Growth of newly settled red drum *Sciaenops ocellatus* in different estuarine habitat types

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ABSTRACT: We examined growth of recently settled juvenile red drum in salt marsh, seagrass, oyster reef, and on nonvegetated bottom areas in the Galveston Bay system of Texas (USA). We estimated growth using otolith microstructure from free-ranging fish collected in different habitat types and also measured growth of red drum in experimental enclosures where fish movement was restricted. Otolith growth was closely related to somatic growth in fish of 13 to 33 mm SL, and we used daily otolith increments from the last 10 d before capture as an indicator of growth following settlement into estuarine habitats. Growth rates of red drum captured at marsh, nonvegetated, and seagrass sites were not significantly different; no fish were collected on oyster reef. While reducing potential problems of a lagged response between otolith growth and somatic growth, the use of a 10 d growth period may have increased the likelihood of fish movement among habitats affecting our comparisons. The overall post-settlement growth rate of 0.45 mm d^{-1} was similar to rates reported in the literature. Movement among habitat types was eliminated in experiments employing 24 solid-walled enclosures (60 cm diameter). Growth rates in enclosures over the 7 d experiment were 0.12 mm d^{-1} in oyster reef, 0.21 mm d^{-1} on nonvegetated bottom, 0.40 mm d^{-1} in salt marsh, and 0.42 mm d^{-1} in seagrass; rates in vegetated enclosures approximated natural growth rates. Significantly higher growth in marsh and seagrass enclosures suggests that growth potential for red drum may be highest in these vegetated areas. However, growth results in enclosures need to be evaluated carefully, because fish movement among habitat types may be important in these shallow estuarine systems.

KEY WORDS: Growth · Habitat · Habitat comparisons · Red drum · Estuaries · *Sciaenops ocellatus*

INTRODUCTION

Rapid growth may confer ecological advantages and increase survivorship of early juvenile fishes (Sogard 1997). Many young marine fishes use shallow estuarine habitats (Weinstein 1979, Heck & Thoman 1984) where they exploit abundant food supplies to maintain rapid growth (Boesch & Turner 1984, Kneib 1993). These high growth rates may reduce the time young fish spend in size classes more vulnerable to predators. Because variability in predation on juvenile fish can

have dramatic effects on population dynamics (Hixon 1991), the selection of appropriate habitats to maximize growth has important demographic consequences (Parker 1971, Cushing 1975, Houde 1987, Werner & Hall 1988, Post & Evans 1989, Forrester 1990, Sogard 1992, Levin et al. 1997, Petrik et al. 1999); rapid growth during early stages of development influences successful recruitment to adult populations (Houde 1987, Forrester 1990, Connell & Jones 1991, Leggett & Deblois 1994). High growth rates may also provide other physiological advantages such as increased swimming speed (Webb & Corolla 1981), ability to detect and escape predators (Fuiman 1994), and enhanced sur-

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vival during winter months (Henderson et al. 1988, Post & Evans 1989, Able 1999).

Many estuarine fishes use a variety of putative nursery grounds throughout their ranges and may use several habitat types in a single location (Rozas & Minello 1998, Rozas & Zimmerman 2000); the value of these habitat types is often based on density patterns associated with these areas. While these density patterns provide insight as to habitat value, functional relationships such as growth rate also need to be examined (Heck et al. 1997, Beck et al. 2001). However, habitat-specific growth measurements are difficult to obtain. Only limited data are available to compare the growth rates of juvenile fishes among various estuarine habitats (Nadeau 1991, Sogard 1992, Heck et al. 1997, Levin et al. 1997, Phelan et al. 2000), and these studies have focused on growth rates between vegetated and nonvegetated habitat types.

Daily patterns recorded in otolith microstructure are useful for measuring growth rates of fish at various life history stages (Neilson & Geen 1985, Radtke 1989, Sogard 1991, Sogard & Able 1992, Secor & Houde 1995, Rooker & Holt 1997). Daily increment deposition, first demonstrated by Pannella (1971), provides a method to age individuals and has been used for a wide variety of species (Campana & Neilson 1985). Additionally, experimental studies demonstrating a coupling of somatic and otolith growth have made it possible to calculate historic and recent post-settlement patterns of growth by measuring incremental widths (Wilson & Larkin 1982, Neilson & Geen 1985, Radtke 1989, Secor & Dean 1989, Sogard 1991). Otolith growth can thus be used as a proxy for fish growth during this time period (Suthers et al. 1989, Sogard & Able 1992, Levin et al. 1997, Baltz et al. 1998).

Field enclosure experiments also provide a means to measure growth rates over a short time period in a fish's natural habitat (e.g. Werner & Hall 1988, Nadeau 1991, Sogard 1992, Sogard & Able 1992, Duffy et al. 1996, Hayse & Wissing 1996, Phelan et al. 2000). Enclosing fish in a particular habitat can provide information on growth potential, but restricting fish movement may also have unanticipated effects (Peterson & Black 1994). Enclosure growth measurements may not always reflect fish growth under natural conditions (Sogard & Able 1992, Duffy et al. 1996).

Red drum *Sciaenops ocellatus* are estuarine-dependent fishes that were historically subject to an intense commercial fishery throughout the Gulf of Mexico and the SE United States, and presently, this species supports an important recreational fishery (Pattillo et al. 1997). Red drum spawn during early fall in offshore waters near passes and inlets, where the pelagic eggs and larvae are carried by tides and currents into shallow bays and estuaries (Holt et al. 1989, Comyns et al.

1991). Following a short pelagic stage, larval fish (ca. 6 to 8 mm) settle primarily into vegetated seagrass habitats and remain in these areas during their early juvenile stages (≤40 mm) (Holt et al. 1983, Rooker & Holt 1997, Rooker et al. 1998).

Many studies have documented the importance of submerged aquatic vegetation to fishes (Heck & Orth 1980, Bell & Westoby 1986, Rozas & Odum 1988, Sogard 1992, Worthington et al. 1992, Heck et al. 1997), and seagrass appears to be an important nursery habitat for red drum (Holt et al. 1983, Rooker et al. 1998). Nevertheless, estuarine systems lacking extensive seagrass beds, such as Galveston Bay, Texas, often support large populations of red drum (Fuls & Hensley 1998). In such estuaries, red drum potentially use salt marsh, nonvegetated bottom, and oyster reefs as juvenile habitat (Stunz et al. 2002). However, differences in the ability of these habitats to support red drum growth have been largely unexplored. The purpose of our study was to determine the growth rates of newly settled red drum among various estuarine habitat types using both otolith increment analysis and field enclosures.

MATERIALS AND METHODS

Study site. Our study site was Christmas Bay, Texas, in the Galveston Bay system ($\sim$1420 km^2); this small satellite bay ($\sim$26 km^2) contains most of the remaining ($\sim$113 ha) seagrass meadows (primarily *Halodule wrightii*) within the estuary (Pulich & White 1991, Sheridan et al. 1998). The dominant shoreline vegetation is *Spartina alterniflora*, and other major habitat types include oyster reefs and sandy nonvegetated bottom. Seagrass in Christmas Bay often grows to the marsh edge (the interface of open water and the emergent salt marsh vegetation), and oyster reef and nonvegetated bottom are often interspersed within the seagrass meadows and along the marsh edge. Thus, all of the habitat types examined are adjacent or in close proximity to one another, and the fish can move among habitat types. The daily tide range in the bay system is 0.3 m (Galveston Pier 21, National Ocean Service, NOAA), and the highest-elevation habitat type we examined (vegetated intertidal marsh edge) remains flooded about 78% of the year, with higher flooding durations during the fall and spring (Minello & Webb 1997).

Otolith analysis. We used bag seines to collect red drum for otolith analysis from Christmas Bay during the peak recruitment period in November 1997. We seined over *Spartina alterniflora* marsh-edge areas without seagrass, nonvegetated bottom, oyster reef *Crassostrea virginica*, and seagrass *Halodule wrightii*.

Fish were immediately placed in 70% ethanol. We measured fish to the nearest 0.1 mm SL and did not adjust for shrinking during preservation (Fey 1999).

Using otolith microstructure, we examined differences in growth rates among fishes collected from different habitat types. Because no fish were collected on oyster reef, we only compared growth rates for marsh edge, nonvegetated bottom, and seagrass. David et al. (1994) determined that asterisci otoliths contain the most accurate increments for estimating age in young red drum. We dissected the right asteriscus for the first 48 red drum we collected from each habitat type following the procedures of Secor et al. (1991) and stored the otoliths in immersion oil for at least 1 wk. Daily increments were clearly visible from the core to the otolith margin, and otoliths did not require additional processing. Since daily increment deposition has been validated by Rooker & Holt (1997), we aged the fish by enumerating the daily growth rings using a digital image analysis system (Optimas 4.0). Each otolith was examined independently by 2 observers. If the 2 counts were not identical, the otolith was read a 3rd time. If the 3rd reading differed from both of the first two, the otolith was discarded from the analysis. While asterisci provide the best estimate of age for young red drum, they underestimate the true age, because they are not formed until 6 d post-hatch (David et al. 1994); therefore, 6 d were added to all increment counts. We compared the growth rates among the different habitat types integrated over the life of the fish using analysis of covariance (ANCOVA). First we used an interaction regression model to test for the assumption of no interaction between the treatment (Habitat) and the effect of the covariate (Age) on the dependent variable (Fish Length), by comparing slopes of the length-age regression. We also used ANCOVA to test for differences in y intercepts.

We further examined otolith microstructure to assess recent post-settlement growth (last 10 d before capture) among habitat types. Because there was a significant relationship between otolith diameter and fish length, we used otolith measurements as a proxy for size. A regression analysis of recent 10 d growth on age indicated that growth rates for our sample of red drum were not significantly related to age during this 10 d period ($R^2 = 0.001$, n = 144, p = 0.684). We then measured the distance from the margin of the otolith back to the 10th ring to examine fish growth during the previous 10 d. A 1-way analysis of variance (ANOVA) was used to test the hypothesis that growth did not vary among habitat types, using the mean increment distance of each fish as the observation.

Field enclosure experiment. We also used field enclosures to examine fish growth rates among different habitat types. Enclosures restricted fish to a habitat type but allowed access to the bottom substrate for foraging. We constructed 24 field enclosures from polypropylene barrels (0.283 m^2; 60 cm diameter × 1 m height) with the top and bottom removed. Six enclosures, approximately 1 m apart, were pressed 15 cm down into each substrate type (marsh edge [∼500 culms m^{-2}], nonvegetated bottom, oyster reef, and seagrass [∼10 000 shoots m^{-2}]) and anchored from the outside with metal stakes. We removed predators by sweeping the enclosures with dip nets and covered the tops of the enclosures with 1 mm mesh nylon netting. All habitat types were within an area of ∼250 m^2 (5 m × 50 m) and mean water depth was ∼30 cm.

The solid-walled enclosures held water at low tide by restricting water exchange, thereby allowing the experiments to be conducted in intertidal areas that may periodically be drained at low tide. Temperature was monitored hourly inside and just outside of 1 enclosure of each habitat type using temperature recorders (Environmental Sensors). Because we expected the largest potential enclosure effects would occur in the marsh, we measured dissolved oxygen and salinity levels hourly inside and just outside of a marsh edge enclosure using 2 DataSonde 3 multiparameter water quality dataloggers (Hydrolab).

We began the experiment on November 9, 1998, by stocking each enclosure with 3 young red drum (mean = 19 mm SL, SE = 0.6, n = 72) seined from adjacent seagrass meadows. To reduce handling stress, we used distinct pelvic fin clips to identify experimental fish, rather than invasive tags. Fish were measured to the nearest 1 mm and held for less than 3 h before being placed in enclosures. The fish remained in the enclosures for 7 d and were recovered by using dip nets or draining the enclosures with a pump. The fish were immediately preserved in 70% ethanol; lengths were measured within 24 h. We determined growth rates by identifying individual fish, measuring them to the nearest mm, and subtracting the original length measurements. We did not adjust measurements for possible shrinking during preservation. Data collected on *Sprattus sprattus* by Fey (1999) indicated larval fish may shrink during alcohol preservation, but in preliminary laboratory trials we found no significant shrinkage (paired $t = 0.168$, n = 16, p = 0.868) of red drum preserved in alcohol; the overall mean length of red drum was 18.7 mm SL (SE = 1.54) before and 18.3 mm SL (SE = 1.57) after a 2 wk period in alcohol.

We used a 1-way ANOVA to test the null hypothesis that red drum growth rates did not vary among habitat types, using the mean growth in each enclosure as the observation. Growth estimates were $\log(x + 1)$-transformed to reduce heteroscedasticity. Significant habitat effects (p < 0.05) were further examined with Fisher's protected least significant difference (PLSD) to
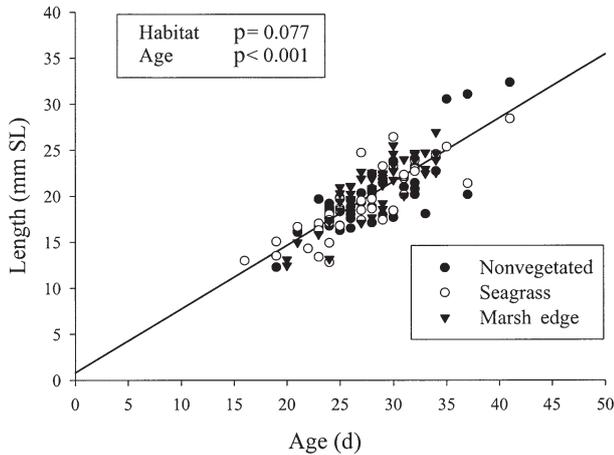
Fig. 1. *Sciaenops ocellatus.* Relationship between age (d) and SL of red drum from marsh edge interface, nonvegetated bottom, and seagrass habitat types in Christmas Bay, Texas. The box shows results of an ANCOVA comparing the slopes of the age-length regression lines (homogeneity of *y* intercepts model) showing no significant differences among age-length regressions on the habitat types (48 fish from each habitat type). The regression line is from pooled age-length relationship from all 3 habitats. SL = 0.815 + 0.692 (Age); R^2 = 0.69

Fig. 2. *Sciaenops ocellatus.* The relationship between fish SL (mm) and diameter (µm) of the asteriscus otolith in red drum collected from marsh edge interface, nonvegetated bottom, and seagrass habitat types in the Galveston Bay system, Texas. Regression model: diameter = 68.597 + 15.097(SL); n = 144, R^2 = 90.0, p < 0.001

test for differences among treatment means. A significance level of 0.01 was used in these PLSDs to buffer against problems caused by multiple testing and uncontrolled experimental error (Day & Quinn 1989).

RESULTS

Otolith analysis

We examined 144 red drum otoliths (48 each from marsh edge, nonvegetated, and seagrass habitat types). The overall mean age of red drum was 27.7 (SE = 0.36) d. The mean age in days was 28.2 (SE = 0.52) for marsh edge, 27.7 (SE = 0.66) for nonvegetated bottom, and 27.2 (SE = 0.70) for seagrass and did not differ significantly among habitats types (ANOVA *F* = 0.601, df = 2,141, p = 0.550). The overall mean length of red drum was 20.0 mm SL (SE = 0.30). The mean length was 20.9 mm (SE = 0.48) for marsh, 19.7 (SE = 0.54) for nonvegetated bottom, and 19.4 (SE = 0.54) for seagrass and did not differ significantly (ANOVA *F* = 2.27, df = 2,141, p = 0.11) among the 3 habitat types.

In our ANCOVA using fish SL as the dependent variable and age in days (otolith increments + 6) as the covariate, we found a significant overall age-length relationship (*F* = 312.11, df 1,140, p < 0.001). There was no significant interaction (ANCOVA interaction model, *F* = 0.722, df = 2,138, p = 0.487), indicating that the slopes of the regression lines (growth rates) were not different among the habitat types examined; and the

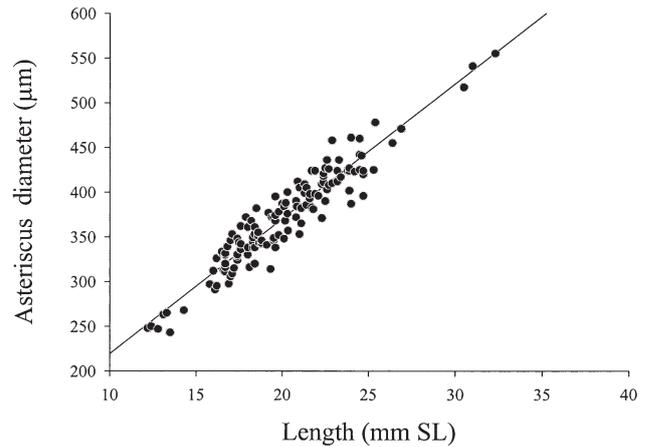main effect of Habitat was not significant (ANCOVA *F* = 2.62; df = 2,140; p = 0.077), indicating that size-at-age was not different among the habitat types (Fig. 1). Overall, this otolith analysis suggests that there was no difference in the growth history of red drum caught in the 3 habitat types. The equation best describing growth of fish for size at age is SL = 0.815 + 0.692 (Age), R^2 = 0.69, where SL equals standard length in mm, and the overall growth rate from hatching to collection was 0.69 mm d^{-1}.

We also examined differences among habitat types in recent (during last 10 d) post-settlement growth. The relationship between fish length and asteriscus diameter (Fig. 2) was highly significant (R^2 = 0.90,
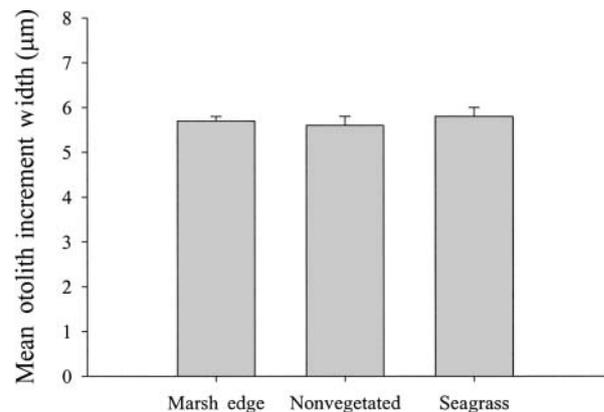

Fig. 3. *Sciaenops ocellatus.* Mean otolith increment widths (± SE) for the last 10 d of growth for newly settled red drum collected from marsh edge interface, nonvegetated bottom, and seagrass habitat types in the Galveston Bay system (48 fish from each habitat type). An ANOVA comparing mean increment width among the 3 habitat types had a p-value of 0.618
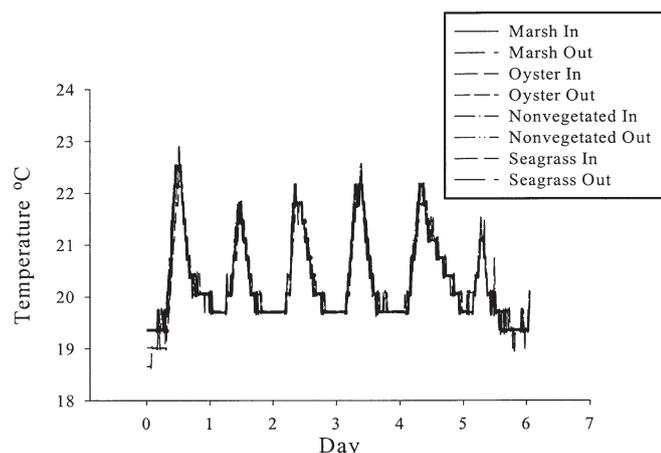
Fig. 4. Hourly temperature inside and outside of the field enclosures over the 7 d experiment in marsh, nonvegetated bottom, oyster reef, and seagrass habitat types

n = 144, p < 0.001); therefore, we used otolith measurements as a proxy for recent post-settlement somatic growth. Within this restricted age category, red drum growth rates were not related to age (R^2 = 0.001, n = 144, p = 0.684). Recent post-settlement growth rates were 0.449 mm d^{-1} (SE = 0.001) for marsh edge, 0.448 mm d^{-1} (SE = 0.002) for nonvegetated bottom, and 0.448 mm d^{-1} (SE = 0.002) for seagrass (Fig. 3). Analysis of variance on the mean increment width for the last 10 d indicated that recent post-settlement growth was not significantly different (F = 0.484, df = 2,141, p = 0.618) among habitat types.

Field enclosure experiment

Throughout the course of the experiment, the 4 habitat types we examined remained flooded, and water depth was generally between 15 and 53 cm. We observed lagged water level fluctuations within the enclosures, probably due to sediment pore water exchange (Harvey et al. 1987). Temperature over the 7 d period ranged from 19 to 23°C and did not appear to vary between inside and outside of the enclosures (Fig. 4). Salinities ranged from 19.8 to 31.1‰ over the 7 d experiment and varied little between inside and outside of the marsh enclosure (Fig. 5). Dissolved oxygen levels over the course of the experiment ranged from 0.83 to 7.69 mg l^{-1} outside and from 0.89 to 6.92 mg l^{-1} inside the marsh enclosure (Fig. 5). The dissolved oxygen inside the enclosure generally tracked the level outside the enclosure, but levels inside often did not reach as high or as low as levels outside.

Fish recovery rates were 100% for seagrass, 95% for both marsh edge and nonvegetated, and 40% for oyster reef. We recovered fish from all 6 replicate enclosures for nonvegetated bottom, marsh, and seagrass; and we recovered fish from 4 of 6 oyster reef enclosures. Mean growth rates for red drum from the enclosure experiment differed significantly (F = 8.355, df = 3,18, p = 0.001) among the habitat types (Fig. 6). Fisher's PLSD that indicated that growth rates were highest in the seagrass (0.42 mm d^{-1} [SE = 0.05]) and marsh edge (0.40 mm d^{-1} [SE = 0.10]) and lower in the nonvegetated (0.21 mm d^{-1} [SE = 0.03]) and oyster (0.12 mm d^{-1} [SE = 0.01]) habitat types.

DISCUSSION

Our objective in this study was to compare growth of recently settled juvenile red drum in different estuarine habitat types from Galveston Bay, Texas, including salt marsh, seagrass, oyster reef, and nonvegetated bottom. Red drum settle in estuarine habitats at
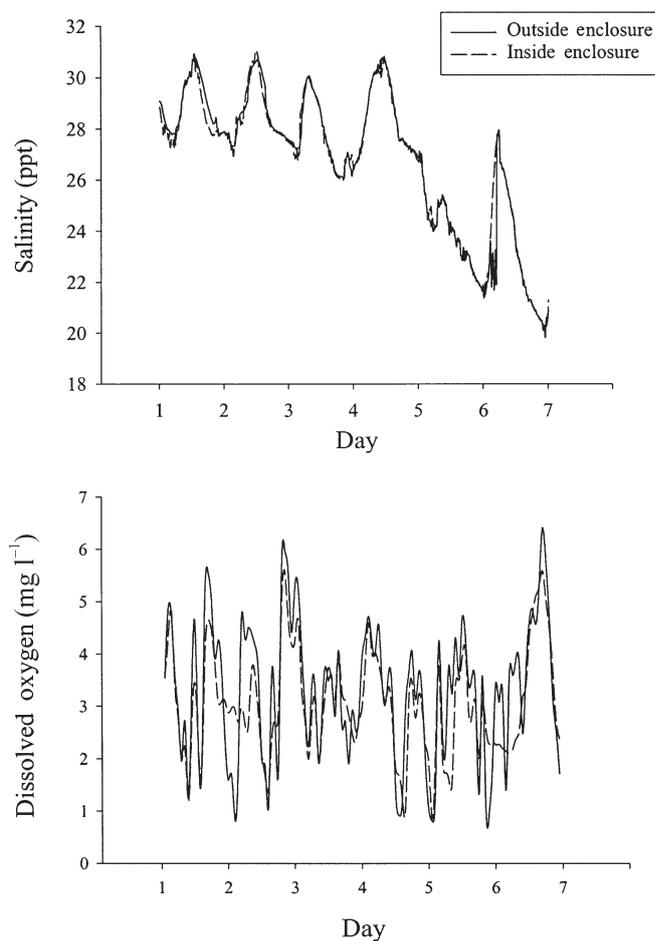

Fig. 5. Hourly salinity and dissolved oxygen levels inside and outside of 1 marsh enclosure over the 7 d field enclosure experiment
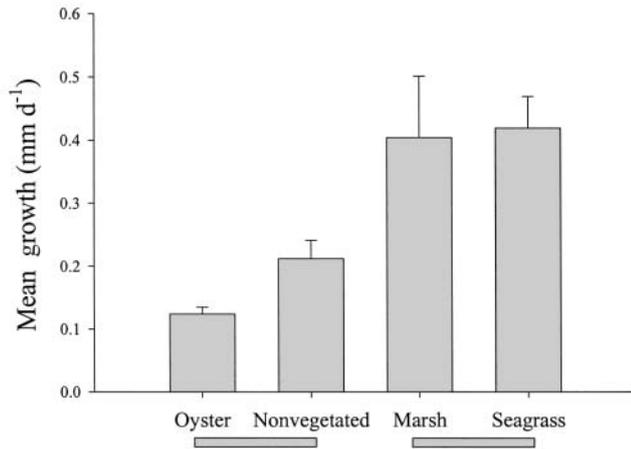
Fig. 6. *Sciaenops ocellatus*. Mean growth rates (mm d^{-1} ± SE) in field enclosures at various estuarine habitat types. There were 6 replicate enclosures for nonvegetated bottom, marsh, and seagrass, and 4 for oyster. An ANOVA comparing mean growth rate among all 4 habitats had a p-value of 0.001. Horizontal bars below the *x*-axis indicate results of Fisher's PLSD, and habitat types sharing the same bar are not significantly different (p > 0.01)

approximately 6 to 8 mm (SL) in size (Holt et al. 1983, Stunz et al. 2002). We estimated growth using otolith microstructure from free-ranging fish collected in different habitat types and also measured growth of red drum in experimental enclosures where fish movement was restricted.

Otolith microstructure has been used to measure daily growth in a wide variety of fish species (Campana & Neilson 1985). We collected red drum between 13 and 33 mm SL (16 to 41 d in age) from salt marsh, seagrass, and nonvegetated bottom (fish could not be collected on oyster reef). When we examined age-length relationships, we found no significant difference in the slopes of the regression lines for different habitat types, suggesting a similar growth history for all fish examined. Such analyses that compare growth rates integrated over the life of the fish, however, may not be particularly useful in measuring habitat-related growth following settlement, because pre-settlement events affecting growth as ichthyoplankton may mask differences in post-settlement growth rates (Gutierrez & Morales-Nin 1986, Secor & Dean 1989, Bradford & Geen 1992, Bestgen & Bundy 1998). Accordingly, we also estimated growth rates following settlement and just prior to capture; these measurements were justified because of a strong linear coupling of somatic and otolith growth (Neilson & Geen 1985, Secor & Dean 1989, Sogard & Able 1992, Francis et al. 1993, Bestgen & Bundy 1998, Szedlmayer 1998).

Associations between short-term otolith growth and habitat conditions can be misleading because there is

some potential for an uncoupling of otolith and somatic growth (Secor & Dean 1989, Bradford & Geen 1992, Sogard & Able 1992, Francis et al. 1993, Bestgen & Bundy 1998, Szedlmayer 1998), and differences among habitat types may be masked by a lagged response in this relationship (Neilson & Geen 1985, Gutierrez & Morales-Nin 1986, Molony & Choat 1990, Rooker & Holt 1997). We measured otolith growth over a 10 d period before capture and found no significant differences among habitat types. This period was selected to reflect growth after settlement into a habitat type while reducing potential problems of a lagged growth response. The overall post-settlement growth rate of 0.45 mm d^{-1} was similar to rates measured by Rooker & Holt (1997) in south Texas (0.45 mm d^{-1}) and Peters & McMichael (1987) in Florida (0.4 to 0.6 mm d^{-1}). While reducing potential problems of a lagged growth response, the use of a 10 d growth period may have increased the likelihood of fish movement among habitats, thus affecting our comparisons.

The degree of post-settlement site attachment for red drum is unknown, and the extent of interhabitat movement will affect the utility of otolith-derived growth rates for habitat comparisons. According to the settle-and-stay hypothesis (Bell & Westoby 1986, Bell et al. 1987), vulnerability to predation should reduce movement of fish once they have settled in a habitat type, especially when movements are across nonvegetated areas. Similarly, Rooker et al. (1998) suggested that newly settled red drum migrate between different seagrass meadows, but not when they are required to cross bare substrate. However, detrimental environmental conditions, such as hypoxia, may increase interhabitat movement. We recorded hypoxia in the salt marsh during early morning hours, but low oxygen levels also occurred in the other habitat types we examined (pers. obs.). Because all of the habitat types were adjacent to one another or in close proximity, we believe that red drum movement among them was likely.

Movement among habitat types is eliminated in caging and enclosure experiments, and this approach has been used to measure fish growth rates in a variety of habitats (de Lafontaine & Leggett 1987, Cowan & Houde 1990, Cowan et al. 1992, Sogard 1992, Reinert 1993, Duffy & Epifanio 1994, Phelan et al. 2000). Results from enclosure experiments address potential growth or comparative habitat value, but possible impacts of restricting fish movement must be considered. Growth rates measured in enclosures should reflect differences among habitat types if there is no effect of the enclosures on fish growth, or when any effect on growth is constant among habitat types (Peterson & Black 1994, Underwood 1997). Overall growth in our enclosures over the 7 d experiment was 0.27 mm d^{-1}, with the highest mean rates of 0.40 mm

d^{-1} and 0.42 mm d^{-1} in salt marsh and seagrass enclosures. These rates in vegetated areas were similar to our otolith estimates of 0.45 mm d^{-1} for a 10 d period before capture and suggest that growth in some of our enclosures approximated natural fish growth.

The use of solid-walled enclosures to measure growth in shallow water and intertidal habitats has both advantages and potential disadvantages. The enclosures can hold water in the intertidal zone at low tide preventing stranding of experimental animals and allowing continuous access to areas periodically unavailable to nekton under natural conditions. The enclosures also can be drained to improve recovery of experimental animals. The marsh surface was constantly flooded during our experiment, but reduced water exchange was evident because low-tide water levels inside marsh enclosures remained higher than levels outside. By reducing water exchange, the solid walls may alter physicochemical conditions inside the enclosures that might affect growth (Neill et al. 1994, Miller et al. 2000). Measurements inside and just outside of the enclosures, however, indicated that the enclosure walls did not substantially alter temperature, salinity, or dissolved oxygen. In contrast to mesh walls that allow water and prey organisms to move in and out of the cages (and also may attract small prey), solid walls prevent re-nourishment of prey within the enclosed area from outside of the enclosure. The effect of this restricted prey movement on predator growth depends upon the density of enclosed predators and prey and the duration of the experiment. Young red drum in the size classes used in our study primarily feed on mysid shrimp, copepods, amphipods, tanaids, decapod crustaceans, and small fishes (Bass & Avault 1975, Minello et al. 1989, Baltz et al 1998, Soto et al. 1998). We did not measure available food in the enclosures but attempted to match the enclosure size and estimated prey densities to the potential food requirements of the experimental red drum based on natural growth rates. The increased growth observed in seagrass and salt marsh enclosures compared with nonvegetated bottom coincides with elevated abundances of infauna and other prey often reported in these habitat types (Kneib 1984, Sogard 1989, Whaley 1997, Rozas & Minello 1998, Zimmerman et al. 2000, Sheridan et al. in press).

Handling of experimental fish also can cause problems in any growth experiment, and reduced foraging and growth during initial stages of an experiment may be related to handling stress (Minello et al. 1989, Nadeau 1991, Reinert 1993). We attempted to minimize handling stress by holding the fish for less than 3 h after collection and before placement in experimental enclosures. Mean growth rates of 0.42 mm d^{-1} in seagrass enclosures were near natural rates of 0.45 mm d^{-1} and suggest that stress-induced growth reduction was not a serious problem in these experiments.

Our enclosure results suggest that growth potential for red drum is greatest in vegetated habitats such as seagrass and salt marsh. Care should be taken in reaching such general conclusions regarding habitat value, because results of cage growth experiments can vary among estuaries and years (Sogard & Able 1992, Phelan et al. 2000). However, our results are also supported by habitat differences in food availability. Increased food resources appear to be associated with high growth rates in vegetated habitats (Summerson & Peterson 1984, Sogard 1992, Levin et al. 1997), although the generality of this conclusion for seagrass has been questioned (Heck et al. 1997). Levin et al. (1997) demonstrated that food supply could limit pinfish growth in estuaries, and that food resources were more efficiently utilized in vegetated habitats. In tidal freshwater marsh creeks, Rozas & Odum (1988) found that foraging profitability was greater in submerged aquatic vegetation than in nonvegetated areas. Foraging on the vegetated marsh surface also appears productive for some estuarine nekton (Rozas & LaSalle 1990, McTigue & Zimmerman 1998), and marsh exploitation appears to increase growth rates in red drum (Baltz et al. 1998) and decapod crustaceans (Zimmerman et al. 2000).

The nursery value of estuarine habitats for nekton is related to the contribution of a habitat type to adult production (Beck et al. 2001) and can be reflected by higher densities, increased survival, or increased growth of young in a habitat type. Seagrass meadows appear to be a primary nursery habitat for young red drum as evidenced by high densities (Holt et al. 1983, Rooker & Holt 1997, Minello 1999, Stunz et al. 2002) and potentially increased survival of juveniles (Stunz & Minello 2001); fish growth results in our enclosures support this conclusion. In Galveston Bay, however, seagrass cover is minimal, and the presence and use of alternate habitat types may be important. Oyster reefs are extensive in the bay system (10 800 ha, covering 10.4% of the bay bottom; Powell 1993), but Stunz et al. (2002) found no red drum on oyster reef and oyster rubble shorelines. Only a few other studies have assessed the value of oyster reefs for juvenile fish species, but none have reported high densities of red drum in oyster reef habitat (Zimmerman et al. 1989, Coen et al. 1999, Minello 1999). These distribution data, along with the results from our field enclosure growth experiment, suggest that oyster reefs may not be an important habitat type for young red drum. In areas of Galveston Bay where seagrass was absent, Stunz et al. (2002) found the highest densities of young red drum along the marsh edge. In Louisiana, Baltz et

al. (1993) also found relatively high concentrations of red drum on the marsh edge ecotone, and suggested that marsh edge functions as a nursery for this species. Selection for marsh vegetation has been observed in laboratory experiments (Stunz et al. 2001), and predation risk in salt marsh vegetation is lower than on nonvegetated bottom (Stunz & Minello 2001). Salt marshes are abundant in the Galveston Bay system, and these marshes are highly reticulated with a large amount of edge (Minello & Rozas 2002). Considering the comparable red drum growth rates we observed in seagrass and salt marsh enclosures, salt marshes likely function as an important nursery habitat for young red drum in this estuarine system.

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