing rates of salinity change than decreasing rates (Moser & Miller 1994), and size-dependent changes in this sensitivity appear to correspond with seasonal shifts in distribution with growth as ambient temperature increases. Ross (2003), however, noted that salinity did not appear to influence significantly field otolith growth in spot or Atlantic croaker in North Carolina.

Clearly, water temperature is a controlling factor for a number of fishes (Neill et al. 1994, Miller et al. 2000) as well as those in our studies. Somatic growth of young spot was significantly lower in 12 compared to 17 or 22°C, suggesting that if all else was equal, cohorts recruiting to the estuary when water temperature was low would have reduced growth compared to those cohorts recruiting at a later date. In fact, during our laboratory experiments we noted spot reduced activity and feeding in the coldest treatment conditions regardless of salinity, suggesting a synergism between thermally-induced lower metabolism and reduced feeding may exist. This reinforces the idea that abiotic factors may predetermine the capacity for recruitment through reduced metabolism and feeding and increased mortality.

Spot peak spawning occurs in the northern Gulf of Mexico between December-late February (Pattillo et al. 1997) and young typically recruit in

multiple cohorts to estuaries between February and April. Sequential cohorts would thus grow differentially when water temperatures are increasing. Indeed, Moser & Hettler (1989) noted metabolic rates of spot increase significantly with increasing temperature; mean metabolic rate increased 9.5% per degree of increase in temperature, whereas there was only a 2% mean increase in metabolic rate per part per thousand salinity. Miller et al. (2000) estimated that abiotic differences among estuaries could account for at least a threefold difference in growth rates of juvenile fishes. Since both water temperature and salinity can vary within and among estuaries, we suggest that variability in growth rates for many nekton is predetermined by these different abiotic conditions, which can vary regionally.

Spring-summer spawners pulse into estuaries under a different set of environmental conditions than winter spawners. The timing of recruitment is driven, in part, by the environmental conditions and the physiological capabilities of the species. For example, laboratory experiments on the effects of water temperature and salinity on growth of young mullet, *Mugil* sp. (Peterson et al. 2000), indicated maximum growth occurred at temperatures $\geq 25^\circ\text{C}$ ($20 < 25 = 30^\circ\text{C}$), while within each temperature, peak growth occurred at 17 psu ($3 = 10 < 17 > 24$ psu). A comparison of these lab-based results with simultaneous field estimates of growth from two locations only 45 km apart indicated a modal SL shift over 7 days of 3.4 mm ($0.486 \text{ mm day}^{-1}$) at the more saline location (6.54–11.47 psu) whereas at the less saline location (1.58–4.39 psu), the modal SL shift was only 2.2 mm ($0.314 \text{ mm day}^{-1}$). These shifts in SL over 7 days, coupled with the salinity and temperature data from these locations, parallel the differences observed in our laboratory growth experiments. These physical data suggest salinity differences between locations could have driven growth differences in young mullet, although differences in water temperature likely reinforced the growth difference within this spatial context. In fact, it has been suggested that because young mullet recruit into varying estuarine environments, their survival and growth may be differentially influenced by exposure to variable abiotic factors (Marais 1978, Nordlie et al. 1982, Cardona 2000). Contrasting results were found for a major spring-summer

spawning sciaenid, the white trout *Cynoscion arenarius* (Rakocinski et al. 2002). In this case, weekly modal shifts in length distributions of white trout were strongly related to changes in weekly mean water temperature. Salinity, however, did not appear to have much effect on growth within this temporal context. Thus, estuarine-dependent species that one would expect to have similar physiological capabilities pulse into a dynamic estuarine environment leading to different survival and growth trajectories may be driven by different controlling factors.

Estuaries encompass an array of environments along coastal landscapes with habitat nested within an abiotic background (Peterson 2003). Understanding the use of this dynamic landscape as a nursery for young nekton requires detailed knowledge of abiotic and biotic influences on vital rates. Understanding the influences of either abiotic or biotic factors alone, however, does not provide enough information to predict distribution, vital metrics, and community assembly of young estuarine nekton. For example, a series of field and laboratory studies of factors influencing recruitment success of estuarine-dependent weakfish, *Cynoscion regalis*, into nursery habitat (Goshorn & Epifanio 1991, Lankford & Targett 1994, Greycay & Targett 1996a, b), indicates that physico-chemical gradients and natural variability (spatial and seasonal) of prey along those gradients influence the value of particular estuarine zones as nurseries by affecting the energetics of feeding and growth. In fact, there is a size-dependent behavioral tradeoff between optimal temperature/salinity conditions, prey availability, and predation that provides a mechanism for the well-documented emigration from oligohaline nurseries to down-estuary habitats with increasing size (Lankford & Targett 1994). These findings further suggest that the overlap of physico-chemical and biotic gradients such as prey availability determine nursery ground suitability and the potential contribution of specific locations to recruitment success and production. The influence of environmental variability on growth and production during estuarine occupation by nekton is ultimately exported to offshore ecosystems as new biomass (Deegan 1993, Beck et al. 2001) and may partially explain geographic differences in estuarine production and export. Clearly, controlled

laboratory experiments can provide robust and complementary data to field studies concerned with processes such as survival, growth, and reproduction in variable environments. Linking variability associated with natural environmental factors and anthropogenic alteration (Rose 2000) to estuarine landscapes through a detailed examination of vital metrics for a suite of similar species under such conditions will foster better prediction and management of fisheries sustainability.

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