



Nursery Habitat Quality Assessed by the Condition of Juvenile Fishes: Not All Estuarine Areas Are Equal

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Abstract

High-quality nursery habitats support greater numbers of juveniles that survive to adulthood, but characteristics underlying high-quality habitats remain elusive because their productivity varies spatially and temporally and may be species-specific. Fish condition is an energy-integrative measure of ecological interactions, stress, and activity within a habitat, such that juvenile fish condition is representative of the quality of nursery habitats. We apply spatially explicit models to examine patterns in nursery habitat quality of Virginia estuaries based on nutritional condition for Atlantic croaker *Micropogonias undulatus*, summer flounder *Paralichthys dentatus*, and striped bass *Morone saxatilis*. Environmental factors (water temperature, dissolved oxygen, salinity, and depth) positively influenced the condition of Atlantic croaker but had mixed effects on striped bass and summer flounder condition, despite co-location of these species. Over the observed range of environmental conditions, the potential impact of salinity was 1.7 to 6 times that of other environmental factors. The condition of Atlantic croaker was negatively influenced by conspecific density, indicating local abundance mediates habitat quality. Regional habitat effects on fish condition were apparent after adjusting for broad-scale environmental effects: on average, striped bass condition was 22% greater in habitats near tributary mouths, Atlantic croaker condition was 28% greater in upestruary habitats, and the adjusted mean condition of summer flounder associated with coastal lagoons and the eastern side of Chesapeake Bay was 100% greater than conspecifics from other regions. Not all habitats are equally suitable for juvenile stages of estuarine species, but locations that produce well-conditioned individuals reveal the environmental characteristics associated with high-quality nursery habitats that contribute to species-specific productivity.

Keywords Hepatosomatic index · Subdermal lipid · Fish fatmeter · Bioenergetics · Chesapeake Bay

Introduction

Ecosystem-based fisheries management requires consideration of relevant ecosystem characteristics that impact production and recovery of fish populations through effects on recruitment (Link 2002; Pikitch et al. 2004). In particular, the dynamics between essential habitats and productivity must be understood to implement comprehensive management strategies (Marshak and Brown 2017). Quality nursery habitats are

thought to contribute disproportionately to the adult population by supporting increased densities, better survival, faster growth, and successful movement of recruits to adult habitats (Beck et al. 2001). Yet, even though the contribution of individual habitats to the overall abundance of fish is one of the key criteria for defining essential fish habitat (Essential Fish Habitat Final Rule 2002), estimation of habitat-specific productivity for a given species has proved elusive (Beck et al. 2001). Habitat productivity is known to vary with anthropogenic impacts, hydrological conditions, intensity of predation, and prey availability, due to the influence of these factors on fish growth and survival (Mittelbach 1986; Gilliers et al. 2006; Searcy et al. 2007; Amara et al. 2007, 2009). Estuarine nursery areas in coastal Virginia encompass diverse habitat types and exhibit a wide range of environmental and physical characteristics that may influence habitat quality and productivity, including hydrodynamic conditions, depth, extent and type of vegetated habitat, and water quality (e.g., temperature and salinity). Variation in these physicochemical features among

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estuaries in coastal Virginia influences the value of nursery habitats for different species, and as a result, estuarine habitats in Virginia may not be equally suitable as nurseries for all fishes that use coastal waters during the juvenile stage.

Juvenile fish condition has been used as a measure of nursery habitat quality (Stevenson and Woods 2006; Fonseca et al. 2015) because fish condition is considered an integrative metric of environmental stress, ecological interactions (e.g., diet and predation), and fish activity. Habitats that support well-conditioned juveniles may disproportionately contribute to the adult stock because the condition of individual fish influences their survival (Wicker and Johnson 1987; Thompson et al. 1991; Brodersen et al. 2008; Evans et al. 2014). However, the biotic and abiotic drivers of spatial patterns in fish condition are not well understood. Here, we apply spatial models to infer habitat quality by examining geographic patterns in condition indices of juvenile fishes from nursery areas in Virginia estuaries, focusing on three species: Atlantic croaker *Micropogonias undulatus*, summer flounder *Paralichthys dentatus*, and striped bass *Morone saxatilis*. These species were selected because previous research indicated that condition indices reflect energy storage at key periods of their juvenile life stages: prior to migration and during winter (Schloesser and Fabrizio 2016). Specifically, subdermal lipids increase prior to emigration of young Atlantic croaker and summer flounder from the Chesapeake Bay in the fall, and liver lipid stores are elevated for juvenile striped bass (obligate estuarine residents) during winter (Schloesser and Fabrizio 2016). For the juvenile stage of these species, subdermal lipid content and the liver lipid stores also positively correlate with energy density in the whole fish (Schloesser and Fabrizio 2017).

The factors that shape the spatial distribution of these species within estuaries, such as water quality, abundance of food resources, and availability of refuges from physiological stressors and predation (Wiens 1976), are also likely to influence the condition of individuals occupying estuarine nursery habitats. Regarding water quality, juvenile Atlantic croaker occupy diverse estuarine habitats and tolerate a wide range of temperatures (0–36 °C); as they grow, they occupy areas with higher salinities (0–15 psu in spring and 6–26 psu in summer; Diaz and Onuf 1985). Temperature, dissolved oxygen, depth, and salinity influence the habitats occupied by juvenile summer flounder in temperate estuaries (Sackett et al. 2008), and temperature is thought to be one of the key environmental factors influencing habitat quality for juvenile flatfish (Gibson 1994). For juvenile striped bass, winter temperature, salinity, and conspecific density are known to influence the suitability of nursery habitats (Hurst and Conover 2002; Martino and Houde 2012). Variation in environmental preferences results in differential use of nursery habitats by juveniles, such that any given area may be used as a nursery habitat by one species, but not another. In occupied habitats, the abundance of food resources and availability of refuges

may be influenced by conspecific density, which would alter the value of nursery habitats through the effects of competition (e.g., Martino and Houde 2012). Therefore, local density may mediate habitat quality for juvenile fishes.

Individuals within a localized area have likely been exposed to similar environmental conditions and are likely to have been feeding on similar prey. Therefore, fish from a given sampling location (say, replicate tows from nearby sites) may yield multiple observations of individual condition, but these observations are not likely to be independent; instead, such observations are likely spatially autocorrelated. As a result, observations from a limited spatial area may bias estimates of condition of the population of juvenile fish and prejudice the factors influencing individual fish condition. Spatial autocorrelation must be addressed to appropriately assess environmental and biological effects of sampling location on mean fish condition. Simultaneous autoregressive (SAR) models address the effect of spatial autocorrelation by describing patterns in the measured response from nearby locations that share similar environmental properties. Models that account for spatial correlations have been used to describe species distribution and abundance (Fabrizio et al. 2000; Dormann et al. 2007; Kissling and Carl 2008; Elith and Leathwick 2009), but have not been widely used to describe geographic patterns in population traits, such as condition.

Here, we apply spatial models to examine geographic heterogeneity in fish condition and to infer variation in habitat quality among temperate estuaries in Virginia. Specifically, we use SAR models to assess the effect of environmental factors, conspecific density, and sampling region on mean condition of juvenile Atlantic croaker, summer flounder, and striped bass. Our objectives were to (1) describe geographic patterns in condition for these three species and to (2) associate the observed spatial variability in condition with environmental, regional, and density-dependent effects.

Methods

All fish capture, handling, and euthanasia procedures were approved by the College of William & Mary Institutional Animal Care and Use Committee (protocols 2008-05-19-5360-mcfabr, 2010-07-20-6788-mcfabr, and 2011-06-06-7347-tdtuck) and were consistent with all applicable state and federal guidelines.

Field Collections

Atlantic croaker, summer flounder, and striped bass were sampled monthly between November 2010 and June 2014 from Virginia's coastal waters; a portion of these juveniles was assessed for condition. Condition measures of Atlantic croaker and summer flounder focused on months when long-

distance movements of fish were expected to be minimal. Juvenile Atlantic croaker ($n = 2960$) were collected between June and September because Atlantic croaker emigrate from temperate estuaries in the fall (e.g., from September to October for Delaware Bay, Miller and Able 2002); for Chesapeake Bay, we considered October the month of peak migration for Atlantic croaker and, thus, collected our samples prior to October. Similarly, summer flounder ($n = 973$) were measured for condition between July and October because the peak of summer flounder emigration from Virginia estuaries occurs around November (Desfosse 1995; Henderson 2012; Capossela et al. 2013). Juvenile striped bass typically do not undertake coastal migrations but remain within their natal river system throughout the first year of life (Massmann and Pacheco 1961; Williams 2010); we assessed the condition of juvenile striped bass ($n = 714$) from November to March, representing the winter of their first-year residency in nursery areas.

We randomly sampled habitats throughout Virginia coastal waters that were occupied by juvenile Atlantic croaker, summer flounder, and striped bass to maximize the contrast in fish density and environmental factors among sampling sites and, thus, allow for detection of these effects. Most samples were collected using a 9.14-m otter trawl in the Chesapeake Bay and estuaries of the James, York, and Rappahannock Rivers (Fig. 1); collections followed random stratified sampling protocols described in Tuckey and Fabrizio (2013), and depth strata were used to delineate the regions we examined for differences in condition. Additionally, Atlantic croaker and summer flounder were collected in Mobjack Bay (random stratified sampling) and in a small coastal lagoon (simple random sampling) along the eastern shore of Virginia using a 4.88-m otter trawl because these habitats are used as nursery areas by these species (Fig. 1). All juvenile summer flounder and striped bass collected were immediately euthanized in an ice slurry and returned to the laboratory for condition measurements, but due to high abundances of juvenile Atlantic croaker, no more than 10 randomly selected individuals were typically euthanized per trawl tow. The total number of each species collected in each tow was recorded. Area swept was estimated using the mean net width and the mean distance traveled during a 5-min tow and was assumed to be constant for each gear. Catch numbers and area swept were used to estimate conspecific density at each sampling site (individuals per 100 m²). Temperature (°C), salinity (psu), and dissolved oxygen (mg/L) were measured near the bottom at each sampling site, and site depth was recorded in meters. Because of the relatively small area and high tidal flushing, most of the variability in temperature, salinity, and dissolved oxygen in the coastal lagoon was associated with tidal cycles (not spatial differences), and therefore, daily mean temperature, salinity, and dissolved oxygen in this region were used as factors to explain spatial variability in condition.

Condition Measurements

We assessed condition using relative estimates of subdermal lipid for Atlantic croaker and summer flounder and the hepatosomatic index (HSI) for striped bass; these metrics are positively correlated with energy content in juveniles of these species (Schloesser and Fabrizio 2017). In a previous study, we identified nonlethal estimates of subdermal lipid with the Distell fish fatmeter as a suitable technique to measure condition in juvenile fishes that store energy as subdermal lipids prior to migration and HSI as suitable for species storing energy during winter months (Schloesser and Fabrizio 2016).

Upon return to the laboratory, fish length was recorded to the nearest millimeter. We considered only those individuals that were large enough to effectively sample with the fatmeter (R. Schloesser, *personal observation*), but small enough to be considered juvenile fish based on monthly length thresholds described by Tuckey and Fabrizio (2016). Therefore, condition was assessed for juvenile Atlantic croaker between 117 and 214 mm total length (TL) and summer flounder between 156 and 289 mm TL. Striped bass between 117 and 200 mm fork length (FL) were examined for HSI.

Subdermal lipid content of individual Atlantic croaker and summer flounder was measured with the Distell fish fatmeter (model FFM-992). This instrument uses low-power microwaves to estimate subdermal lipid content based on the water content of tissues beneath the skin (Kent 1990), which is a measure of the energy stored in subdermal lipid reserves and associated muscle tissues. Measurements were taken along the midline of the body and behind the operculum. At this location, four measurements from the noneyed side of summer flounder and a mean of four readings from each side of Atlantic croaker (eight readings total) were used to estimate relative subdermal lipid content. These locations best represent energy and lipid content for these species (Schloesser and Fabrizio 2017) and result in low measurement error (mean coefficients of variation were 0.09 for Atlantic croaker and 0.18 for summer flounder). Here, reported fatmeter readings are interpreted relative to measures from other individuals, such that higher values indicate a higher degree of subdermal lipid storage. The consistency of measurements over time was checked relative to a standard. Accuracy of the fatmeter varies depending on the lipid content of the sample and is reported as $\pm 1.5\%$ for lipid content between 2 and 15% (Anonymous 2010). The relative subdermal lipid readings for Atlantic croaker correspond to a lipid content range of 0.63 to 8.23% wet weight, and the lipid content of summer flounder ranged from 0.72 to 2.24% wet weight (Schloesser and Fabrizio 2017).

The HSI measures lipid storage in the liver (Jensen 1979; Lambert and Dutil 1997). The hepatosomatic index was calculated from estimates of body and liver mass (wet weight) measured with a Mettler Toledo XA204 balance

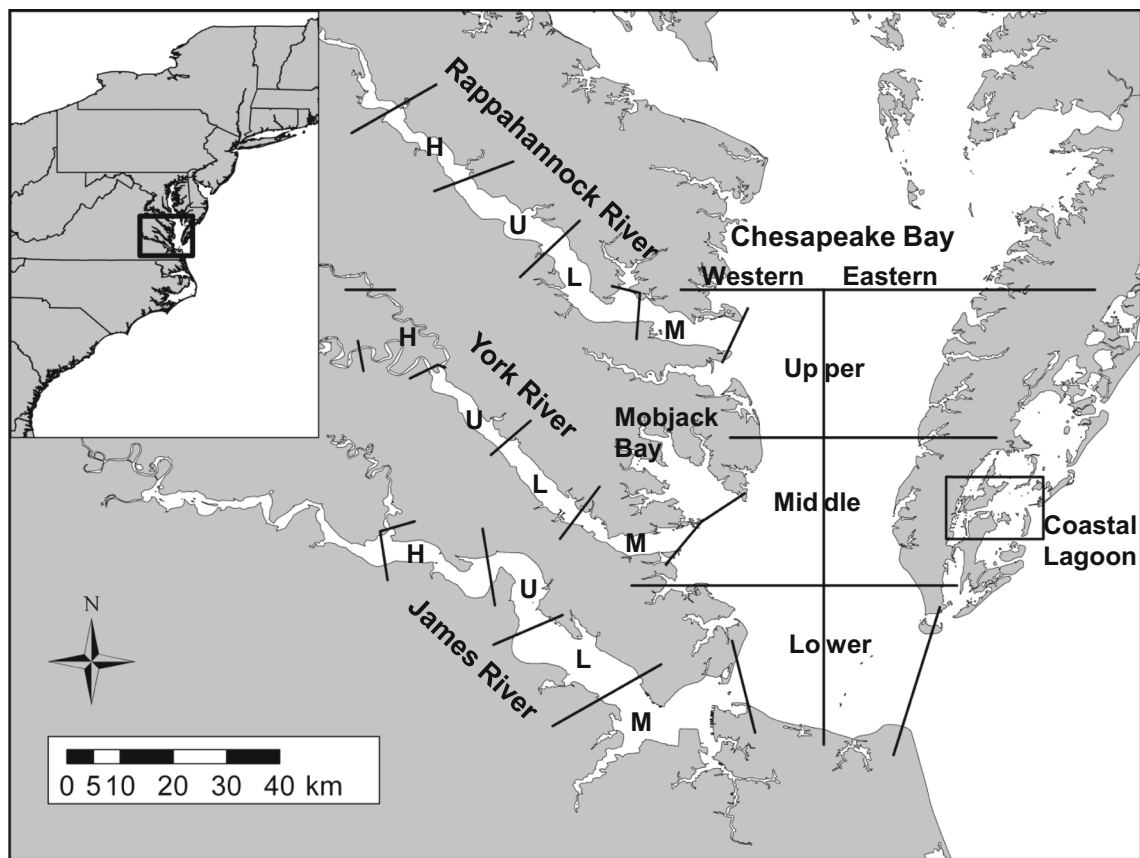


Fig. 1 Sampling regions in Virginia from which Atlantic croaker, summer flounder, and striped bass were collected for analysis of geographic patterns in condition. Solid lines denote region borders, and

H = head, U = upper, L = lower, and M = mouth regions within each riverine subestuary

(accurate to 0.1 mg). The HSI was calculated for striped bass using:

$$\text{HSI} = 100(W_{\text{liver}}/W) \quad (1)$$

where W_{liver} = wet mass of liver (g) and W = wet body mass (g).

Spatial Analysis

Because of the high variability in condition indices among individuals and the large sample sizes required to detect variation in nursery habitat quality (> 30 individuals per area; e.g., Gilliers et al. 2004, 2006), the intense sampling necessary to examine such variation required attention because sampling sites may not represent independent replicates. Thus, we used SAR models to examine spatial patterns in the condition of juvenile Atlantic croaker, summer flounder, and striped bass among nursery areas in coastal Virginia because this approach allowed us to model the spatial autocorrelation in mean condition among nearby sampling sites. We also considered models that ignored spatial relationships (hereafter, nonspatial models) to determine if simpler models could capture spatial

patterns in fish condition. We examined patterns in mean condition of juvenile fishes among four regions in each of three subestuaries (the James, York, and Rappahannock River subestuaries), seven regions in the lower Chesapeake Bay (including Mobjack Bay), and a coastal lagoon (Fig. 1). The coastal lagoon encompassed a single region because it is a relatively smaller system (1774 ha; Fig. 1). Because most of our regions were large (17,000 to 66,200 ha per region in the lower Chesapeake Bay; 2400 to 29,400 ha per region in the subestuaries), the likelihood of mixing of fish from neighboring regions was reduced. Application of spatial models requires the assumption of population closure, which was reasonable given the scale of our regions, the short time span of sampling, and early-life residency behaviors of the species examined. In particular, samples were collected during months when long-distance movements of fish were expected to be minimal (Massmann and Pacheco 1961; Miller and Able 2002; Henderson et al. 2014).

To ensure condition estimates for fish from a given region were not biased by collection date, we detrended the raw condition data (summarized in Table 1) using simple linear models with year and month as categorical predictors (Table 2; see Schloesser and Fabrizio 2016 for more information on the

Table 1 Statistical properties of the condition indices for juvenile (a) Atlantic croaker, (b) summer flounder, and (c) striped bass by sampling region

Region	Number of fish	Mean	Variance	Minimum	Median	Maximum
(a) Atlantic croaker relative subdermal lipid						
Rappahannock Head	138	24.8	65.4	9.7	22.6	46.6
Upper Rappahannock	139	24.7	56.4	8.6	23.2	45.5
Lower Rappahannock	104	24.2	53.6	8.5	22.7	43.7
Rappahannock Mouth	141	25.6	66.9	11.6	24.6	49.4
Western Upper Bay	131	27.4	69.3	9.4	27.0	51.3
Eastern Upper Bay	194	27.9	75.4	8.3	27.7	48.0
York Head	18	21.0	12.6	14.8	21.0	28.6
Upper York	199	20.8	49.7	7.3	20.6	40.0
Lower York	174	22.8	63.6	8.5	21.1	48.1
York Mouth	188	25.4	77.2	7.7	24.4	46.9
Mobjack Bay	320	24.0	60.7	11.7	22.5	47.4
Western Middle Bay	115	25.9	61.8	7.2	25.0	47.2
Eastern Middle Bay	199	27.4	62.5	7.7	27.5	47.8
James Head	154	27.2	75.1	6.6	26.9	50.5
Upper James	125	24.5	76.7	6.4	22.6	53.9
Lower James	150	22.4	84.2	6.8	20.7	50.3
James Mouth	234	21.3	79.7	6.4	18.9	51.8
Western Lower Bay	75	20.2	61.3	7.1	18.9	38.1
Eastern Lower Bay	121	21.5	68.9	7.8	20.4	42.8
Coastal lagoon	41	21.9	67.1	11.0	19.8	50.7
(b) Summer flounder relative subdermal lipid						
Rappahannock Head	3	7.1	0.1	6.8	7.3	7.3
Upper Rappahannock	17	3.2	5.3	0.1	3.0	7.4
Lower Rappahannock	30	3.2	5.5	0.1	3.7	7.7
Rappahannock Mouth	36	3.7	5.6	0.1	4.8	8.1
Western Upper Bay	53	2.4	4.3	0.1	1.4	8.1
Eastern Upper Bay	93	3.9	7.7	0.1	4.2	8.0
Upper York	23	4.2	6.6	0.1	4.6	7.3
Lower York	10	1.6	5.1	0.1	0.6	7.4
York Mouth	41	1.5	3.7	0.1	0.8	7.4
Mobjack Bay	73	2.2	3.9	0.1	1.4	6.7
Western Middle Bay	64	1.8	3.1	0.1	1.3	7.7
Eastern Middle Bay	135	3.1	6.6	0.1	2.3	8.2
Lower James	29	4.8	5.1	0.1	5.2	7.9
James Mouth	48	3.8	4.2	0.4	4.1	7.6
Western Lower Bay	48	1.6	2.8	0.1	1.2	7.6
Eastern Lower Bay	106	3.4	5.7	0.1	2.7	8.0
Coastal lagoon	164	2.7	3.4	0.1	2.5	6.5
(c) Striped bass hepatosomatic index values						
Rappahannock Head	34	1.67	0.09	1.07	1.70	2.25
Upper Rappahannock	82	1.74	0.19	1.16	1.70	3.10
Lower Rappahannock	203	2.19	0.34	0.96	2.20	3.92
Rappahannock Mouth	9	2.04	0.82	0.89	1.63	3.52
York Head	23	2.31	0.44	1.49	2.19	3.81
Upper York	115	2.04	0.20	0.86	2.03	3.14
Lower York	130	2.28	0.35	1.05	2.24	5.71
York Mouth	3	2.03	0.09	1.70	2.13	2.27
James Head	48	1.59	0.32	1.03	1.49	4.81

Table 1 (continued)

Region	Number of fish	Mean	Variance	Minimum	Median	Maximum
Upper James	33	1.72	0.19	1.19	1.66	3.10
Lower James	34	1.92	0.17	1.22	1.88	2.93

temporal patterns in condition). For these models, subdermal lipid readings were square-root-transformed and HSI values were log-transformed because these transformations most suitably met the linear model assumption of homogeneous variances. We calculated mean condition indices for each sampling site from the time-adjusted (detrended) data to use as the response in the subsequent analyses. The time-adjusted means reflect the average condition of Atlantic croaker in September and summer flounder in October, which is prior to fall emigration of these species, and the average condition of striped bass in November, prior to the onset of winter.

Table 2 The temporal distribution of the sampling sites used to examine spatial patterns in condition for (a) Atlantic croaker, (b) summer flounder, and (c) striped bass, and the year and month corrections used to ensure condition estimates for fish from a given region were not biased by collection date. Note that subdermal lipid readings (a, b) were square-root-transformed and HSI values (c) were log-transformed. Time-adjustment values of 0 indicate that measures of condition reflect Atlantic croaker in September 2013, summer flounder in October 2013, and striped bass in November 2013

	Time period	Number of sites	Mean correction	Standard error
(a)	2011	18	0.3137	0.0798
	2012	386	0.3254	0.0282
	2013	246	0	–
	June	136	–0.9002	0.0428
	July	167	–0.6095	0.0411
	August	178	–0.4036	0.0419
	September	169	0	–
	(b)	2011	114	–0.2514
2012		232	–0.7782	0.0415
2013		138	0	–
July		80	–0.1288	0.0736
August		117	–0.2609	0.0627
September		134	–0.1400	0.0557
(c)	October	153	0	–
	2010	31	0.0395	0.0306
	2011	50	0.2380	0.0209
	2012	23	0.0388	0.0423
	2013	54	0	–
	November	12	0	–
	December	21	0.1103	0.0609
	January	48	0.2565	0.0538
	February	36	0.2222	0.0533
	March	41	0.3213	0.0544

SAR models were used to estimate the mean condition of juveniles at each sampling site as a linear function of environmental predictors and conspecific density at each site and the mean condition of individuals from neighboring sites, whereas the nonspatial models did not account for the effect of neighboring sites on observed mean condition. In addition to spatial effects on fish condition, we investigated the fixed effects of site-specific temperature, dissolved oxygen, salinity, depth, and conspecific density. These factors varied among sampling sites from which individuals were captured, and although environmental factors exhibited general patterns among the regions examined (Table 3), no multicollinearity was detected among factors. We also examined the fixed effect of ‘region’, which represented the cumulative effects of unobserved environmental factors that were not explicitly specified in the model but that may contribute to variation in energy and lipid storage in fishes (e.g., substrate type, prey availability, predator abundance, and availability of refuges; Adams et al. 1982; Lloret and Planes 2003).

Spatial autocorrelation in condition was represented by a variance-covariance matrix that used spatial weights to describe the relationship of fish condition among neighboring sampling sites. A spatial weight can be estimated for each site based on the neighborhood distance (i.e., the maximum distance to be considered a neighbor) and a given weighting scheme (i.e., approach for weighting each neighbor). Here, we considered a variety of neighborhood distances and neighbor-weighting schemes. Specifically, we allowed neighbor distances to range from 0 to 25 km at about 1.11 km intervals (corresponding with 0.01° of latitude) and considered three weighting schemes: binary weighting (sites are either included or excluded as neighbors), standardized weighting (covariances are scaled by the number of neighbors for each site), and variance-stabilized weighting (a method that balances multiple weighting schemes; see Tiefelsdorf et al. 1999). These three weighting schemes were examined using inverse-distance weighting and equal weighting among neighbors. To identify the neighbor distances and weighting schemes that best described spatial variation in condition for each species, we used the estimated minimum residual spatial autocorrelation (minRSA) metric and Akaike information criteria (AIC) following Kissling and Carl (2008). First, we calculated minRSA to determine a range of neighbor distances that reduced the spatially dependent error; this resulted in multiple models for each combination of species, condition index, and weighting scheme. Next, from among these

Table 3 Mean environmental conditions (T = temperature (°C), DO = dissolved oxygen (mg/L), S = salinity (psu), and Dp = depth (m)) and conspecific density (Dn, individuals per 100 m²) among sampling regions from which juvenile fish were collected, representing the average habitat

conditions of (a) Atlantic croaker from June to September, (b) summer flounder from July to October, and (c) striped bass from November to March. Observed minima and maxima are presented to permit evaluation of the potential impact of each factor on fish condition (see Table 6)

Region	Number of sites	T	DO	S	Dp	Dn
(a) Atlantic croaker environmental factors						
Rappahannock Head	33	27.66	5.66	7.48	4.42	3.75
Upper Rappahannock	25	26.80	5.32	12.79	5.89	6.13
Lower Rappahannock	26	26.13	4.60	14.56	9.65	4.40
Rappahannock Mouth	35	26.10	4.42	16.40	13.31	3.10
Western Upper Bay	26	25.51	4.53	18.55	8.82	3.20
Eastern Upper Bay	41	25.18	4.37	21.05	11.92	4.11
York Head	6	27.75	5.13	8.30	6.40	5.15
Upper York	40	26.75	4.77	13.40	6.13	9.99
Lower York	30	25.95	4.61	18.08	7.38	5.85
York Mouth	41	25.24	4.37	20.64	11.59	6.20
Mobjack Bay	74	26.93	6.19	19.87	4.88	1.72
Western Middle Bay	19	25.20	5.36	22.33	9.57	8.70
Eastern Middle Bay	38	24.79	5.09	23.91	12.84	4.76
James Head	40	26.78	6.76	2.98	7.76	1.91
Upper James	24	27.24	6.09	7.67	6.64	5.50
Lower James	34	24.94	6.19	17.28	7.28	6.34
James Mouth	50	23.92	6.01	21.67	10.24	5.88
Western Lower Bay	15	22.14	5.68	24.91	9.23	9.29
Eastern Lower Bay	26	22.70	6.16	26.80	12.00	12.08
Coastal lagoon	27	25.05	5.58	30.49	2.98	0.22
Minimum among all sites		16.26	0.68	0.17	1.50	0.07
Maximum among all sites		31.62	11.14	32.04	27.70	147.08
(b) Summer flounder environmental factors						
Rappahannock Head	2	19.02	7.78	11.64	4.10	0.10
Upper Rappahannock	7	21.06	6.44	16.06	8.61	0.22
Lower Rappahannock	14	21.80	6.44	16.15	12.09	0.16
Rappahannock Mouth	22	23.69	5.42	16.67	12.67	0.15
Western Upper Bay	28	23.96	5.58	18.76	8.07	0.18
Eastern Upper Bay	40	23.68	5.60	21.76	10.57	0.28
Upper York	9	23.65	6.12	15.52	3.98	0.20
Lower York	6	24.35	5.49	19.71	4.87	0.14
York Mouth	21	24.24	5.38	20.34	9.54	0.29
Mobjack Bay	56	25.45	6.15	18.43	5.15	0.22
Western Middle Bay	30	24.29	6.32	20.98	8.18	0.22
Eastern Middle Bay	50	24.35	5.88	24.15	10.93	0.28
Lower James	19	23.36	6.02	16.91	7.21	0.18
James Mouth	31	23.15	6.12	22.46	9.87	0.15
Western Lower Bay	14	22.30	7.02	23.91	7.35	0.28
Eastern Lower Bay	48	22.66	6.80	26.86	10.11	0.18
Coastal lagoon	87	25.54	5.62	30.76	2.73	0.52
Minimum among all sites		17.37	0.68	10.09	1.50	0.07
Maximum among all sites		29.23	9.32	32.04	27.70	4.17
(c) Striped bass environmental factors						
Rappahannock Head	14	7.23	11.19	6.28	5.28	0.38
Upper Rappahannock	16	7.16	10.50	11.31	8.03	0.59

Table 3 (continued)

Region	Number of sites	T	DO	S	Dp	Dn
Lower Rappahannock	13	6.66	10.80	13.22	14.86	1.92
Rappahannock Mouth	4	7.51	11.30	13.92	14.35	0.42
York Head	8	6.28	10.76	7.05	6.06	0.56
Upper York	39	6.34	10.50	12.28	7.42	0.45
Lower York	17	6.89	9.62	16.17	8.67	0.78
York Mouth	1	8.40	9.34	16.72	13.70	0.75
James Head	25	7.69	11.38	2.48	7.34	0.25
Upper James	14	7.54	11.30	5.58	7.11	0.39
Lower James	7	8.66	10.65	13.22	8.44	0.83
Minimum among all sites		1.27	7.32	0.12	1.80	0.07
Maximum among all sites		14.97	13.54	20.29	18.90	5.71

models, we selected the model with the combination of neighbor distance and weighting scheme that resulted in the lowest AIC value.

We built SAR models that incorporated environmental factors and conspecific density to describe patterns in condition indices for each species (Kissling and Carl 2008; Plant 2012). The global species-specific model was:

$$Y_{ij} = \mu + \alpha_i + \beta_1(T)_j + \beta_2(DO)_j + \beta_3(S)_j + \beta_4(Depth)_j + \beta_5(Density)_j + \lambda W_{ij} + \varepsilon_{ij} \quad (2)$$

where

- Y_{ij} the time-adjusted mean condition of individuals from sampling site j in region i as measured by square-root-transformed subdermal lipid estimates (Atlantic croaker and summer flounder) or log-transformed HSI values (striped bass);
- μ the intercept, representing the overall mean condition of individuals from all regions;
- α_i the relative effect of region i when density and environmental factors are held constant;
- β_{1-5} the partial regression coefficients for temperature (T), dissolved oxygen (DO), salinity (S), depth, and conspecific density at site j ;
- λ the spatial autoregression coefficient;
- W the spatial weights matrix identified in Table 4;
- u_{ij} the spatially dependent error at site j in region i ; and
- ε_{ij} the spatially independent and normally distributed residual error for site j in region i .

The global model was reduced to a nonspatial model by allowing $u_{ij} = 0$. We examined ~30 reduced models for each species to identify the combination of density, environmental, and spatial effects that best explained patterns in mean condition using AIC (Table 5). The final model was the ‘best’ model

as determined by AIC. Nonspatial models were fit to the data using the `gls` function, and SAR models were fit using the `spautolm` function in R (`spdep` package; R Core Team 2017).

The potential impact of environmental factors and conspecific density on fish condition was determined by calculating the magnitude of the difference between the predicted condition of fish experiencing the range extremes of temperature, dissolved oxygen, salinity, depth, and conspecific density. For example, the potential impact of temperature on adjusted mean condition was given by multiplying the partial regression coefficient for temperature by the difference between the maximum and minimum observed temperature among sites occupied by a species (see Table 3). In addition, after adjusting for broad-scale environmental effects, the model-based mean condition values for selected regions were compared to identify areas with high-quality nursery habitats. These predictions were based on the selected SAR model for each species.

Results

The observed geographic patterns in the mean condition of fish were unique to each species (Table 1). After adjusting for temporal patterns in condition, subdermal lipids were higher for juvenile Atlantic croaker in much of the Chesapeake Bay than for individuals from the lower regions of the James River

Table 4 Neighborhood distances (km) and weighting schemes used to develop spatial weight matrices among sampling sites. Binary weighting refers to equal weighting of neighboring sites and exclusion of sites outside the neighborhood distance, and variance stabilization balances multiple weighting schemes (see Tiefelsdorf et al. 1999)

	Distance (km)	Weighting scheme
Atlantic croaker	6.66	Binary
Summer flounder	16.66	Variance stabilization
Striped bass	8.88	Variance stabilization

Table 5 Reduced models considered for the evaluation of environmental and density effects on geographic patterns in mean condition of juvenile fishes from Virginia estuarine waters. Sampling region and spatial effects always reduced AIC values and were included in all models but not shown here. Bold AIC values indicate the combination of temperature (T), dissolved oxygen (DO), salinity (S), depth (Dp), and conspecific density (Dn) that were included as partial regressors in the final model for each species

	Partial regressors (β s)					AIC		
	T	DO	S	Dp	Dn	Atlantic croaker subdermal lipid	Summer flounder subdermal lipid	Striped bass HSI
						1572.3	1133.6	54.6
	X	X	X	X	X	1575.8	1133.3	54.0
	X	X	X		X	1577.7	1137.3	52.8
	X	X		X	X	1648.5	1171.4	73.9
	X		X	X	X	1587.4	1131.6	57.4
		X	X	X	X	1626.4	1157.4	55.6
	X	X	X			1579.2	1137.2	52.4
	X	X		X		1661.8	1173.1	75.0
	X		X	X		1590.3	1131.4	57.3
		X	X	X		1633.3	1159.5	56.4
	X	X			X	1674.8	1169.4	73.1
	X		X		X	1588.6	1135.8	56.4
		X	X		X	1625.5	1170.6	55.0
	X			X	X	1648.6	1169.9	72.7
		X		X	X	1683.1	1186.7	74.4
			X	X	X	1627.9	1170.5	55.5
	X	X				1682.2	1171.1	73.9
	X		X			1590.4	1135.9	56.8
		X	X			1631.5	1173.9	56.9
	X			X		1660.9	1171.5	74.1
		X		X		1699.0	1190.7	77.4
			X	X		1634.1	1173.0	55.9
	X				X	1673.0	1168.0	71.5
		X			X	1695.2	1187.5	72.7
			X		X	1626.3	1176.8	54.8
				X	X	1681.1	1199.4	72.5
	X					1680.6	1169.5	72.5
		X				1706.3	1191.8	75.4
			X			1632.2	1180.2	56.3
				X		1697.6	1203.8	75.7
					X	1695.3	1197.6	70.8

subestuary and southwest Chesapeake Bay (Fig. 2a). Conversely, juvenile summer flounder from the lower James River subestuary exhibited high mean subdermal lipids (Fig. 3a). High mean subdermal lipid values in juvenile summer flounder were also observed in the upestuary regions of the tributaries and in the eastern regions of Chesapeake Bay, particularly in the northeastern region (Fig. 3a). For juvenile striped bass, mean HSI was high for individuals from the York River subestuary and the mouth of the Rappahannock River between November and March compared with those from the James River subestuary (Fig. 4a).

The SAR models described the observed patterns in juvenile fish condition better than nonspatial models which ignored spatial correlations among condition indices. The neighborhood distance and weighting scheme that best described the spatial

correlation in condition differed among species (Table 4), but for all species, equal weighting among neighbors yielded better-fitting models than inverse-distance weighting. Region was an important descriptor of patterns in condition of juvenile Atlantic croaker, summer flounder, and striped bass, but the role of site-specific environmental conditions and conspecific density in driving geographic patterns varied among species (Table 6; Figs. 2, 3, and 4b). Thus, environmental and density effects were explored separately for each species.

Environmental and Density Effects

For Atlantic croaker, density had a significant negative effect on mean condition such that individuals in high condition were observed in areas with low local densities (~ 1–4

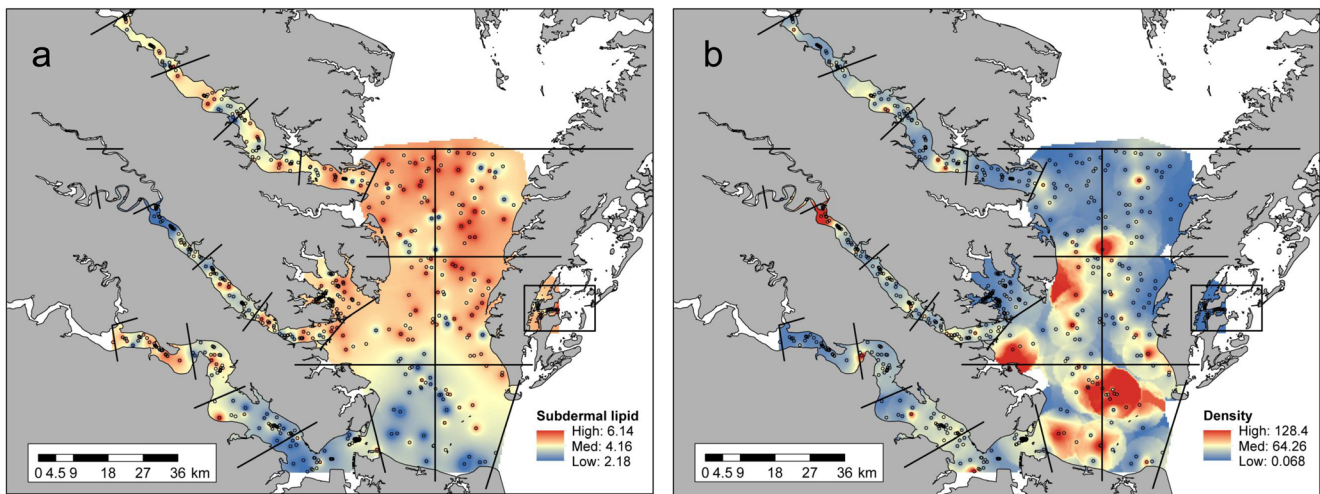


Fig. 2 Geographic patterns in square-root-transformed, time-adjusted subdermal lipid estimates (a) and density (individuals per 100 m²; b) of juvenile Atlantic croaker from sampled sites (circles) between June and September (2011–2013). Red denotes high mean condition or density

values, and blue denotes low mean values. Images were interpolated over neighborhood distances determined by the ‘best’ spatial weight matrices (Table 4)

individuals per 100 m², such as the upper Chesapeake Bay, Fig. 2). All the environmental factors examined had a significant positive influence on mean subdermal lipid values for juvenile Atlantic croaker, indicating that mean condition was higher for individuals associated with warmer, saltier, deeper, and more oxygen-enriched waters. In general, temperature increased from the Chesapeake Bay mainstem to upestuary regions for sites from which Atlantic croaker were collected (Table 3a), implying upestuary regions may support juvenile Atlantic croaker in relatively high condition when all other factors are held constant. However, the potential impact of salinity was more than twice that of temperature (Table 6), so the decrease in salinity from the mouth of the rivers to the upestuary regions would mediate the positive influence of

temperature in these upestuary regions. The positive influence of depth on mean condition of Atlantic croaker indicates that individuals with high subdermal lipids resided in deeper waters of the Chesapeake Bay and tributary mouths, but the potential impact of salinity was six times that of depth (Table 6). Even though deep waters in Chesapeake Bay may exhibit hypoxic (<2 mg/L) conditions in summer, 98.7% of Atlantic croaker were collected from waters with dissolved oxygen concentrations that exceeded 2 mg/L.

Depth had a positive effect on condition of juvenile summer flounder in Virginia coastal waters, but salinity and temperature had negative effects with a greater potential impact on subdermal lipid values (Table 6). Deep areas at the mouths of subestuaries (Table 3b) supported individuals with high

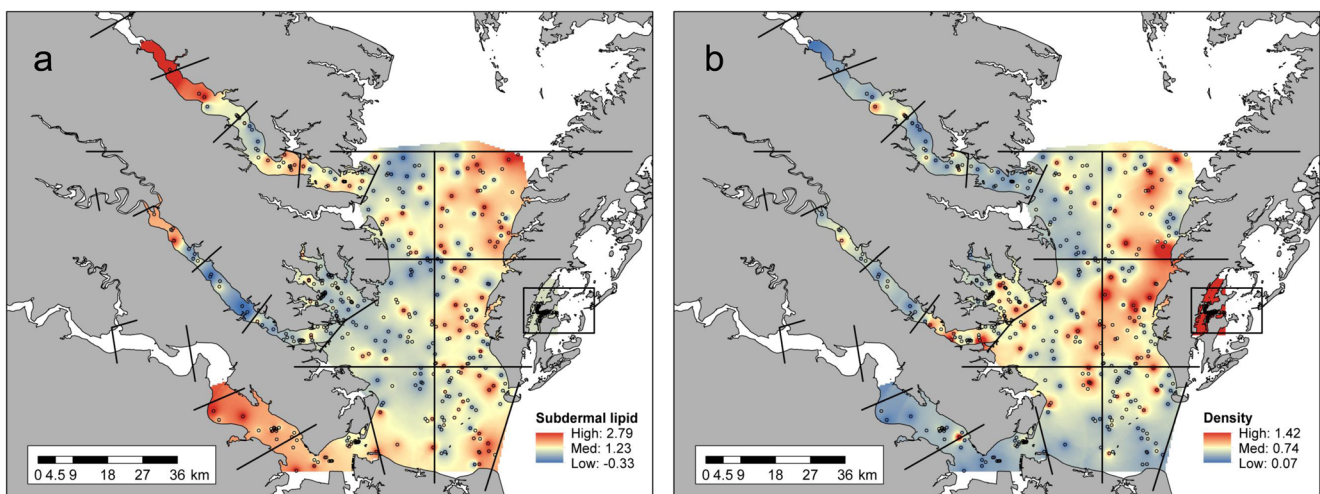


Fig. 3 Geographic patterns in square-root-transformed, time-adjusted subdermal lipid estimates (a) and density (individuals per 100 m²; b) of juvenile summer flounder from sampled sites (circles) between July and October (2011–2013). Red denotes high mean condition or density

values, and blue denotes low mean values. Images were interpolated over neighborhood distances determined by the ‘best’ spatial weight matrices (Table 4)

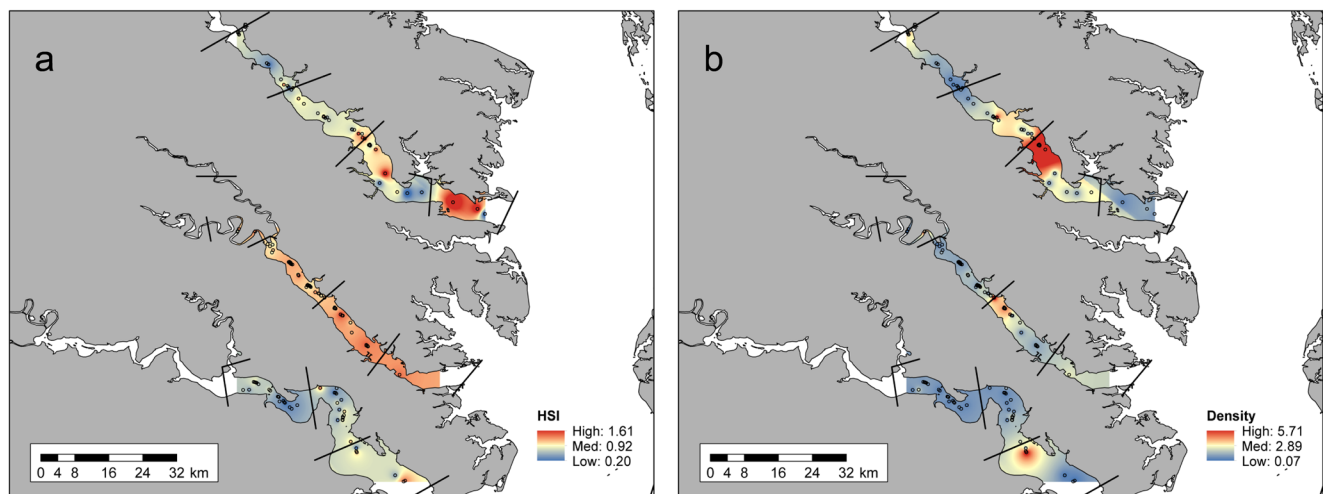


Fig. 4 Geographic patterns in log-transformed, time-adjusted hepatosomatic index (HSI) values (**a**) and density (individuals per 100 m²; **b**) of juvenile striped bass from sampled sites (circles) between November and March (2010–2013). Red denotes high mean condition or density values, and blue denotes low mean values. Images were

interpolated over neighborhood distances determined by the ‘best’ spatial weight matrices (Table 4). Juvenile striped bass were not collected from the Chesapeake Bay, Mobjack Bay, or the coastal lagoon during the time period examined

subdermal lipids, as did lower salinity waters typically observed in upestuary regions (Table 3b). Juvenile summer flounder typically exhibited low mean subdermal lipid content in warmer environments (Table 6), such as those observed in Mobjack Bay (Table 3b). Although the ‘best’ model did not identify conspecific density as a significant factor, several models within 2 AIC units indicate conspecific density could be a reasonable explanatory factor influencing summer flounder subdermal lipid in some systems.

Environmental conditions significantly influenced HSI values for juvenile striped bass between November and March (Table 6). A negative effect on mean HSI values was detected for juvenile striped bass occupying warmer waters, such as the lower region of the James River subestuary (Table 3c). A negative effect on mean condition was also detected for fish occupying relatively high salinity waters, such as

those at the lower regions of the York River subestuary (Table 3c), and the potential impact of salinity was almost twice that of temperature (Table 6). The upper regions of the James River subestuary exhibited mean oxygen concentrations that were higher than those observed in other regions (Table 3c), and the low mean condition of striped bass in the upper James River likely resulted in the observed negative effect of dissolved oxygen on striped bass condition, even though dissolved oxygen concentrations were above 5 mg/L at all sites where striped bass were collected. No significant effect of conspecific density on striped bass HSI values was detected.

Regional Patterns in Condition

Regional patterns in adjusted mean fish condition were evident for all three species. Because environmental conditions

Table 6 Environmental and density effects on the mean condition of juvenile fishes as measured by relative subdermal lipids or the hepatosomatic index (HSI) and determined from the simultaneous autoregressive (SAR) models indicated in Table 5 (bold values). Table values are partial regression coefficients of environmental and

density effects; the potential impact on adjusted mean fish condition was calculated over the range of observed conditions as indicated in Table 3. NA indicates that the environmental factor was not included in the final model

	Atlantic croaker subdermal lipid			Summer flounder subdermal lipid			Striped bass HSI		
	Effect	Standard error	Potential impact	Effect	Standard error	Potential impact	Effect	Standard error	Potential impact
Water temperature (°C)	0.113	0.015	1.735	-0.079	0.012	-0.938	-0.025	0.010	-0.340
Dissolved oxygen (mg/L)	0.117	0.028	1.219	NA	NA	NA	-0.061	0.024	-0.379
Salinity (psu)	0.132	0.015	4.219	-0.128	0.019	-2.812	-0.032	0.006	0.645
Depth (m)	0.026	0.009	0.679	0.027	0.011	0.716	NA	NA	NA
Density (individuals/m ²)	-0.009	0.004	1.281	NA	NA	NA	NA	NA	NA

(i.e., temperature, salinity, dissolved oxygen, and depth) and conspecific density significantly affected the mean observed condition of juvenile fishes, we used adjusted means from the SAR model to examine regional patterns in condition. Due to the manner in which spatial models were parameterized, adjusted means represent the deviation from the adjusted mean condition of individuals collected from the mouth of the James River (Atlantic croaker and summer flounder) or the mouth of the Rappahannock River (striped bass; no individuals were collected from the mouth of the James River).

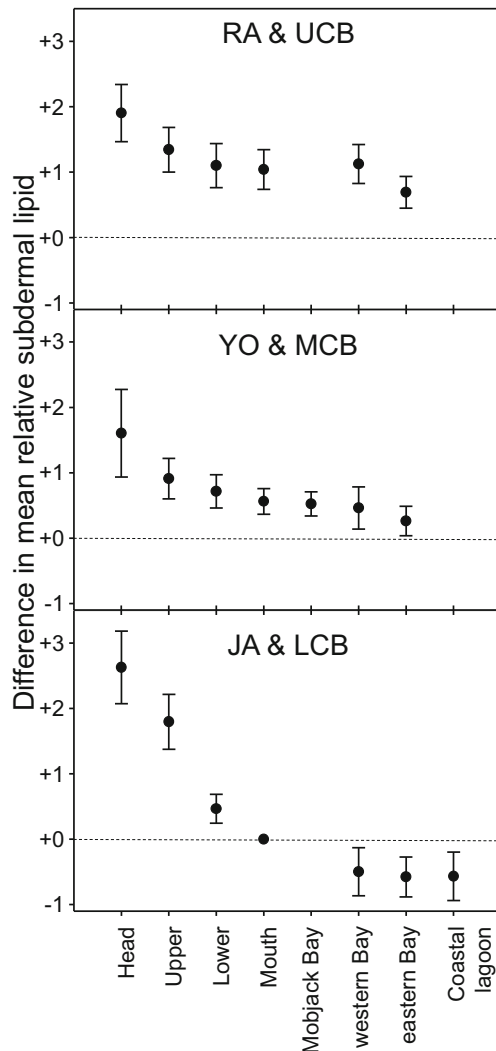


Fig. 5 The effect of region on square-root-transformed, time-adjusted subdermal lipid estimates of juvenile Atlantic croaker with the effect of environmental factors and conspecific density held constant. Values are expressed as the difference in mean condition ($\pm 95\%$ confidence interval) of fish relative to those from the mouth of the James River subestuary (mean condition = 3.70, dotted lines). Regions on the x-axis are organized from west to east, starting at the most upestuary region, and the panels are organized from north to south: RA & UCB = Rappahannock River and upper Chesapeake Bay; YO & MCB = York River, Mobjack Bay, and middle Chesapeake Bay; JA & LCB = James River, lower Chesapeake Bay, and the coastal lagoon

Relative to the mouth of the James River, juvenile Atlantic croaker exhibited high mean condition in upestuary regions after adjusting for broad-scale environmental effects (Fig. 5). The adjusted mean condition of individuals from the upper Chesapeake Bay and from the head and upper regions of the James, York, and Rappahannock River subestuaries exhibited values 28% greater than that from individuals in other regions. In the three subestuaries, the adjusted mean condition declined from upestuary regions to the mouth, and this decline was most pronounced in the James River subestuary (Fig. 5). In contrast, adjusted mean condition indices were similar among regions throughout the middle and lower regions of Chesapeake Bay and the coastal lagoon.

Relative to the James River mouth, adjusted mean condition of juvenile summer flounder was highest in the coastal lagoon (Fig. 6), indicating coastal habitats along the oceanfront of Virginia are of high quality for juvenile summer flounder. Individuals collected on the eastern side of Chesapeake Bay proper also exhibited high subdermal lipid stores, such that the adjusted mean condition of individuals associated with habitats in the coastal lagoon and eastern Chesapeake Bay regions was 100% greater than that for individuals from all other regions. For summer flounder collected in the James, York, and Rappahannock subestuaries, adjusted mean values of subdermal lipids were generally lower in the intermediate areas of these subestuaries (Fig. 6).

Adjusted mean condition indices of juvenile striped bass exhibited similar patterns among the Rappahannock, York, and James River subestuaries during winter (Fig. 7). Although variability in the mean HSI for striped bass was too high to permit detection of statistically significant differences in condition of juveniles among most neighboring regions, our data indicate that the fish inhabiting the upper areas of the Rappahannock, York, and James River subestuaries had lower mean HSI values relative to fish from regions near the mouths of the subestuaries (Fig. 7). Adjusted mean condition of juvenile striped bass from the lower and bottom regions of the subestuaries was 20% greater than the condition of individuals from the head and upper regions.

Discussion

The condition of juvenile Atlantic croaker, summer flounder, and striped bass varied widely among regions in Virginia estuaries. The spatial patterns in condition of juvenile Atlantic croaker that we observed indicate that upestuary habitats produce juveniles with relatively high mean condition. For summer flounder, mean subdermal lipid estimates were generally higher for the eastern side of the Chesapeake Bay compared with the western side and were also higher in some of the intermediate salinity areas of the tributaries, particularly the James and Rappahannock subestuaries. Juvenile striped bass

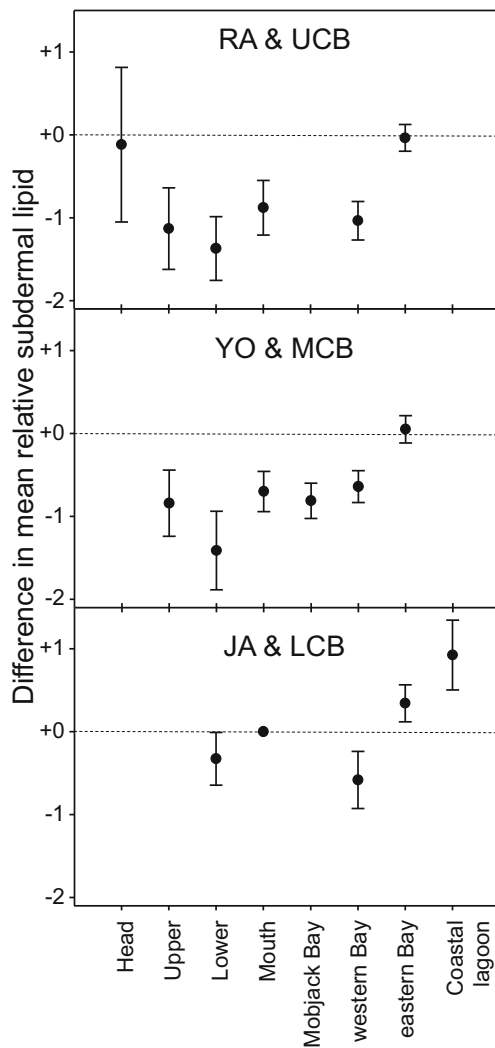


Fig. 6 The effect of region on square-root-transformed, time-adjusted subdermal lipid estimates of juvenile summer flounder with the effect of environmental factors held constant. Values are expressed as the difference in mean condition (\pm 95% confidence interval) of fish relative to those from the mouth of the James River (mean condition = 1.81, dotted lines). Regions on the x-axis are organized from west to east, starting at the most upestuary region, and the panels are organized from north to south: RA & UCB = Rappahannock River and upper Chesapeake Bay; YO & MCB = York River, Mobjack Bay, and middle Chesapeake Bay; JA & LCB = James River, lower Chesapeake Bay, and the coastal lagoon. No summer flounder were collected at the head of the York River, or in the head and upper region of the James River

of higher mean condition were observed in the York River and at the mouth of the Rappahannock River. Individuals with high condition indicate that these areas are potentially high-value habitats for these species, but these areas were not necessarily contiguous. Although environmental characteristics such as temperature, salinity, dissolved oxygen, and depth directly influenced the condition of individuals in these Virginia subestuaries, the observed noncontinuous spatial patterns in condition are likely due to complex interactions among biotic and abiotic factors. In addition, these spatial

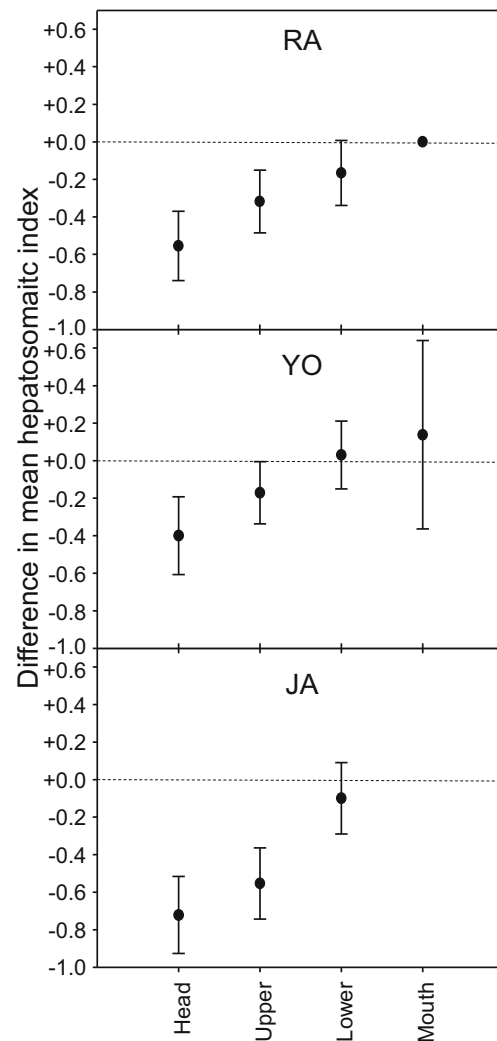


Fig. 7 The effect of region on log-transformed, time-adjusted hepatosomatic index (HSI) values of juvenile striped bass with the effect of environmental factors held constant. Values are expressed as the difference in mean condition (\pm 95% confidence interval) of fish relative to those from the mouth of the Rappahannock River (mean condition = 2.37, dotted lines). Regions on the x-axis are organized from west to east, starting at the most upestuary region, and the panels are organized from north to south: RA = Rappahannock River, YO = York River, JA = James River. No striped bass were collected at the mouth of the James River, or from the Chesapeake Bay, Mobjack Bay, or the coastal lagoon

patterns in condition likely reflected regional habitat characteristics that we were not able to explicitly consider in these models (e.g., prey availability, substrate type, predator abundance, and habitat complexity). Ultimately, the spatial variation in mean condition of juvenile fishes indicates that not all estuarine habitats in Virginia are equally suitable as nursery areas for Atlantic croaker, summer flounder, and striped bass.

Spatial models, such as SAR models applied here, accounted for the lack of independence among fish from neighboring sites and allowed the examination of density-dependent and density-independent effects. Spatial autocorrelation was evident over a

larger distance for summer flounder relative to Atlantic croaker and striped bass, which exhibited correlations over similar distances. Differences in these neighborhood distances among species and indices may reflect the spatial scale of habitat characteristics that influence juvenile condition for these species. For example, neighborhood distances may reflect variability in the abundance and distribution of important prey resources. Spatially intensive surveys that collect detailed information on the planktonic and benthic prey resources in Virginia estuaries are needed to examine the association between prey communities and neighborhood distances. Condition indices also respond differently to changes in feeding rate or starvation ('latency'; Ferron and Leggett 1994) and may influence the distances over which spatial correlations in condition are observed. Condition indices that respond more rapidly to feeding rates would likely result in lower critical distances than if a more conservative condition index were examined.

Environmental and Density Effects

The spatial distribution of high- and low-conditioned individuals provides insight on the biotic and abiotic factors that influence habitat quality for juvenile Atlantic croaker, summer flounder, and striped bass. After accounting for spatial autocorrelation among neighboring sites, temperature and salinity remained important factors influencing the mean condition of these three species, whereas dissolved oxygen described spatial patterns in the condition of Atlantic croaker and striped bass only, and depth described the patterns in the condition of Atlantic croaker and summer flounder. Over the observed range of environmental conditions occupied by these species, the potential impact of salinity on mean condition was 1.7 to 6 times that of the other environmental factors examined. Conspecific density significantly influenced the mean condition of juvenile Atlantic croaker, and given the high observed densities for this species, local abundance may mediate habitat quality.

Based on our study of three species in Virginia, temperature may be a key factor discriminating productive nursery habitat among species. Warm temperatures (~24 °C) promote rapid growth of juvenile Atlantic croaker (Searcy et al. 2007), and as seen here, warm temperatures may also promote high condition. The regions with sampling sites that averaged < 24 °C (the mouth of the James River and regions in the lower Chesapeake Bay) also exhibited some of the lowest mean subdermal lipid contents for Atlantic croaker. However, the opposite effect of temperature was observed for summer flounder condition. We suspect that the negative effect of temperature on the condition of summer flounder was associated with the observed low mean condition of fish from the lower York River subestuary, Mobjack Bay, and the middle west bay region, where fish in relatively low mean condition were sampled from relatively high mean temperatures (~24–25 °C),

albeit, these temperatures were still within the range typically associated with juvenile summer flounder habitat (~19–26 °C; Sackett et al. 2008). Although we sampled juvenile striped bass at a different time of year than the other two species, striped bass also displayed a negative relationship between condition (HSI) and water temperature. This negative relationship is consistent with the temperature-dependent energy allocation strategy observed in striped bass. Juveniles allocate more energy to growth with increasing water temperature, resulting in less energy available for storage in the liver (Hurst et al. 2000; Schloesser and Fabrizio 2016).

Similarly, salinity may help discriminate the productivity of nursery habitats: higher salinity had a positive effect on condition of juvenile Atlantic croaker, but a negative effect on summer flounder and striped bass. Mean subdermal lipid content of Atlantic croaker was higher in the middle and upper Chesapeake Bay compared with the tributaries near those regions. Although small juveniles (10–20 mm) may grow faster in low salinity water (5 psu) compared with water at 20 psu in a laboratory setting (Peterson et al. 1999), wild Atlantic croaker occupy higher salinity waters as they grow (Diaz and Onuf 1985). In our study, subdermal lipid content was higher for wild juveniles (> 100 mm) in high salinity water (up to 30 psu); in addition, lipid stores increased with size (Schloesser and Fabrizio 2017). Together, these findings indicate that energy allocation strategies may shift to include lipid storage as Atlantic croaker grow and transition from low to high salinity habitats. High salinity habitats were not preferable for juvenile striped bass, which is consistent with Hurst and Conover (2002), who reported that juvenile striped bass exhibit the highest survival rates at intermediate salinities (15 psu) when exposed to winter conditions and lower survival at 30–35 psu when water temperatures declined below 5 °C or when individuals were in poor condition. Intermediate salinities (12–17 psu) may also provide quality nursery habitat for summer flounder. Even though fewer juvenile summer flounder occurred in these regions, their relatively high condition indicates that juvenile summer flounder habitat may encompass a broader salinity range than traditionally recognized (~25–31 psu; Sackett et al. 2008), particularly because lab-based (Malloy and Targett 1991) and field-based (Nys et al. 2015) studies indicate no significant effect of salinity between 10 and 30 psu on feeding and growth of juvenile summer flounder.

Dissolved oxygen had an inconsistent influence on condition of juveniles. Higher dissolved oxygen levels positively influenced the condition of Atlantic croaker, had no effect on condition of summer flounder, and negatively influenced the condition of striped bass when all other effects were held constant. We do not expect that dissolved oxygen had a direct effect on condition because the majority of Atlantic croaker (98.7%) and all striped bass (100%) were collected from nonhypoxic waters (oxygen concentrations > 2 mg/L). Low

dissolved oxygen (≤ 2 mg/L) may indirectly affect condition due to altered spatial distributions and food web interactions, which negatively impacts feeding rates, growth, and survival of coastal species (Rose et al. 2009; Campbell and Rice 2014). Low-oxygen-induced shifts in spatial distributions of Atlantic croaker result in a lower mean temperature of occupied habitats and increases in conspecific density outside hypoxic waters (Craig and Crowder 2005). Based on our results, the use of habitats with lower temperature and higher densities would indirectly result in lower mean condition of Atlantic croaker. Alternatively, because dissolved oxygen is coupled with primary production in estuarine systems (Odum 1956; Kemp and Boynton 1980), dissolved oxygen may reflect primary and secondary production. Increased production associated with higher levels of dissolved oxygen would be expected to positively influence the condition of Atlantic croaker. But for striped bass, the occupied areas with relatively lower observed oxygen concentrations (~ 9 mg/L) correlated with higher HSI values. This was evident for juveniles captured in the lower York region, indicating that this region could be a particularly productive area for juvenile striped bass.

Similar to dissolved oxygen, depth may not directly influence condition but may instead serve as a proxy for other unmeasured, but important, environmental factors. Healthier Atlantic croaker and summer flounder were associated with the deeper waters sampled in this study (~ 10 – 13 m on average). Juvenile summer flounder use deep (> 8.5 m) habitats (Sackett et al. 2008), as do Atlantic croaker (Diaz and Onuf 1985). Deeper habitats may be characterized by high prey availability or reduced predator abundance, which may directly affect the condition of juvenile Atlantic croaker and summer flounder. For example, habitat selection of juvenile Atlantic croaker is influenced strongly by predation risk: to avoid predators, juveniles select habitats with low dissolved oxygen and low food availability (Froeschke and Stunz 2012). Both summer flounder and Atlantic croaker also prefer nonvegetated bottoms (Packer and Hoff 1999; Froeschke and Stunz 2012), which are more likely to occur in light-limited depths of Chesapeake Bay.

Conspecific density significantly affected spatial patterns in the condition of Atlantic croaker, but not summer flounder or striped bass. We note that the influence of environmental factors has been the primary focus of studies of spatial variation in condition, growth, or survival, yet for Atlantic croaker, some environmental factors were not as effective in describing variation in condition as was conspecific density. Conspecific density exerted a negative effect on condition, such that we observed juvenile Atlantic croaker with high condition indices from habitats that supported low densities of this species. Intraspecific competition resulting from high densities may lead to decreases in food consumption and reduced growth in fish (Post et al. 1999; Amundsen et al. 2007; Searcy et al. 2007). Similarly, reduced food consumption leads to reduced

protein and lipid stores (Bar 2014). Areas where mean condition is reduced due to density-dependent mechanisms such as competition may represent lower quality habitat for some species (e.g., European hake, *Merluccius merluccius*; Cantafaro et al. 2017). Conspecific density may be particularly important for describing patterns in the condition for species that exhibit a wide range of densities among regions (as was observed for Atlantic croaker, but not for summer flounder or striped bass), notably during times when food resources are limited. A low proportion of the sites that we sampled exhibited densities of summer flounder and striped bass > 2 individuals per 100 m^2 , and as a result, our study may not fully characterize the effect of conspecific density on mean condition for these two species. Nevertheless, the wide range in observed conspecific density resulted in a strong influence on the condition of juvenile Atlantic croaker, indicating future field-based studies may benefit from consideration of density-dependent effects on fish condition and habitat quality.

Regional Patterns in Condition

Regional differences in mean condition were apparent after adjusting for broad-scale effects of environmental factors, indicating that not all habitats provide equal opportunities for energy acquisition by juvenile fishes. Upestruary habitats in the James, York, and Rappahannock subestuaries may provide higher quality habitats for coastal species like juvenile Atlantic croaker and summer flounder than previously expected. Improved condition of coastal species in upestruary habitats has been observed for a suite of trophic guilds and life stages (Latour et al. 2017). Juveniles in upestruary habitats may be exposed to energy-rich prey resources that are less available in downestuary regions, or reduced predation pressure in upestruary regions may allow for more frequent feeding activity. Low predation stress (and low stress in general) may also result in lower metabolic costs, and therefore, individuals from such environments may allocate more energy to storage.

Within the subestuaries, a gradient in regional effects on condition was apparent for Atlantic croaker and striped bass, but with opposite patterns. A positive upestruary effect of region on Atlantic croaker condition was discernable in the York and Rappahannock River subestuaries and was most evident in the James River subestuary, most likely due to the more pronounced salinity gradient in this subestuary. The rate of freshwater discharge in the James River is four to seven times higher than that in the York or Rappahannock rivers, and the difference in discharge rates affects the fish community structure within these estuaries (Tuckey and Fabrizio 2013). The observed pattern in regional effects on Atlantic croaker indicates that environmental gradients in the James River subestuary also structure predator and prey communities in a manner that has a strong positive effect on mean condition of juvenile Atlantic croaker in upestruary habitats. For example,

in the James River, fish species diversity is greater in upestuary habitats compared with mid-tributary regions (Tuckey and Fabrizio 2013). However, this community structuring does not have the same impact on the condition of juvenile striped bass; instead, our data indicate that mean condition of juvenile striped bass increases downriver toward the Chesapeake Bay proper, although variability in the mean HSI for striped bass did not permit detection of statistically significant spatial patterns in condition of juveniles among most neighboring regions within tributaries. Even though movements of juvenile striped bass are minimal during winter months (Massmann and Pacheco 1961), higher movement than expected among regions could result in low variability among the regions examined and inhibit the detection of significant differences in mean HSI among neighboring regions. Alternatively, variability in HSI may be high among individuals, regardless of the region they occupy.

Within the Chesapeake Bay, regional variability in mean condition indicates differential preparation for emigration of juvenile Atlantic croaker and summer flounder from the Chesapeake Bay and coastal lagoon. Juvenile Atlantic croaker from the northernmost regions of Chesapeake Bay exhibited high mean subdermal lipids in the late summer, and mean subdermal lipid estimates were generally higher for juvenile summer flounder from the eastern side of the Chesapeake Bay. Subdermal lipids support migration in some fish species (Leonard and McCormick 1999), and subdermal lipid content increases in juvenile Atlantic croaker and summer flounder prior to their emigration from Chesapeake Bay in the fall (Schloesser and Fabrizio 2016). Because well-conditioned juveniles may be better prepared for migration compared with fish in low condition (Litvin et al. 2014), the Atlantic croaker from the upper Chesapeake Bay and summer flounder from the eastern regions likely have sufficient energy reserves for emigration in the fall. Yet not all regions may effectively support individuals that are prepared for emigration. The lower James River subestuary and the southwest region of Chesapeake Bay supported Atlantic croaker in poor condition, as did the western Chesapeake Bay for summer flounder. Because individuals in low condition may suffer higher mortality rates during migration (Brodersen et al. 2008), these habitats in southern Virginia may contribute less to recruitment to the adult stock despite the high density of juveniles. Therefore, the abundance of juveniles in these regions may not accurately reflect nursery habitat quality, highlighting the need to consider survival, movement, and contribution to the population when assessing quality of nursery habitats (Beck et al. 2001). For example, some summer flounder remain in Chesapeake Bay during winter, and a high proportion of those individuals exhibit poor condition (Schloesser and Fabrizio 2016). Juvenile summer flounder from downestuary regions of the Rappahannock River had the lowest mean condition when correcting for environmental variability. If a higher proportion of these summer flounder

reside in Chesapeake Bay during winter, then they may be susceptible to mortality during winter (Schloesser and Fabrizio 2016), and thus, the downestuary regions of the Rappahannock River would not represent high-quality nursery habitats for juvenile summer flounder in Virginia.

Although we sampled a single coastal lagoon, our results indicate that such areas have a strong positive influence on the condition of juvenile summer flounder. These habitats also support high densities of adult summer flounder (Wyanski 1990). Our observation of relatively high densities of juvenile summer flounder in a coastal lagoon is consistent with other studies that indicate the distribution of juvenile summer flounder is influenced by salinity, such that individuals preferentially occupy high salinity marsh habitats (Packer and Hoff 1999; Sackett et al. 2008). Yet, because these habitats are saltier and warmer, we would have expected to observe lower mean condition of juvenile summer flounder from the coastal lagoon. The observation that this region supports juvenile summer flounder in relatively high condition indicates that factors not explicitly examined in the models drive habitat quality in the coastal lagoon. For example, individuals may use coastal lagoons due to abundant prey resources, such as mysid shrimp (Latour et al. 2008; Buchheister and Latour 2011). Unfortunately, little is known about the spatial distribution and relative abundance of mysid shrimp or juvenile fishes in general in Virginia coastal lagoons. Coastal lagoons, such as the one near Oyster, VA, where we sampled, and lagoonal systems near Wachapreague and Chincoteague, VA, may serve as important nursery areas for juvenile summer flounder, but we currently lack synoptic fisheries surveys from these systems. Given the results of our study and the economic importance of summer flounder in the mid-Atlantic region (National Marine Fisheries Service 2016), we recommend monitoring the abundance and condition of juvenile summer flounder in coastal lagoons of Virginia.

Conclusions

Although numerous fish species occupy estuarine waters, a given habitat within the estuary may not be equally suitable for all species. Instead, a particular area or habitat type may disproportionately support juveniles of one species due to the influence of spatially varying environmental factors and conspecific density. Complex interactions among environmental factors may affect energy allocation strategies of fishes, which ultimately manifests as spatial patterns in condition indices. Our research demonstrated that mean condition indices of juvenile fishes exhibit spatial patterns; when such indices are detrended for temporal variability and when spatial models are used to take into account the spatial correlation among neighboring observations, condition indices of juvenile fishes may infer the quality of estuarine nursery habitats. Habitats in

tributary mouths conferred a 22% increase in striped bass condition, upestuary habitats conferred a 28% increase in Atlantic croaker condition, and the mean effect of habitat on condition of summer flounder associated with coastal lagoons and the eastern side of Chesapeake Bay was twice that of conspecifics from other regions after adjusting for broad-scale environmental effects. Such an approach can provide information on the comparative value of nursery habitats throughout the geographic range of the species. For example, the spatial scale of sampling can be expanded to encompass the full range of nursery areas occupied by summer flounder along the eastern US coast, and a comparative assessment of habitat quality may be obtained using observations of the mean condition of fish. The temporal stability of nursery habitat quality also needs further examination as habitat quality of a given area may not be time invariant. Environmental conditions in Chesapeake Bay exhibit decadal oscillations (Austin 2002), and such environmental changes and fluctuations in annual productivity of estuarine organisms are expected to influence the quality of nursery habitats. In any given year, estuarine habitats in Virginia may not be equally favorable for the production of recruits of multiple species, and assessing spatial patterns in juvenile fish condition to identify locations that produce well-conditioned juveniles will reveal the environmental characteristics associated with high-quality nursery habitats that may contribute to species-specific productivity.

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