

INFERRED GROWTH OF JUVENILE FRENCH GRUNTS, *HAEMULON FLAVOLINEATUM*, AND SCHOOLMASTER, *LUTJANUS APODUS*, IN MANGROVE AND SEAGRASS HABITATS

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ABSTRACT

Growth, survival, and abundance of young, and their connectivity to adult populations are four primary factors used to define nursery habitats. In the present study, we examined the relative quality of mangrove and seagrass habitats for juvenile French grunt, *Haemulon flavolineatum* (Desmarest, 1823), and schoolmaster, *Lutjanus apodus* (Walbaum, 1792), reef fish populations in St. Croix and Puerto Rico by using otolith microstructure to compare growth in these habitats. Mean daily otolith increment widths during the post-settlement period (30–60 d) of surviving late juvenile French grunts and schoolmaster collected in 2007 were compared between mangrove and seagrass habitats within each island. Increments widths were significantly wider during the post-settlement period in mangrove habitats at both study locations for both species. Our inferred growth interpretations indicate that mangroves may support faster growing fishes than seagrass habitats. However, due to the fact that the observed growth rates reflect the traits of the surviving cohorts among habitats, other factors, such as size-selective mortality/emigration and previous larval growth history, should also be considered in the interpretation of the observed growth patterns.

Many marine fishes have complex life histories in which juveniles and adults occur in spatially distinct habitats (Gillanders et al. 2003). For many species, juveniles may simultaneously occupy more than one habitat type (e.g., mangrove, seagrass, patch reef, coral rubble). When this occurs, it is likely that habitats will vary in their relative quality. Relative quality is frequently assessed by comparing abundance, growth, and survivorship of juveniles in two or more habitat types (e.g., Wilson et al. 1990, Irlandi and Crawford 1997, Rozas and Minello 1997, Meng et al. 2000).

Habitats that promote rapid growth are generally assumed to be high-quality areas for juvenile fishes, because rapid growth implies that sufficient food is available and that juveniles will be less vulnerable to size-selective mortality due to predation and environmental stress (Sogard 1997). Individuals attaining a larger size at the end of the juvenile period may be more successful in completing the process of migration to the adult habitat. Therefore, a habitat that promotes higher growth rates may contribute more and larger juveniles to the adult population (Beck et al. 2001, Bergenius et al. 2002, but see Gagliano et al. 2007).

Variation in growth among juvenile habitat types and locations, especially in shallow water estuarine environments, has been well documented (Beck et al. 2001). However, the majority of these studies have been conducted in geographic regions where estuaries are large and numerous, and contain many estuarine dependent species (e.g., northern Gulf of Mexico and the US Atlantic Coast; Houde and Rutherford

1993, Hales and Able 2001, Heck et al. 2003, Minello et al. 2003). In contrast, there are few studies comparing relative growth of fishes that settle to mangroves, seagrasses, and coral reef habitats in tropical latitudes.

The French grunt, *Haemulon flavolineatum* (Desmarest, 1823), and the schoolmaster, *Lutjanus apodus* (Walbaum, 1792), are economically and ecologically important fish species in the Caribbean. Juveniles of these two species are dependent upon mangrove and seagrass nearshore habitats as nursery areas (Rooker and Dennis 1991, Sedberry and Carter 1993, Rooker 1995, Nagelkerken et al. 2000a,b,c, Adams and Ebersole 2002). Since nearshore habitats throughout the Caribbean are under threat from anthropogenic stressors, data are needed to quantify the importance of specific nearshore habitat types in sustaining fish populations.

The purpose of our study was to evaluate the relative quality of mangrove and seagrass habitats for juveniles of two reef fish species in the US Caribbean by comparing growth rates in each habitat type. Using otolith increment widths as a proxy for growth, we examined whether there are habitat-specific differences in juvenile growth within each species.

MATERIALS AND METHODS

SITE DESCRIPTION

Our initial design consisted of two mangrove and two seagrass stations in each island (see below) to compare habitat specific growth. However, both fishes were not found at some stations, thus additional areas were added within each island to maintain adequate sample sizes.

St. Croix Stations.—Five stations were sampled on St. Croix, US Virgin Islands. The seagrass stations were Teague Bay, Turner Hole, and Great Pond, while the mangrove stations were Salt River and Altona Lagoon. Teague Bay, Turner Hole, and Great Pond are part of a bank-barrier reef system that surrounds the northeast and southeast coasts of St. Croix. For details on the station locations, see Mateo et al. (2010). In all of these shallow (1–5 m) embayments, there is a large back-reef lagoon with the distance from the shore to the reef varying from 500 to 700 m (Mateo and Tobias 2001). Most of the bottom is covered by seagrass [e.g., *Thalassia testudinum* Banks & Soland ex. Koenig and *Syringodium Filiforme* (Kütz)] in beds of varying density, with small, scattered patch reefs. The Salt River estuary is a shallow (1–4 m) red mangrove, *Rhizophora mangle* Linnaeus, fringed lagoon on the north shore of St. Croix separated from the open ocean by a fringing reef (Adams and Tobias 1999). Altona Lagoon is an enclosed, red mangrove-fringed lagoon, connected to a large back-reef lagoon by a single narrow channel < 10 m wide, with a maximum depth of 3.5 m. Altona Lagoon is located on the north coast of St. Croix.

Puerto Rico Stations.—In Puerto Rico, samples were collected from two general areas: La Parguera (Montalva Bay, Corral, El Palo Keys) and Guayanilla Bay (Punta Guayanilla, Maria Langa). There were two seagrass stations (Corral, El Palo Keys) and three mangrove stations (Montalva Bay, Punta Guayanilla, and Maria Langa). Montalva Bay is a non-estuarine, coastal system fringed by red mangroves, with shallow (1–2 m) water areas (i.e., sand, mud) covered with seagrass beds (Aguilar-Perera and Appeldoorn 2007). Corral and El Palo Keys are emergent reefs with shallow coral reefs and seagrass beds. The lagoons in all of these sites are < 3 m deep and have no mangroves. In Guayanilla Bay, Punta Guayanilla has nearby shorelines dominated by red mangroves, while Maria Langa is a red mangrove-covered island ~2 km from the shoreline (Vicente and Associates 2003, Mateo et al. 2006). Depths range from 1 to 2 m at both study sites.

Table 1. Mean water temperature and salinity taken at site of capture in St. Croix and Puerto Rico. Station abbreviations for St. Croix: AL = Altona Lagoon, SR = Salt River, TB = Teague Bay, TH = Turner Hole, GP = Great Pond. Station abbreviations for Puerto Rico: CO = Corral, EL = El Palo, ML = Maria Langa, MO = Montalva, GU = Punta Guayanilla. Habitat abbreviations: MG = Mangrove, SG = Seagrass.

Date	Habitat	Station	Temp °C	Salinity
St. Croix				
5/5/2007	MG	SR	29.8	35.0
5/7/2007	MG	AL	28.4	36.0
5/11/2007	SG	TB	28.7	35.0
5/16/2007	SG	TH	28.6	37.0
5/25/2007	SG	GP	28.6	36.0
Puerto Rico				
6/13/2007	MG	MO	28.4	36.7
6/14/2007	SG	CO	29.5	35.5
6/18/2007	MG	GU	30.0	36.5
6/20/2007	MG	ML	29.7	36.7
6/22/2007	SG	EL	28.7	35.2

SAMPLING METHODS

Young-of-the-year (YOY, Age-0 to < 1 yr) fishes were collected in 2007 during May in St. Croix and June in Puerto Rico using fish traps and seine nets at each station (Table 1). Twenty to 25 French grunts and schoolmaster 3–12 cm fork length (FL) were caught at each station and kept frozen until processed for otolith removal. Mean water temperatures taken with a hand held YSI meter at the time of capture ranged from 28.4 to 29.8 °C in St. Croix and 28.4 to 30.0 °C in Puerto Rico. Mean salinity values ranged from 35.0 to 37.0 in St. Croix and 35.2 to 36.7 in Puerto Rico (Table 1).

PREPARATION AND ANALYSIS OF JUVENILE OTOLITHS

FL was measured for each fish prior to dissection and otolith removal. Both sagittal otoliths were removed, cleaned of endolymphatic tissue, rinsed three times with Milli-Q water, and allowed to dry in a Class 100 laminar-flow hood. Samples were placed in acid-washed 2.5-ml snap-cap containers. A total of 186 otoliths were prepared for growth studies (French grunt $n = 96$, schoolmaster $n = 90$).

Transverse thin sections of 400 μm of each otolith were made with a Buehler low-speed saw. Each section was mounted on a microscope petrographic slide with thermoplastic glue and ground to the core in the sagittal plane with lapping film (30, 15, 9, and 3 μm). Otoliths were examined under an Olympus MX-51 transmitted light microscope at 400 \times at the National Marine Fisheries Services laboratory in Narragansett, Rhode Island, USA. Using Image-Pro image analysis software 6.1 (Media Cybernetics 2006), increments were enumerated and increment widths measured along the anterior dorsal section of the otolith from the core to the outer edge. Based on preliminary analysis, a consistent reading axis was selected that was not the longest axis of the juvenile otolith growth area, but one along which increments were visible to the edge. Based on age validation studies by Hein (1999) and Lindeman (1997), each increment was assumed to reflect 1 d of growth. We followed a standard protocol for reading and interpreting the otoliths (Searcy and Sponaugle 2000).

A subset of individuals with FL of 5–9 cm (French grunts) and 5–10 cm (schoolmaster) was selected for analyzing differences in inferred growth among habitats within islands. This size range was used to avoid problems in growth interpretation due to differences in size at capture among stations. Differences in mean FL and age among habitats within islands were examined using one-way ANOVA. Natural log transformation of otolith increment width data was carried out to meet the assumptions of homogeneity of variances and normality

(Sokal and Rohlf 1981). The relationships between otolith growth and fish growth for French grunt and schoolmaster was confirmed by analyzing the relationships between the residuals from the regressions of otolith length on age and of fish size on age. Slopes of the relationships between otolith length and fish length among islands were tested using ANCOVA homogeneity of slopes tests. The reference point for the division between larval and juvenile-settlement increments was 30 d, based on previous studies for grunts and snappers as the upper limit of the larval to post-settlement transition (Brothers and McFarland 1981, Lindeman 1997, Shaw 1997). Given that daily growth data are auto-correlated because the same individuals are compared at different ages, and because otolith daily increment data taken on individual fish are longitudinal in nature (sequential measurements were made on each otolith examined), repeated-measures MANOVA was used to test for among-group differences in growth trajectories (Chambers and Miller 1995, Searcy et al. 2007). A repeated multivariate approach was preferred to a repeated univariate test because our data did not meet the assumptions of sphericity and compound symmetry. Pillai's Trace V was used as the test statistic since it is more robust than Wilk's Λ in the case of unequal sample sizes and for situations in which covariances are not homogeneous.

We used a repeated-measures MANOVA (SYSTAT v9.1) on natural log-transformed data for all comparisons of otolith increment widths among groups. We compared increment widths in the intervals from 30 to 60 d as dependent response variables (a total of 30 dependent response variables). We report the summary of the multivariate analysis on the overall Pillai's Trace V test for differences between groups. The between groups factors were habitat (mangrove, seagrass) and island (St. Croix, Puerto Rico).

Potential problems may arise in interpreting growth in fishes with different individual ages because these individuals would have grown in different months of the year with different temperature regimes. We calculated the temperature for a particular month on which an individual would have grown during their day 30 to day 60 period based on examining hatching dates and temperature data from October 2006 through June 2007. The sea surface temperature data came from the National Oceanic and Atmospheric Administration's (NOAA) Integrated Coral Observing Network program. These stations are located in Salt River, St. Croix, and in La Parguera, Puerto Rico. Temperature, age, and FL were used as covariates in our MANOVA tests to account for potential factors that might affect interpretation of growth differences among habitats and islands.

RESULTS

SIZE DISTRIBUTION

There were no significant differences in mean FL and age of French grunts among habitats within islands [mean FL (STX: $F_{1,61} = 3.16$, ANOVA: $P < 0.081$; PR: $F_{1,66} = 1.106$, ANOVA: $P = 0.297$), mean age (STX: $F_{1,61} = 0.714$, ANOVA: $P < 0.401$; PR: $F_{1,66} = 2.218$, ANOVA: $P = 0.149$); Table 2]. For schoolmaster, mean FL and age of individuals captured was significantly larger in seagrass habitats only in Puerto Rico [mean FL (STX: $F_{1,56} = 0.739$, ANOVA: $P < 0.394$; PR: $F_{1,34} = 14.398$, ANOVA: $P = 0.001$), mean age (STX: $F_{1,56} = 0.714$, ANOVA: $P < 0.739$; PR: $F_{1,34} = 14.470$, ANOVA: $P = 0.001$); Table 3].

RELATIONSHIP BETWEEN FISH GROWTH AND OTOLITH GROWTH

The residuals of otolith size on age and fish size on age were significantly positively related, indicating that otolith increments are valid proxies of growth (French grunt STX: $r = 0.97$, $P < 0.001$; French grunt PR: $r = 0.98$, $P < 0.001$; Schoolmaster STX: $r = 0.87$, $P < 0.001$; Schoolmaster PR: $r = 0.84$, $P < 0.001$). For French grunt and schoolmaster, the slopes of the linear relationships between otolith length and FL did not differ significantly between islands (French grunt ANCOVA: $F_{1,128} = 0.841$, $P = 0.361$; Schoolmaster ANCOVA: $F_{1,91} = 0.564$, $P = 0.455$).

Table 2. Mean (\pm SE) fork lengths (FL, cm) of French grunts and schoolmaster by station, habitat, and year. See Table 1 for abbreviations.

Habitat	Station	n	FL
French grunt, St. Croix			
MG	AL	12	4.37 (0.15)
MG	SR	18	8.49 (0.15)
SG	TB	16	4.89 (0.18)
SG	TH	24	6.97 (0.18)
French grunt, Puerto Rico			
MG	MO	16	5.88 (0.31)
MG	ML	21	8.97 (0.18)
SG	CO	23	7.24 (0.21)
SG	EL	23	7.42 (0.21)
Schoolmaster, St. Croix			
MG	AL	21	5.50 (0.28)
MG	SR	19	7.04 (0.54)
SG	TB	8	7.74 (0.87)
SG	GP	21	5.73 (0.35)
Schoolmaster, Puerto Rico			
MG	MO	17	6.73 (0.49)
MG	GU	10	5.57 (0.63)
SG	CO	7	10.11 (0.57)
SG	EL	10	9.07 (0.33)

OTOLITH MICROSTRUCTURE

Mean increment widths over the period of day 30 to day 60 were significantly larger in mangroves compared with seagrass for both French grunt [Puerto Rico (7.68 ± 0.24 vs $6.33 \mu\text{m} \pm 0.15$), St. Croix (8.25 ± 0.21 vs $7.06 \mu\text{m} \pm 0.20$)], and schoolmaster [Puerto Rico (8.55 ± 0.31 vs $5.90 \mu\text{m} \pm 0.21$), St. Croix (8.27 ± 0.23 vs $6.28 \mu\text{m} \pm 0.24$); Fig. 1].

There were no significant differences in otolith increment widths between islands for either species (Table 4). For both species, increment widths between habitats (both islands combined) were significantly larger in mangrove than in seagrass habitats (Table 4). There was no significant interaction for increment width between islands and habitat among species, indicating that the habitat effect on growth rate

Table 3. Mean (standard error) number of otolith increments (= age in days) of French grunts and schoolmaster used to assess growth by habitat and year for St. Croix and Puerto Rico. n = Number of individuals, MG = Mangrove, SG = Seagrass.

Species	Island	Habitat	n	Number of increments
French grunt	St. Croix	MG	30	196.3 (15.7)
		SG	32	173.0 (13.5)
	Puerto Rico	MG	32	219.0 (11.1)
		SG	36	234.0 (5.1)
Schoolmaster	St. Croix	MG	30	91.8 (8.9)
		SG	27	141.7 (15.8)
	Puerto Rico	MG	15	152.2 (19.9)
		SG	19	229.0 (17.7)

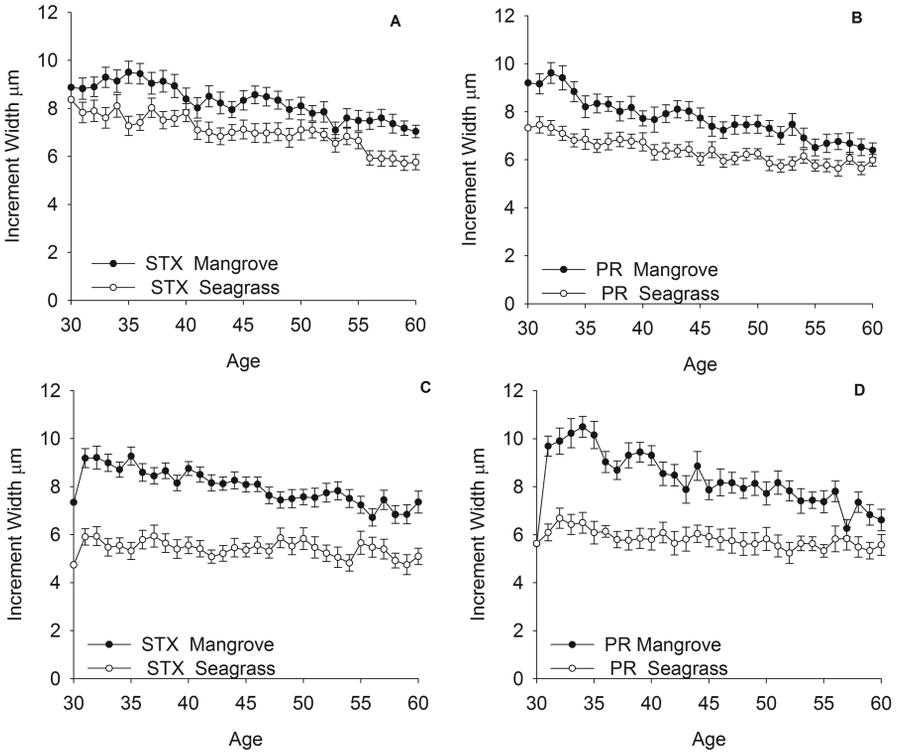


Figure 1. Mean otolith increment widths (μm) for each daily increment (age) from 30 to 60 d post-hatch for French grunts from (A) St. Croix and (B) Puerto Rico, and schoolmaster from (C) St. Croix and (D) Puerto Rico.

for both species was similar between islands. There was also no significant effect of temperature, age, or FL on increment widths in either species (Table 4).

DISCUSSION

In the present study, we used apparent inferred growth of early juveniles reflected by surviving later juveniles as a metric for evaluating the relative quality of different habitats as nurseries for juvenile fishes. We found that surviving late juvenile French grunt and schoolmaster from mangrove habitats had significantly wider otolith increments during their early juvenile period than individuals from seagrass habitats in both Puerto Rico and St. Croix. However, interpretation of this result is still not straightforward; there are many factors that can influence apparent growth differences and not all of these may be indicative of a selective advantage for fishes in mangrove habitats. The most important factors to consider are size selective mortality/emigration, larval history, temperature, and the role of shelter in reducing energy costs.

Previous growth history, as well as size-selective mortality, may influence interpretation of juvenile growth rates (Meekan and Fortier 1996, Searcy and Sponaugle 2001, Bergenius et al. 2002, Searcy et al. 2007). For example, traits that are beneficial

Table 4. Repeated measures multivariate analysis of variance (MANOVA) of the significance of island (St. Croix, Puerto Rico) and habitat (mangrove, seagrass) on increment widths over the period of 30–60 d for French grunt and Schoolmaster with temperature, fork length (FL), and age as covariate. Only summary results of the overall multivariate tests for between factor analyses are reported.

Source	Pillai Trace	df	F-ratio	P
French grunt				
Island	0.208	30	1.044	0.755
Habitat	0.360	30	1.956	0.017
Island × habitat	0.227	30	0.893	0.627
Temperature	0.198	30	0.749	0.813
FL	0.273	30	1.138	0.313
Age	0.235	30	0.931	0.575
Error		91		
Schoolmaster				
Island	0.447	30	0.890	0.624
Habitat	0.750	30	3.301	0.001
Island × habitat	0.600	30	1.649	0.081
Temperature	0.427	30	0.820	0.707
Age	0.519	30	1.187	0.314
FL	0.614	30	1.752	0.111
Error		34		

in the larval stage, such as fast growth, may become disadvantageous to juvenile survival (Gagliano et al. 2007) if the direction of differential size selective mortality reverses. Shelter from predation may interact with size-selective mortality to influence not only growth rates, but size-dependent survival (Meekan and Fortier 1996, Searcy and Sponaugle 2001, Bergenius et al. 2002, Searcy et al. 2007). For example, fast growing juvenile fishes may suffer greater predation than slower growers (Sogard 1997, Gagliano et al. 2007), especially if shelter provided by the habitat favors smaller fishes.

Searcy et al. (2007) recommended that prior to the use of growth as an index of habitat quality, it is important to recognize that growth rates may be affected by mechanisms other than habitat quality, such as selective mortality of slower (or faster) growing individuals, previous growth history, and negative density dependence (i.e., lower growth at higher conspecific densities). Incorporation of selective mortality into growth-based assessment of habitat quality is important because the removal of either slower or faster growing individuals from the population will bias interpretation of overall cohort growth. In our study, it is possible to hypothesize potential scenarios for size selective mortality, but the key is to identify processes that would act differentially among habitats. For example, mangrove prop roots and their associated fouling community may not favor a particular fish size, whereas faster growing fishes in seagrass may have outgrown the shelter provided by seagrass and thus may have either emigrated or been preyed upon more readily, as predicted by Werner and Gilliam (1984; see Appeldoorn et al. 2009, Grol et al. 2011 for application to grunts). Therefore, since we cannot discount that the pattern of growth we observed might have been influenced by size-selective mortality, we can only conclude that the observed growth rates reflect the traits of the surviving cohorts.

Abiotic factors, such as temperature, could have influenced the observed growth. Reichert and van der Veer (1991) and Baltz et al. (1998), for example, found that warmer water temperatures were responsible for faster growth rates in a variety of juvenile fish species. In contrast, growth rates of juvenile flatfish were negatively affected by rising water temperature (Sogard 1992, Meng et al. 2000, Manderson et al. 2002). These contrasting results are likely because the growth-temperature relationship is parabolic; growth rates tend to increase with temperature to an optimum beyond which growth rates decline rapidly (Williams and Caldwell 1978, Reichert and van der Veer 1991). In our study, samples were obtained at the same time of year in an attempt to eliminate any potential effect of seasonal temperature variations. Yet, differences in the ages of fishes sampled indicate that the time of settlement, and hence season of growth studied, varied substantially, and testing the effect of temperature under this scenario would require year-round temperature records for each site. For this reason, we examined growth differences among habitats using monthly temperature from ICON/CREWS sea surface temperature records at the time of settlement, as well as age and FL, as covariates in our MANOVA analyses; the analysis showed no evidence that temperature, age, and FL were factors in our growth interpretations.

Finally, the structure of mangrove habitats likely provided sufficiently better protection from predation to explain much of the differences in growth. Predation has often been considered the largest source of mortality for juvenile fishes and the risk of predation can influence growth rates by either forcing young fishes into suboptimal foraging habitats or reducing the amount of time spent foraging (Gilliam and Frazer 1987, Sogard 1992, Walters and Juanes 1993). Comparisons of predation risk among mangrove, seagrass, and reef habitats in the Caribbean are few. Using tethering experiments in Belize, Chittaro et al. (2005) found lower predation risks for *Haemulon chrysargireum* Günther, 1859, a related grunt species, in mangrove/seagrass habitats compared to coral reefs. In Curaçao, overall comparisons of cumulative survival of tethered *H. flavolineatum* among habitats (seagrass, mangrove, reefs) showed that survival was significantly highest in the mangroves compared to other habitats (Dorenbosch et al. 2009, Grol et al. 2011). This is not surprising because mangrove ecosystems are the most structurally complex of the shallow water coastal habitats (Nagelkerken et al. 2000a,b,c, Cocheret et al. 2002, Mumby et al. 2004). They provide protection for small fishes in several ways: prey visibility is reduced, predator and prey encounter rates are low, and the ability of predators to search for and capture prey is greatly reduced (Chittaro et al. 2005, Dorenbosch et al. 2009). Growth will potentially be increased because less time is spent sheltering from predators and more time can be spent foraging and feeding (Beck et al. 2001). The differences in inferred growth we observed between mangrove and seagrass habitats are consistent with this concept.

In summary, our study showed that post-settlement otolith increment widths from late surviving juvenile fishes were significantly wider in mangrove habitats than in seagrass habitats. These observations may indicate that mangroves support faster growing fishes than seagrass habitats. However, due to the fact that the observed growth rates reflect the traits of the surviving cohorts among habitats, other factors such as size-selective mortality/emigration must also be considered when interpreting the observed growth patterns. A better understanding of the conditions affecting growth, as well as assessment of multiple indices of relative habitat quality

over several years, may enable researchers to successfully characterize essential fish habitat and evaluate the importance of shallow water fish nursery areas to adult fish populations.

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