Is growth a reliable indicator of habitat quality and essential fish habitat for a juvenile estuarine fish?

Steven P. Searcy, David B. Eggleston, and Jonathan A. Hare

Abstract: A common assumption throughout the marine ecological and fisheries literature is that growth is a valid indicator of habitat quality and can be used as a criterion for designation of essential fish habitat (EFH). In this study, the validity of growth as an index of habitat quality was tested by examining how variability in otolith growth was related to abiotic and biotic environmental conditions and could be biased by previous growth history, density dependence, and selective mortality. The study was conducted with juvenile Atlantic croaker (*Micropogonias undulatus*) collected in two North Carolina, USA, estuaries during two seasons of two recruitment years. Water temperature, a component of habitat quality, explained nearly 40% of the variability in juvenile otolith growth. There was also evidence that estimates of growth could be biased by density dependence (slower growth at higher conspecific abundance) and by selective mortality (higher mortality of individuals with relatively slower larval and juvenile otolith growth). Studies using growth-based assessment of habitat quality that fail to identify factors underlying growth rate differences among habitats may reach incorrect decisions regarding quality of different habitats and assignment of EFH.

Résumé : On présume couramment dans l'ensemble de la littérature sur l'écologie marine et les pêches que la croissance est un indicateur valide de la qualité de l'habitat et qu'elle peut servir de critère pour la désignation des habitats essentiels des poissons (« EFH »). Dans notre étude, nous évaluons la validité d'utiliser la croissance comme indice de qualité de l'habitat en examinant comment la variabilité de la croissance des otolithes est reliée aux conditions abiotiques et biotiques du milieu et comment la croissance pourrait être faussée par l'histoire de la croissance antérieure, la densité-dépendance et la mortalité sélective. Nous avons fait notre travail sur de jeunes grondeurs de l'Atlantique (*Micropogonias undulatus*) récoltés dans des estuaires de Caroline du Nord au cours de deux saisons durant deux années de recrutement. La température de l'eau, une composante de la qualité de l'habitat, explique presque 40 % de la variabilité de la croissance des otolithes chez les jeunes. Il y a aussi des indications que les estimations de la croissance peuvent être faussées par la densité-dépendance (une croissance ralentie aux densités plus élevées de poissons de même espèce) et par la mortalité sélective (mortalité accrue des individus ayant des larves et des jeunes à croissance des otolithes plus lente). Les études qui utilisent une évaluation de la qualité des habitats basée sur la croissance et qui n'identifient pas les facteurs sous-jacents responsables des différences de taux de croissance entre les habitats peuvent arriver à des conclusions erronées concernant la qualité des différents habitats et la détermination des EFH.

[Traduit par la Rédaction]

Introduction

Worldwide, coastal development and degradation threaten nearshore and estuarine environments that are vital to the early growth and survival of many important fishery species (National Research Council (NRC) 1992; Hinrichsen 1998). In the United States, recognition of the importance of interactions between species and habitat variables has led to the legislative mandate to protect essential fish habitat (EFH), which is defined as waters and substrate necessary for spawning, breeding, feeding, or growth to maturity (Magnuson–Stevens Fishery Conservation and Management Act, amended 1996). To help refine this broad categorization, the National Marine Fisheries Service identified four criteria (presence–absence, density, growth, and production) that may be used as guidelines to assess EFH (reviewed in Able 1999). In particular, examination of individual fish growth rates is one method that has been used to compare habitat quality among different juvenile nursery areas (e.g., Sogard 1992; Meng et al. 2000; Necaise et al. 2005).

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S.P. Searcy[1,2] and D.B. Eggleston. Department of Marine, Earth, and Atmospheric Sciences, North Carolina State University, Raleigh, NC 27695-8208, USA.
J.A. Hare.[3] NOAA NOS NCCOS, Center for Coastal Fisheries and Habitat Research, 101 Pivers Island Road, Beaufort, NC 28516-9722, USA.

[1] Corresponding author (e-mail: ssearcy@umassd.edu).
[2] Present address: University of Massachusetts – Dartmouth, School for Marine Science & Technology, 838 South Rodney French Boulevard, New Bedford, MA 02744-1221, USA.
[3] Present address: NOAA NMFS NEFSC, Narragansett Laboratory, 28 Tarzwell Drive, Narragansett, RI 02882–1199, USA.

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The use of growth as an index of habitat quality is based on the assumption that larger, faster-growing fish are healthier and have experienced more favorable abiotic and biotic conditions than smaller, slower-growing fish (e.g., Able et al. 1999). Before using growth as an index of habitat quality and assignment of EFH, it is important to understand how growth rates change as a result of habitat-specific environmental conditions, as well as other factors including selective mortality of slower- (or faster-) growing individuals, previous growth history (positive or negative correlation between earlier and later growth), and negative density dependence (i.e., lower growth at higher conspecific densities). Unless the basis for spatial and temporal growth rate differences among habitats can be accounted for, certain habitats may be prioritized for conservation for the wrong reasons.

Perception of habitat quality based on back-calculated growth rates may change depending on timing of growth estimates. For example, examining growth rates after a period of selective mortality of relatively slower-growing fish (e.g., Searcy and Sponaugle 2001; Bergenius et al. 2002) may result in the perception of a higher quality habitat than what preselection growth rates would indicate. Alternatively, loss of faster-growing individuals (e.g., Litvak and Leggett 1992) will decrease perception of habitat quality. Growth rates may also reflect habitat quality of a previously occupied habitat if current growth is negatively (e.g., Sogard and Olla 2002) or positively (e.g., Tupper and Boutilier 1995) related to prior growth. Finally, negatively density-dependent growth, which describes lower growth at higher population densities, presents an apparent dichotomy to growth-based assessment of juvenile habitat quality. Although habitats that support higher abundances of juvenile fishes are considered to be important nurseries (e.g., Minello 1999), higher fish densities that lead to a reduction in growth rates will diminish the perception of habitat quality based on growth and may lead to misidentification of EFH based solely on growth rate data.

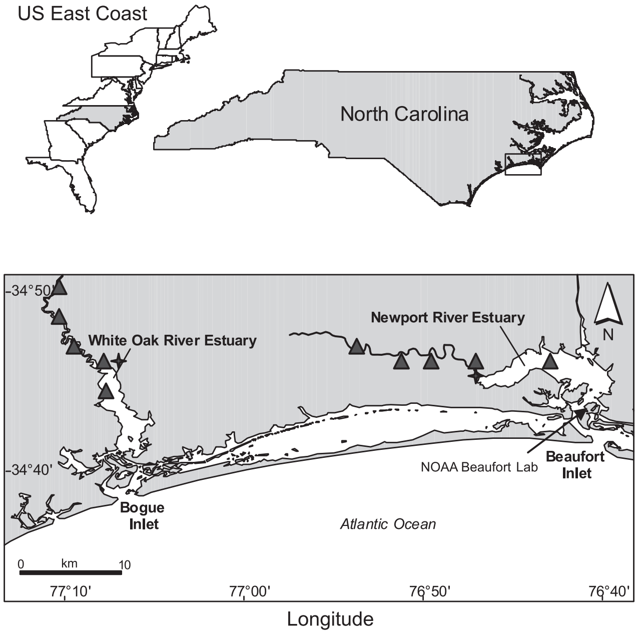
In this study, we (*i*) examined how juvenile otolith growth of Atlantic croaker, *Micropogonias undulatus*, was affected by abiotic and biotic factors typically associated with habitat quality (i.e., feeding success, predator abundance, competitor abundance, temperature, salinity) and, after accounting for these effects, (*ii*) determined whether growth-based measures of habitat quality could be biased by previous larval growth history, density dependence, and selective mortality. To the extent that these "biasing" factors affect growth rate, the use of growth as a measure of habitat is diminished. Thus, the results from this study test the assumption that high growth reflects "good" habitat for Atlantic croaker and allow us to refine the use of growth as a criterion for identifying habitat quality and EFH.

Materials and methods

Study species

Atlantic croaker is an economically and ecologically important fish in southeastern United States (US) and Gulf of Mexico estuaries. Along the east coast of the US, adults spawn on the continental shelf, and following offshore pelagic development, late-stage larvae ingress into estuaries and settle in low-salinity nursery areas (Weinstein 1979). We use ingress into estuaries to differentiate larval (marine) from juvenile (estuarine) periods. Atlantic croaker is an ideal study species to investigate processes that influence early juvenile growth because juveniles typically remain in nursery creeks for the first year of development (Miller and Able 2002). Additionally, in the southeastern US, adults have a protracted spawning season that extends from August to May (Hettler and Chester 1990), allowing for tracking of multiple cohorts over a range of different environmental conditions.

Fig. 1. Location of White Oak River and Newport River estuaries, North Carolina, USA. Inset shows location of beam-trawl stations (triangles).



Fish sampling and habitat characterization

Atlantic croaker growth was investigated in two similar estuaries in southeast North Carolina (US): Newport River and White Oak River (Fig. 1). These estuaries were selected because they contain oligohaline nurseries that are isolated from other low-salinity habitats, thereby minimizing the chance of postsettlement movement. In each estuary, Atlantic croaker were sampled weekly at one mid-estuary station that targeted croaker at the end of their larval phase following initial entry into the estuaries and at four river stations that collected juvenile croaker after settlement to nursery areas (Fig. 1). Fish were collected from a small boat (~6 m) using a 1 m beam trawl (1 mm mesh upper and side panels and a 3 mm mesh bottom panel). Beam trawl catch efficiency is known to vary according to species and size of the targeted animal (e.g., Kuipers et al. 1992); however, because of the narrow size range of Atlantic croaker targeted (10–15 mm), catch efficiency was not corrected for. Samples collected at the river stations were also used to identify potential competitors of juvenile Atlantic croaker, e.g., early juvenile flounder (*Paralichthys* sp. < 20 mm) and spot (*Leiostomus xanthurus* < 20 mm), and potential predators, e.g., flounder (*Paralichthys* sp. > 100 mm). Although our 1 m beam trawl collections likely underestimated total predator abundance, we assume that we were able to effectively estimate the abundance of small flounder, which are important predators of recently settled Atlantic croaker in the study system (Searcy 2005).

In the Newport River estuary, sampling was conducted for 7 weeks during each fall (November–December) and spring (February–April) of two recruitment seasons (2001–2002 and 2002–2003). In the White Oak River estuary, sampling was conducted for 7-week periods during the fall of 2002 and the spring of 2002 and 2003. Because of the shallow nature of both estuaries, beam trawl tows were restricted to the last 2 h of daytime floodtide, and three replicate tows were made at each station, typically for 1 min each, covering an area of ~60 m^2. Trawls were always pulled against prevailing currents and tow speed was standardized by gauging speed against emergent features in the water (i.e., crab pot buoys and stakes) or the shoreline. Trawl samples were sorted in the field, and all fishes were identified and preserved in 95% ethanol. Temperature and salinity were measured following sampling at each station using a handheld YSI-85 instrument (YSI, Yellow Springs, Ohio).

Fish and otolith processing

In the laboratory, fishes collected from each sampling location were identified and measured to the nearest 0.1 mm standard length. To estimate whether Atlantic croaker were feeding on each sampling date, 30 fish from the river sampling stations of each estuary were randomly chosen for stomach content analysis. Feeding ability for each estuary was recorded as the proportion of croaker that had empty stomachs.

Atlantic croaker have a continuous pattern of larval ingress into estuaries (Warlen and Burke 1990), therefore identification of cohorts within a recruitment season required otolith ageing of individual fish. For each sampling date, within each estuary, sagittal otoliths were dissected from 30 randomly selected croaker collected before settlement (mid-estuary stations; Fig. 1) and a minimum of 30 randomly selected croaker that had settled to the river nursery areas. The right sagitta was attached to a slide with mounting medium and archived. The left sagitta was mounted in epoxy, sectioned along both sides of the frontal plane using a dual-blade low-speed ISOMET saw, and polished to the core. The polished otolith section was then examined using a transmitted light microscope at 400×. Unclear otoliths and those with a nonlinear growth axis were discarded. The images of remaining otoliths were captured with a frame grabber, and increment count and widths (distance between two sequential increments) were measured using Image Pro Plus 4.5 image analysis software (Image Processing Solutions, North Reading, Massachusetts) and digitally enhanced to 800×. One person read all otoliths twice independently. If the two increment counts differed by two or fewer increments, then one reading was randomly chosen for further analysis. If the two increment counts differed by three or more increments, the otolith was read again. If the third increment count was two or fewer increments away from a previous reading, then one of these two similar counts was randomly chosen for analysis. If the third reading was three or more increments away from previous readings, the otolith was discarded from analysis. In total, 1396 of 1550 (89%) otolith counts were retained from the Newport River estuary, and 855 of 1000 (86%) otoliths counts were retained from the White Oak River estuary.

To estimate age of all croaker collected, separate age–length keys (3-day bins for age and 1 mm bins for length) were created for each weekly collection of Atlantic croaker from each estuary. The use of age–length keys allowed us to incorporate variability in size at age (Campana and Jones 1992) and assign croaker to individual cohorts that were hatched during the same 1-week period (weekly hatch-date cohorts). Relative abundance of each weekly hatch-date cohort was calculated as the total number of fish from that cohort collected during all three tows at the four river sampling stations and standardized to the typical total tow duration of 12 min (i.e., three 1-min tows at four stations). Peak cohort abundance refers to the largest relative abundance of a weekly hatch-date cohort. It was assumed that on the day of peak cohort abundance, a cohort had fully recruited to the estuary with no subsequent immigration or emigration.

Data analyses

Daily increment deposition and a positive relationship between otolith and somatic growth has been validated for juvenile Atlantic croaker (Searcy 2005). However, to avoid any error and assumptions of back-calculating somatic growth from otolith measurements, estimates of larval and juvenile growth were based solely on otolith growth measurements (i.e., Chambers and Miller 1995; Searcy and Sponaugle 2001). It is also important to note that this study utilizes length-based growth measures, which are a conservative measure of actual fish growth as actual fish growth includes changes in both length and weight (Wootton 1990).

Selective mortality

To determine whether relatively faster- or slower-growing Atlantic croaker from each weekly hatch-date cohort had higher mortality, back-calculated otolith growth over the same time period was compared between earlier (initial-group) and later (survivor-group) collections. Selection for larval otolith growth was examined from 11 to 30 days after hatching. The 11- to 30-day period of growth was chosen to represent larval growth that occurred in the marine environment as previous otolith analysis indicated that during the study periods examined, 30 days was the minimum age of croaker at estuarine ingress (Searcy 2005). For selective mortality analysis of larval growth, the initial group was comprised of individuals collected on the day of peak cohort abundance, and survivor-group growth was comprised of individuals collected 1 week later. To examine selection for juvenile growth, daily otolith growth was measured the week following peak cohort abundance within river nurseries and compared between an initial group collected 1 week after peak cohort abundance and a survivor group collected 2 weeks after peak cohort abundance. Finally, to examine whether selective mortality could bias between estuary comparisons of growth, contrasts were made between initial groups and between surviving groups of hatch-date cohorts collected from each estuary. The potential for selective mortality to bias between-estuary comparisons of habitat quality would be indicated if growth between estuaries varied following a period of mortality (survivor-group comparisons) but not prior to selection (initial-group comparisons).

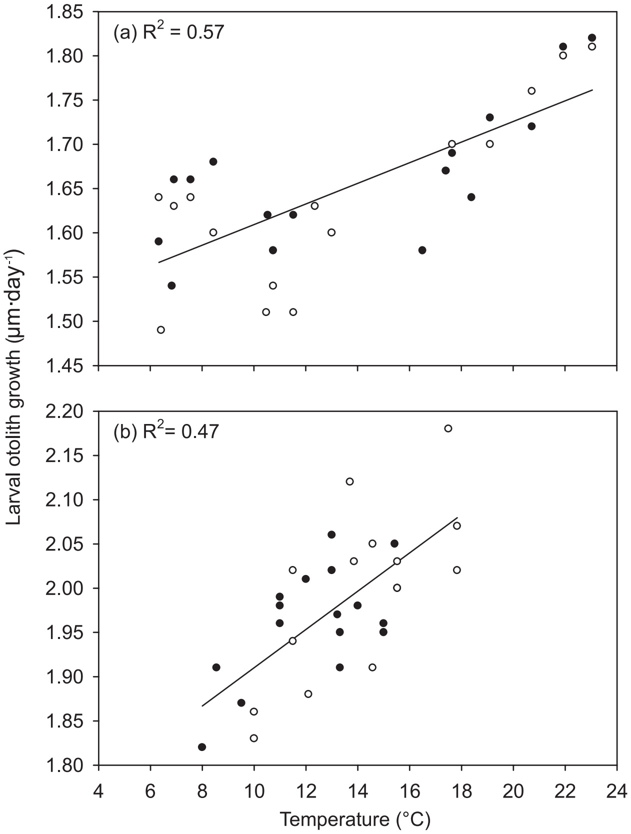
Otolith increment growth was natural log (ln) transformed as preliminary analysis indicated that variance in otolith increment width increased with age. Because otolith growth measurements taken on individual fish are longitudinal in nature (i.e., sequential measurements were made on each otolith examined), a repeated-measures multivariate analysis of variance (MANOVA; SAS 2002) was used to test the null hypothesis that there was no difference in growth between initial and survivor groups of croaker (Chambers and Miller 1995). The statistic used for determining whether growth varied between initial and survivor groups in the repeated-measures MANOVA analysis was the interaction term for Wilks' λ, which is based on the sample size, number of groups in the comparison, and number of growth intervals being analyzed (Chambers and Miller 1995).

Factors affecting juvenile growth

For each estuary, multiple regression models were used to determine the relative importance of biotic and abiotic factors that influence growth and how growth estimates may be biased by selective mortality, previous growth history, and density dependence. The initial multiple regression model included average juvenile otolith growth (ln-transformed) for the first week following peak cohort abundance of each weekly hatch-date cohort as the dependent variable and biotic explanatory variables of (*i*) feeding ability (the week of peak cohort abundance), (*ii*) average standard length at estuarine ingress (from mid-estuary stations the week before peak cohort abundance within river nurseries), (*iii*) total abundance of competitors (early juvenile flounder and spot < 20 mm), and (*iv*) total abundance of predators (flounder > 100 mm) collected in river sampling stations during the week of peak cohort abundance. Competitor and predator abundance estimates within river nursery areas were standardized to the typical total tow duration of 12 min (i.e., three 1-min tows at four stations). Abiotic explanatory variables included (*v*) average water temperature, (*vi*) average salinity, and (*vii*) maximum change in salinity between the week of and the week after peak cohort abundance.

Before regression analyses, normality was tested using the results of Proc Univariate (SAS 2002), residual plots were examined to determine if variances were heteroscedastic, observations that were outliers (Cook's $D < 4/n$, where n represents the number of observations) were eliminated from the analysis, and multicollinearity among independent variables was examined using variance inflation factors (Sokal and Rohlf 1995). To meet model assumptions, competitor and predator abundance were $\log(x + 1)$-transformed, salinity and temperature were log-transformed, and feeding success was arcsine-square-root transformed. A stepwise, backwards elimination procedure was then used in the multiple regression analysis to reduce the number of independent variables. Backwards elimination starts with all predictors in the model, removes the variable that is least significant (largest p value), and refits the model until all remaining variables are significant (in this study $p < 0.10$). The overall significance was tested with the adjusted R^2 value, and squared partial correlation coefficients were calculated to examine the proportion of variance explained uniquely by each independent variable.

Fig. 2. Relationship between (*a*) nearshore water temperature and average ln-transformed larval Atlantic croaker (*Micropogonias undulatus*) otolith growth (11–30 days after hatch) and (*b*) estuarine water temperature and average ln-transformed Atlantic croaker juvenile otolith growth (first week following peak croaker abundance) within the White Oak River (open circles) and Newport River (closed circles) estuaries, North Carolina, USA.



Growth as an index of habitat quality

Multiple regression models were run for each estuary to determine whether growth-based interpretation of juvenile croaker habitat quality could be biased by previous growth history (correlations between average larval growth from 11 to 30 days after hatching and average juvenile growth the week following peak cohort abundance), density-dependent growth (total abundance of conspecifics within river nursery areas), and selective mortality (see previous section). As water temperature was found to be a dominant factor influencing fish growth (see Results), before statistical analysis, both larval and juvenile otolith growth were standardized across cohorts by taking the residuals from the linear regression of growth on water temperature. Near-inlet water temperature recorded at the NOAA Beaufort Laboratory (Fig. 1) was used to correct for larval growth, and estuarine water temperature recorded at river stations was used to correct for juvenile growth (Fig. 2).

In the multiple regression analysis, the importance of previous growth history would be indicated by either a significant positive or negative relationship between residual juvenile growth and residual larval growth. Evidence for

Table 1. Tests for selective mortality of larval otolith growth (11–30 days after hatch) for Atlantic croaker (*Micropogonias undulatus*) cohorts within the White Oak River and Newport River estuaries, North Carolina, USA.

		White Oak River				Newport River			
Season	Hatch	λ	*F*	df	*p* (%)	λ	*F*	df	*p* (%)
Fall 2001	16 October	—	—	—	—	0.83	0.52	9,23	NS
	22 October	—	—	—	—	0.79	0.37	9,13	NS
Spring 2002	27 December	—	—	—	—	0.52	1.30	9,13	NS
	2 January	0.48	1.31	9,11	NS	—		—	—
	8 January	0.88	0.36	9,25	NS	0.70	1.14	9,24	NS
	14 January	0.85	0.29	9,15	NS	0.63	0.96	9,15	NS
	20 January	0.66	1.31	9,23	NS	—		—	—
	26 January	0.23	4.94	9,13	**(6%)	—		—	—
Fall 2002	5 October	0.64	1.35	9,22	NS	0.75	1.30	9,36	NS
	11 October	0.76	0.76	9,22	NS	0.77	1.59	9,47	NS
	17 October	0.74	1.20	9,31	NS	0.70	1.25	9,26	NS
	23 October	0.76	0.97	9,27	NS	0.74	1.29	9,34	NS
	29 October	0.49	1.14	9,10	NS	0.83	0.74	9,33	NS
Spring 2003	9 January	—	—		—	0.69	0.59	9,12	NS
	15 January	0.60	1.82	9,25	NS	—		—	—
	21 January	0.58	1.94	9,24	*(8%)	0.78	0.69	9,22	NS
	27 January	0.88	0.25	9,17	NS	0.53	1.61	9,17	NS
	2 February	0.79	0.54	9,18	NS	0.51	1.59	9,15	NS
	8 February	0.55	0.90	9,10	NS	0.71	1.07	9,24	NS

Note: Results are for repeated-measures multivariate analyses of variance (MANOVAs) between initial (back-calculated growth from day of peak abundance) and surviving groups of fish collected 1 week later. —, no comparison was possible; λ, Wilks' λ; **, $p < 0.01$; *, $p < 0.05$; NS, $p > 0.05$. Where significant, the number within the parentheses indicates the percent difference of average otolith growth between initial and surviving groups of croaker cohorts.

Table 2. Tests for selective mortality of juvenile otolith growth for Atlantic croaker (*Micropogonias undulatus*) cohorts within the White Oak River and Newport River estuaries, North Carolina, USA.

		White Oak River				Newport River			
Season	Hatch	λ	*F*	df	*p* (%)	λ	*F*	df	*p* (%)
Fall 2001	22 October	—	—	—	—	0.46	2.97	6,15	*(7%)
Spring 2002	27 December	—	—	—	—	0.91	0.18	6,11	NS
	8 January	—	—	—	—	0.64	0.85	6,9	NS
	14 January	—	—	—	—	0.62	1.85	6,18	NS
	20 January	0.17	5.58	6,7	*(15%)	—	—		—
	26 January	—	—		—	—	—		—
Fall 2002	5 October	0.61	1.28	6,12	NS	0.31	4.51	6,12	*(7%)
	11 October	0.82	1.14	6,32	NS	0.80	0.95	6,23	NS
	17 October	0.82	0.49	6,14	NS	0.88	1.7	6,74	NS
	23 October	0.93	0.39	6,30	NS	0.71	1.7	6,24	NS
	29 October	—	—		—	0.90	0.78	6,42	NS
Spring 2003	9 January	—	—		—	0.72	1.14	6,18	NS
	15 January	0.78	0.37	6,8	NS	—	—		—
	21 January	0.83	0.64	6,18	NS	0.83	0.92	6,26	NS
	27 January	0.57	3.59	6,29	**(10%)	0.94	0.34	6,34	NS
	2 February	0.71	0.87	6,13	NS	0.87	0.79	6,33	NS
	8 February	0.46	1.37	6,7	NS	0.46	2.97	6,15	*(10%)

Note: Results are for repeated-measures multivariate analyses of variance (MANOVAs) between initial (week following peak abundance) and surviving groups of fish collected 1 week later. —, no comparison was possible; λ, Wilks' λ; **, $p < 0.01$; *, $p < 0.05$; NS, $p > 0.05$. Where significant, the number within the parentheses indicates the percent difference of average otolith growth between initial and surviving groups of croaker cohorts.

density-dependent growth would be supported by a negative relationship between residual juvenile growth and total croaker abundance in riverine stations, and the importance of selective mortality would be supported by relatively faster residual juvenile growth occurring for cohorts that had experienced significant selective mortality. The overall significance of the multiple regressions were tested with the adjusted R^2 value, and squared partial correlation coefficients

Table 3. Somatic growth estimate for early juvenile Atlantic croaker (*Micropogonias undulatus*) collected in the White Oak River and Newport River estuaries, North Carolina, USA.

Season	Regression	r^2	n	SE	p	Specific growth (mm·day^{-1})
White Oak						
Spring 2002	$y = 0.215x + 2.353$	0.82	153	0.008	***	0.185
Fall 2002	$y = 0.229x + 2.837$	0.93	262	0.004	***	0.196
Spring 2003	$y = 0.173x + 3.868$	0.92	313	0.003	***	0.148
Newport						
Fall 2001	$y = 0.222x + 2.159$	0.72	93	0.015	***	0.190
Spring 2002	$y = 0.239x + 1.116$	0.74	119	0.013	***	0.205
Fall 2002	$y = 0.213x + 3.226$	0.79	408	0.005	***	0.183
Spring 2003	$y = 0.152x + 5.307$	0.90	320	0.003	***	0.130

Note: Regression equations listed for each seasonal collection are for the size-at-age relationship with the corresponding average specific growth. r^2, the regression coefficient; n, sample size; SE, standard error of the slope; p, probability; ***, $p < 0.0001$.

Table 4. Repeated-measures multivariate analysis of variance (MANOVA) results for between-estuary (White Oak River and Newport River estuaries, North Carolina, USA) comparisons of initial and survivor group larval Atlantic croaker (*Micropogonias undulatus*) otolith growth.

		Initial group				Survivor group			
Season	Hatch	λ	F	df	p	λ	F	df	p
Spring 2002	8 January	0.71	1.58	9,34	NS	0.80	0.41	9,15	NS
	14 January	0.90	0.24	9,19	NS	0.63	0.73	9,11	NS
Fall 2002	5 October	0.90	0.59	9,48	NS	0.39	1.73	9,10	NS
	11 October	0.71	1.14	9,25	NS	0.78	1.46	9,46	NS
	17 October	0.83	0.64	9,29	NS	0.76	1.01	9,29	NS
	23 October	0.85	0.49	9,26	NS	0.65	2.16	9,36	*(W > N)
	29 October	0.72	1.46	9,34	NS	0.69	1.40	9,28	NS
Spring 2003	21 January	0.67	1.16	9,21	NS	0.53	2.42	9,25	*(W > N)
	27 January	0.60	0.94	9,13	NS	0.60	1.55	9,21	NS
	2 February	0.66	1.14	9,20	NS	0.63	1.51	9,23	NS
	8 February	0.69	1.13	9,23	NS	0.42	1.38	9,9	NS

Note: λ, Wilks' λ; *, $p < 0.05$; NS, $p > 0.05$. Where significant, the text in parentheses indicates whether otolith growth was faster in the White Oak River estuary (W) or Newport River estuary (N).

were calculated to examine the proportion of variance explained uniquely by each independent variable.

Results

Selective mortality

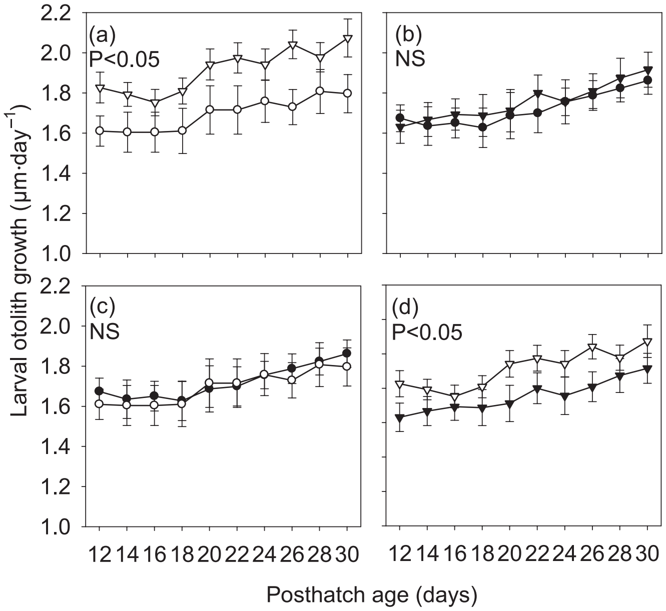
Surviving-group early-juvenile Atlantic croaker in the White Oak River estuary had relatively faster larval (2 of 15 cohorts; Table 1) and juvenile (2 of 10; Table 2) otolith growth than the initial group. In the Newport River estuary, there was no evidence for selection on larval otolith growth, but surviving groups had relatively faster juvenile otolith growth for 3 of 14 cohorts (Table 2). No correction was made for multiple comparisons. For cohorts that did have evidence for selective mortality, survivor groups had 6%–8% faster larval otolith growth (Table 1) and 7%–15% faster juvenile otolith growth (Table 2), which amounts to somatic growth differences of between 0.1 and 0.2 mm·week^{-1} based on estimates of instantaneous growth (Table 3).

Cohorts in which significant selective mortality was detected did not overlap temporally between estuaries (Tables 1, 2). Although larval otolith growth did not differ between initial groups collected in the White Oak River and Newport River estuaries, comparison of the same period of growth for the survivor groups collected within each estuary suggests that croaker in the White Oak River estuary grew significantly faster than croaker in the Newport River for two cohorts (23 October 2002 and 21 January 2003; Table 4; see also Fig. 3 for the 21 January 2003 cohort). Interestingly, for juvenile otolith growth comparisons, there were no between-estuary differences in survivor-group growth for any of the cohorts (Table 5), and the only initial-group growth difference between estuaries was for the 21 January 2003 cohort (Table 1).

Factors affecting juvenile growth

Juvenile otolith growth was significantly related to temperature and competitor abundance (Table 6). These two factors jointly explained 50% of the variability in juvenile otolith growth, with temperature independently explaining more variability in juvenile otolith growth than competitor abundance (squared partial correlation coefficients were

Fig. 3. Comparison of ln-transformed larval Atlantic croaker (*Micropogonias undulatus*) otolith growth (± standard error) for the 21 January 2003 cohort between initial groups (circles; collected at peak cohort abundance) and survivor groups (triangles; collected one week later) within the (*a*) White Oak River and (*b*) Newport river estuaries, North Carolina, USA, and between-estuary comparisons of (*c*) initial and (*d*) survivor groups (where open symbols denote the White Oak River estuary and solid symbols denote the Newport River estuary). For reference, significance of repeated-measures multivariate analysis of variance (MANOVA) for each comparison is noted within each figure panel.



39% and 10% for temperature and competitor abundance, respectively; Table 6).

Growth as an index of habitat quality

To determine whether estimates of juvenile growth were biased by larval growth history, density dependence, or selective mortality, separate multiple regression analyses were calculated for each estuary. In the White Oak River estuary, the three-factor multiple regression model was nonsignificant ($p = 0.52$; Table 7). In the Newport River estuary, the multiple regression model was significant and a total of 51% of the variability in residual juvenile growth was explained by a negative relationship with conspecific abundance (squared partial correlation coefficient of 0.37) and a positive relationship with the occurrence of significant selective mortality (squared partial correlation coefficient of 0.43; Table 7).

Discussion

The main objective of this study was to determine if growth could be used as a criterion to assess habitat quality and assign EFH using juvenile Atlantic croaker as a model study species. Individual juvenile fish growth estimates were obtained from analysis of 2251 otolith growth records collected during two fall and spring recruitment seasons in two North Carolina estuaries. After correcting for water temperature, variability in juvenile otolith growth rates was explained by both selective mortality and density dependence, suggesting that these factors may bias growth-based interpretation of habitat quality.

Selective mortality

Although evidence for selective mortality of larval and juvenile otolith growth was relatively rare, when significant, the survivor groups had relatively faster growth than the initial groups. The relationship between faster growth and higher survival is consistent with previous work examining selective mortality for larval and juvenile fishes (e.g., Searcy and Sponaugle 2001; Wilson and Meekan 2002; Hoey and McCormick 2004). In the current study, because selective mortality was examined between younger and older juvenile fish, selective mortality refers to the loss of juveniles related to previous larval or juvenile traits. For example, selection on growth rates likely reflects mortality of individuals with a characteristic associated with growth such as length or physiological condition. A variety of studies have shown that faster otolith growth and higher physiological condition are correlated (e.g., Suthers et al. 1992), and both body length (Schmitt and Holbrook 1999) and physiological condition (e.g., Booth and Hixon 1999; Hoey and McCormick 2004) can influence the probability of survival of recently settled fishes.

Loss of relatively slower-growing members of weekly hatch-date cohorts was not temporally consistent between the Newport River and White Oak River estuaries. Therefore, occurrence of selective mortality was likely a function of conditions that varied between estuaries, e.g., encounter with patchily distributed prey or predators, rather than characteristics specific to individual cohorts, e.g., range or variability in growth rates. For example, Atlantic croaker entering both estuaries had identical patterns of larval growth; however, there was only evidence of selective mortality of relatively slower-growing larvae in the White Oak River estuary. If slow-growing larvae had characteristics that predestined them to higher mortality, it should have been evident in both estuaries.

Temporal mismatch in selective mortality is important to recognize as selective loss in one estuary and not the other may bias between estuary comparisons of habitat quality. This is represented by the 21 January 2003 cohort, which had significant selective mortality favoring faster larval growth in the White Oak River estuary but not the Newport River estuary. For this cohort, initial-group growth did not vary between estuaries, which is consistent with larvae entering both estuaries being members of the same offshore “larval pool” that experienced similar abiotic and biotic environments. In contrast, survivor-group comparisons did vary between estuaries, which emphasizes that evaluation of habitat quality based on back-calculated otolith growth that was not taken immediately after the growth occurred (i.e., the initial group) would have incorrectly designated the White Oak River as a higher-quality habitat. The difference in otolith growth between the initial and survivor groups ranged between 6% and 15%, which is roughly equivalent to selective mortality results interpreted from previous studies (e.g., Meekan and Fortier 1996; Searcy and Sponaugle 2001;

Table 5. Repeated-measures multivariate analysis of variance (MANOVA) results for between-estuary (White Oak River and Newport River estuaries, North Carolina, USA) comparisons of initial and survivor group juvenile Atlantic croaker (*Micropogonias undulatus*) otolith growth.

		Initial group				Survivor group			
Season	Hatch	λ	*F*	df	*p*	λ	*F*	df	*p*
Fall 2002	5 October	0.80	0.52	6,13	NS	0.54	1.54	6,11	NS
	11 October	0.90	0.72	6,37	NS	0.87	0.44	6,18	NS
	17 October	0.93	0.68	6,57	NS	0.82	1.08	6,31	NS
	23 October	0.71	1.83	6,27	NS	0.95	0.24	6,27	NS
Spring 2003	21 January	0.68	2.15	6,28	*(W > N)	0.82	0.59	6,16	NS
	27 January	0.75	1.80	6,33	NS	0.87	0.72	6,30	NS
	2 February	0.76	1.95	6,37	NS	0.58	1.10	6,9	NS
	8 February	0.50	1.98	6,12	NS	0.62	1.01	6,10	NS

Note: λ, Wilks' λ; *, $p < 0.05$; NS, $p > 0.05$. Where significant, the text in parentheses indicates whether otolith growth was faster in the White Oak River estuary (W) or Newport River estuary (N).

Table 6. Factors selected as significant ($p < 0.10$) for multiple regression analysis of juvenile Atlantic croaker (*Micropogonias undulatus*) otolith growth with data from the White Oak River and Newport River estuaries pooled.

Model	Parameter	df	Par. estimate	SE	*t*	$p > \lvert t \rvert$	Partial corr^2
Adjusted $R^2 = 0.50$	Intercept	1	1.700	0.056	30.45	<0.0001	
$F_{[2,27]} = 15.78$	Temperature	1	0.019	0.005	4.18	<0.001	0.39
$p < 0.0001$	Competitor	1	0.019	0.011	1.75	= 0.09	0.10

Note: Listed are regression parameters (Par.) and squared partial correlation coefficients (Partial corr^2) for the independent variables of temperature and log(x + 1)-transformed competitor abundance. SE, standard error.

Table 7. Regression parameters and squared partial correlation coefficients for multiple regression analysis of residual juvenile Atlantic croaker (*Micropogonias undulatus*) otolith growth (corrected for water temperature) within the White Oak River and Newport River estuaries, North Carolina, USA.

Model	Parameter	df	Par. estimate	SE	*t*	$p > \lvert t \rvert$	Partial corr^2
White Oak							
Adjusted $R^2 = -0.05$	Intercept	1	–0.019	0.252	–0.08	= 0.94	
$F_{[3,9]} = 0.79$	Croaker	1	0.006	0.041	0.15	= 0.88	
$p = 0.52$	Larval growth	1	–0.714	0.467	–1.53	= 0.16	
	Selective mortality	1	–0.004	0.004	–0.86	= 0.41	
Newport							
Adjusted $R^2 = 0.51$	Intercept	1	0.099	0.051	1.94	= 0.08	
$F_{[3,10]} = 5.90$	Croaker	1	–0.022	0.009	–2.42	<0.05	0.37
$p < 0.05$	Larval growth	1	–0.35	0.219	–1.60	= 0.14	
	Selective mortality	1	0.045	0.017	2.74	<0.05	0.43

Note: Independent variables included the abundance of juvenile Atlantic croaker averaged between 1 and 2 weeks following peak cohort abundance (15-min catch per unit effort (CPUE) log-transformed), residual larval otolith growth (corrected for offshore water temperature), and the occurrence of significant selective mortality on juvenile growth evident the first week following peak abundance. Par., regression parameters; Partial corr^2, squared partial correlation coefficients; SE, standard error.

Shima and Findlay 2002). Assignment of EFH and habitat quality according to back-calculated growth rates that vary by ≤15% among habitats should be interpreted cautiously.

Factors affecting juvenile growth

Fish size at estuarine ingress and feeding ability did not have a significant impact on juvenile Atlantic croaker growth. Although fish size is known to be an important factor influencing growth rates (e.g., Baltz et al. 1998), the relatively narrow range in size at ingress (11–13 mm; Searcy 2005) for each weekly hatch-date cohort may be one reason why this factor was not a statistically significant determinant of growth in this study. The lack of a statistically significant relationship between juvenile growth and feeding ability may reflect a temporal mismatch between daily growth estimates obtained from otoliths and the once-weekly measures of stomach contents (which at best is an integral of feeding success over the previous day; Baltz et al. 1998). Future studies relating juvenile growth to feeding history will be better served by using a longer-termed index of previous feeding ability, such as total fish lipid content (e.g., Suthers et al. 1992).

Water temperature explained almost 40% of the variability in juvenile Atlantic croaker otolith growth, with a linear relationship between growth and water temperature found within each estuary. Because of the correlative nature of this field study, we cannot directly attribute variability in growth to water temperature; however, the importance of water temperature is consistent with a large body of work that has demonstrated that water temperature may result in both spatial and temporal variations in juvenile fish growth rates (e.g., Sogard 1992; Lankford and Targett 1994; Rooker and Holt 1997). That slight variations in water temperature may be related to differences in fish growth is particularly important to recognize when evaluating habitat quality among estuarine habitats. At small spatial scales, water temperature may vary among habitats as a function of differential heating and cooling (i.e., water depth, bottom type), as well as estuarine hydrodynamics (i.e., freshwater runoff, tidal- and wind-driven flow). Therefore, growth differences among habitats may simply reflect differences in water temperature rather than other environmental factors that are also associated with habitat quality such as food availability.

Growth as an index of habitat quality

After accounting for variation in water temperature, juvenile growth was significantly affected by selective mortality and conspecific density in the Newport River estuary but not in the White Oak River estuary. In the White Oak River estuary, the lack of a positive relationship between growth and selective mortality despite evidence for higher survival of relatively faster-growing individuals within this estuary (see Selective mortality section) highlights that selective mortality is just one of a suite of factors that can influence growth rates. Regardless, even if selective mortality is relatively rare, it may, on a cohort-by-cohort basis, still bias assessment of habitat quality.

Density-dependent growth also varied between estuaries, with lower growth found at higher croaker abundance in the Newport River estuary but not in the White Oak River estuary. Density-dependent growth is typically associated with resource limitation caused by reduced feeding success (Cowan et al. 2000). Food, however, is not typically considered to be limiting in estuaries (e.g., Miller et al. 1991; Kneib 1993). Indeed, previous field studies of juvenile estuarine fishes (including Atlantic croaker) have failed to find any relationship between fish growth and their density (Ross 1992; Baltz et al. 1998; Eby et al. 2005). These studies, however, were conducted on older juvenile fishes when densities may not have been high enough to elicit a growth response at low food levels. In the current study, densities of juvenile Atlantic croaker were roughly equivalent between the White Oak River and Newport River estuaries (Searcy 2005), which suggests that a factor other than density may have led to food limitation. One possibility is that Atlantic croaker nursery habitat within the Newport River estuary was restricted by the presence of a shallow sill at the base of the river nursery (Kirby-Smith and Costlow 1989). The sill establishes a firm lower boundary for Atlantic croaker nursery habitat that restricts movement into the upper estuary (Searcy 2005), which may lead to local depletion of food resources and reduced growth. Regardless of the mechanism underlying density-dependent growth, future studies that compare growth among habitats should consider the role of conspecific densities on observed growth rates.

Finally, although larval growth history was not considered to be an important factor influencing juvenile growth in the current study, its importance should not be discounted. Juvenile Atlantic croaker may have a positive correlation between larval and juvenile otolith growth during nonfeeding periods following hydrodynamic flushing from river nursery areas (S.P. Searcy, D.B. Eggleston, and J.A. Hare, unpublished data). Other studies have also found that episodic environmental events may influence subsequent growth rates. For example, compensatory growth is a relatively common phenomenon whereby fish respond to periods of reduced growth with subsequent accelerated growth (reviewed in Ali et al. 2003). In a recent laboratory study, juvenile halibut, *Hippoglossus stenolepis*, that were exposed to low temperatures were able to compensate for slow growth by having 20% faster growth than a control group (Hurst et al. 2005). Knowledge of the extent to which growth rates reflect proximate or previous environmental factors is critical before the application of growth-based assessment of habitat quality and EFH.

Accurate evaluation of habitat quality and EFH remains a central issue for both habitat and fishery managers (Mangel et al. 2006). To date, three of the four criteria (presence–absence, density, growth, and production) suggested by the National Marine Fisheries Service (NMFS) to identify EFH (Able 1999) have proven to be unreliable for juvenile fishes. Presence–absence information cannot be used to identify EFH because it forms no basis with which to prioritize habitats for protection (Able 1999). Density may be an inappropriate measure of EFH because habitats that support highest densities of fish may not be the same habitats that contribute most to adult populations (Gillanders and Kingsford 1996; Kraus and Secor 2005). The present study has shown that use of growth as an index of habitat quality may be biased by density dependence and selective mortality. The final NMFS criterion, production, may provide the most rigorous approach to investigating habitat quality and EFH. For example, including both growth and density measures within a habitat provides a measure of habitat quality that is more robust that either measure used independently. Likewise, use of the "nursery role hypothesis" to evaluate habitat quality for a particular species according to whether a habitat's "contribution per unit area to the production of individuals that recruit to adult populations is greater, on average, than production from other habitats in which juveniles occur" (Beck et al. 2001) provides a more rigorous approach to evaluating the importance of different nursery habitats. Although the nursery role of different habitats may be difficult to test empirically (reviewed in Gillanders et al. 2003), misidentification and failure to protect habitats that are most important may have a detrimental effect on adult populations.

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