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Juvenile winter flounder (*Pseudopleuronectes americanus*) and summer flounder (*Paralichthys dentatus*) utilization of Southern New England nurseries: Comparisons among estuarine, tidal river, and coastal lagoon shallow-water habitats

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Abstract

This study evaluated the relative importance of the Narragansett Bay estuary (RI and MA, USA), and associated tidal rivers and coastal lagoons, as nurseries for juvenile winter flounder, *Pseudopleuronectes americanus*, and summer flounder, *Paralichthys dentatus*. Winter flounder (WF) and summer flounder (SF) abundance and growth were measured from May to October (2009–2013) and served as indicators for the use and quality of shallow-water habitats (water depth < 1.5–3.0 m). These bioindicators were then analyzed with respect to physiochemical conditions to determine the mechanisms underlying intra-specific habitat selection. WF and SF abundances were greatest in late May and June (maximum monthly mean = 4.9 and 0.55 flounder/m² for WF and SF, respectively), and were significantly higher in the tidal rivers relative to the bay and lagoons. Habitat-related patterns in WF and SF abundance were primarily governed by their preferences for oligohaline (0.1–5 ppt) and mesohaline (6–18 ppt) waters, but also their respective avoidance of hypoxic conditions (< 4 mg DO/L) and warm water temperatures (> 25 °C). Flounder habitat usage was also positively related to sediment organic content, which may be due to these substrates having sufficiently high prey densities. WF growth rates (mean = 0.25 ± 0.14 mm/d) were negatively correlated with the abundance of conspecifics, whereas SF growth (mean = 1.39 ± 0.46 mm/d) was positively related to temperature and salinity. Also, contrary to expectations, flounder occupied habitats that offered no ostensible advantage in intra-specific growth rates. WF and SF exposed to low salinities in certain rivers likely experienced increased osmoregulatory costs, thereby reducing energy for somatic growth. Low-salinity habitats, however, may benefit flounder by providing refugia from predation or reduced competition with other estuarine fishes and macro-invertebrates. Examining WF and SF abundance and growth across each species' broader geographic distribution revealed that southern New England habitats may constitute functionally significant nurseries. These results also indicated that juvenile SF have a geographic range extending further north than previously recognized.

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Keywords

Summer flounder; Winter flounder; Age-0 juvenile; Shallow-water nursery habitat; Abundance; Growth

Introduction

Estuaries and other inshore habitats serve as important nurseries for juvenile fishes. The functional significance of these nurseries is predicated on the habitat's relative contribution of recruits to adult populations (Beck et al. 2001). There are numerous ecological factors operating concurrently in nursery habitats that affect the survival and recruitment success of juvenile fishes, including food availability and quality (Manderson et al. 2002), resource competition (Modin and Phil 1994), and risk to predation (Taylor 2005). Underlying these regulatory factors, the growth performance of individual fish may explain variations in survival (Houde 1987; Rice et al. 1993). Most notably, a survival advantage is conferred to fast growing fish because of a reduced vulnerability to size-dependent predation (Parker 1971; Anderson 1988; Post and Evans 1989) and increased tolerance to extreme environmental conditions (e.g., over-wintering temperature; Sogard 1997; Schultz et al. 1998). Accelerated growth may also benefit fish by providing a predator size advantage relative to preferred prey, and broadening the breadth of prey on which the fish successfully forages (Sogard 1997; Stehlik and Meise 2000; Latour et al. 2008).

The abundance of juvenile fish is typically higher in nursery habitats that afford maximum growth potential and survival. Accordingly, measurements of these indices are frequently used to assess the functional significance of nurseries; such that high quality nurseries are those in which juvenile fish abundance and growth are optimized (Gibson 1994; Le Pape et al. 2003; Franco et al. 2010). Moreover, juvenile fish may preferentially occupy habitats that augment growth potential (Sogard 1992), provided that rapid growth confers a selective advantage, and growth performance is habitat-specific. Negative biological interactions (i.e., predation and competition), however, may influence the behavioral mechanisms underlying juvenile fish habitat selection (Werner et al. 1983; Halpin 2000; Laegdsgaard and Johnson 2001). For example, juvenile fish may preferentially utilize nurseries that offer suboptimal growth conditions if these respective habitats also provide spatial refuge and decreased risk to predation (Halpin 2000). These biotic factors, as well as physiochemical conditions (e.g., temperature, salinity, and dissolved oxygen), that regulate habitat-specific abundance and growth of juvenile fish are complex, and vary over relatively small spatiotemporal scales (Goldberg et al. 2002; Manderson et al. 2002; Meng et al. 2005). Thus, evaluating the functional significance of nurseries on the basis of fish abundance and growth requires a synoptic examination of multiple habitat types that occurs over sufficiently broad seasonal and annual temporal scales (Beck et al. 2001). These efforts are necessary to properly identify critical nursery habitats and manage essential areas that impact fish year-class strength and recruitment.

The identification of functionally significant nurseries is particularly important for fish species that are susceptible to precipitous population declines (Gibson 1994). Such species

include flatfishes, owing to their complex life history strategies and use of multiple habitat types. Summer flounder, *Paralichthys dentatus*, and winter flounder, *Pseudopleuronectes americanus*, are parichthid and pleuronectid flatfish, respectively, with distinct life history characteristics. Summer flounder (SF) spawn offshore on the continental shelf during the late fall and early winter, producing pelagic, buoyant eggs that hatch ~ 3 d post-spawning (Packer et al. 1999). From October to May, planktonic SF larvae can recruit both passively and actively to inshore nurseries, where they complete their transformation to the juvenile, bottom-oriented form (Packer et al. 1999). Conversely, for winter flounder (WF), spawning of demersal eggs occurs predominantly inshore within estuaries from late winter to early spring (Pereira et al. 1999). After hatching 14–21 d post-spawning, larval WF are pelagic for ~ 60 d (Chambers and Leggett 1987), after which they metamorphose into benthic juveniles during the late spring and early summer (Percy 1962).

SF and WF both utilize estuaries and other inshore areas as nurseries during the juvenile, post-settlement stage (Packer et al. 1999; Pereira et al. 1999); however, the geographic range of their respective nursery habitats in the northwest and mid-Atlantic differs. Juvenile SF occupy more southerly-located habitats within this defined geographic area, ranging from New Jersey to South Carolina (Fogarty 1981; Able et al. 1990), whereas WF are a colder-water species, utilizing estuaries from Maryland northward to Nova Scotia (Schwartz 1964; Pereira et al. 1999). Recent anecdotal observations, however, indicate a spatiotemporal overlap between juvenile SF and WF in the Narragansett Bay (RI and MA, USA); a temperate estuary in southern New England (Taylor, pers. obs.). Accordingly, juvenile SF may have a geographic distribution extending further north than previously recognized (Fogarty 1981; Able et al. 1990). Based on these observations, the main objective of this research was to evaluate over a 5-year period the potential importance of the shallow waters of the Narragansett Bay estuary and associated tidal rivers and coastal lagoons as nursery habitat for juvenile (age-0) SF and WF. Specifically, estimates of SF and WF abundance and growth were used as the principal indicators of habitat use and quality of these ecosystems. These bioindicators were also examined relative to spatially and temporally explicit physiochemical conditions to determine the mechanisms underlying intra-specific habitat selection.

Methods

Study Area

The Narragansett Bay estuary is contiguous with Rhode Island Sound at its mouth and extends northward into Rhode Island (RI) and Massachusetts (MA) (total area ~ 380 km²; mean depth ~ 7.8 m; maximum depth > 40 m; Chinman and Nixon 1985; Fig. 1). The geographically-complex system is comprised of sub-estuaries, bays, and coves, and serves as a drainage basin for several tidally-influenced rivers, including the Narrow River to the southwest (mean depth ~ 2 m; maximum depth at two isolated basins ~ 15–19 m) and the Seekonk and Taunton Rivers to the northwest and northeast, respectively (mean depths ~ 1.3 m; maximum depths in narrow channels ~ 3–4 m) (Chinman and Nixon 1985; Fig. 1). The main estuary is generally well-mixed with a slight down-bay salinity gradient (range ~ 24–33 ppt in the bay proper; Kremer and Nixon 1978), whereas the adjoining rivers have

broader salinity ranges (< 2 to 30 ppt in upper and lower reaches, respectively; this study). Annual water temperatures for the bay and tidal rivers typically range from -0.5 to 25°C (Kremer and Nixon 1978), and portions of the upper bay and rivers are prone to episodic hypoxia during summer months (Desbonnet and Costa-Pierce 2008). Bay and riverine sediments are comprised mostly of fine-grained silts and clays, with fine sands becoming increasingly abundant in shoal areas of the upper bay and in the lower bay (Murray et al. 2007).

Nine shallow, coastal lagoons align the southern shore of RI, four of which were examined in this study: Winnapaug Pond, Quonochontaug Pond, Charlestown Pond, and Point Judith Pond (areas = $1.8\text{--}6.9\text{ km}^2$; mean depths = $1.2\text{--}1.8\text{ m}$; maximum depths in channels $\sim 5\text{ m}$; Meng et al. 2000; Stolt et al. 2011) (Fig. 1). The lagoons are separated from Block Island Sound by barrier spits ($1\text{--}8\text{ km}$ long, $0.8\text{--}3.5\text{ km}$ wide; Boothroyd et al. 1985), but are connected to the Sound by narrow, permanent anthropogenic breachways. Temperature and salinity ranges in the lagoons are comparable to Narragansett Bay (Meng et al. 2000 and references therein), and the sediments are characterized as sands and organic silts in the channels/margins and coves, respectively (Stolt et al. 2011).

Field Sampling

Juvenile (age-0) WF and SF were collected from late spring to early fall over a 5-year period (2009–2013) from the three “habitats” described above: Narragansett Bay (bay), tidal rivers, and coastal lagoons (Fig. 1). For Narragansett Bay, 18 sites across three “locations” (upper, middle, and lower bay) were sampled from June to October using monthly seine hauls (Fig. 1). One haul was conducted at each site per sampling date with a $61 \times 3.1\text{ m}$ seine (0.64 cm mesh size and 0.48 cm bunt). Sampling occurred during daylight ($\sim 0800\text{--}1600$; $\pm 2\text{--}4$ hour of high tide), and the net was deployed by boat and subsequently retrieved from shore (water depth and area sampled per site $\sim 0\text{--}3\text{ m}$ and 542 m^2 , respectively). Field sampling of tidal rivers focused on three “locations”: Seekonk, Taunton, and Narrow Rivers (Fig. 1). For the Seekonk River (SR) and Taunton River (TR), 3 sites per river were sampled fortnightly from May to August/September with a $15 \times 1.8\text{ m}$ beach-seine set (0.64 cm mesh size and 0.48 cm bunt). Sampling occurred during daylight ($\sim 0800\text{--}1600$; $\pm 2\text{ hr}$ of low tide) and sites were accessed by boat, after which seines were deployed by unfurling the net by hand and subsequently pulling the gear to shore (1 haul per site per date; water depth sampled $\sim 0\text{--}1.5\text{ m}$). The area swept at each site was recorded and varied due to tidal stage and beach profiles (average and range of area sampled per site $\sim 841\text{ m}^2$ and $237\text{--}1700\text{ m}^2$). For the Narrow River (NR), 3 sites were sampled monthly from May/June to October with a $40 \times 1.7\text{ m}$ seine (0.64 cm mesh size and 0.48 cm bunt). Sampling occurred during daylight ($\sim 0800\text{--}1600$; $\pm 2\text{--}4$ hour of high tide), and nets were deployed and retrieved in the same manner as the bay survey (1 haul per site per date; water depth and area sampled per site $\sim 0\text{--}1.5\text{ m}$ and 250 m^2 , respectively). Four coastal lagoon “locations” were surveyed, including Winnapaug Pond (WP), Quonochontaug Pond (QP), Charlestown Pond (CP), and Point Judith Pond (PJ), whereby 3–4 sites per lagoon were sampled monthly from May/June to October using the same procedures as the Narrow River (Fig. 1). From 2009–2013, a total of 450, 258, and 399 seine hauls were performed in the bay, rivers, and lagoons, respectively. Flounder captured during field sampling were enumerated and measured to the nearest millimeter for

total length (TL). For a given sampling date, surface temperature (°C), salinity (ppt), and dissolved oxygen (mg/L) were measured at each site using YSI meters (YSI Incorporated, 1700/1725 Brannum Lane Yellow Springs, OH). Sediment characteristics [grain size < 63 µm (% silt-clay) and total organic carbon (TOC, % dry weight)] were available for a subset of the locations sampled in this study, including the Narragansett Bay and the Seekonk and Taunton Rivers. The composition of bay and riverine sediments was assessed in earlier studies between 2000 and 2006 (% silt-clay: $n = 253$; TOC: $n = 232$), and data were accessed from Murray et al. (2007), U.S. EPA (2011), and summarized in Taylor et al. (2012).

Flounder Frequency of Occurrence and Abundance

The frequency of occurrence (%*FO*) and abundance of WF and SF were derived from catch data across sampling sites (Fig. 1), and subsequently analyzed by grouping across habitat-types as described above. The abundance data were standardized to the number of flounder/m² assuming 30% seine efficiency (Pierce et al. 1990; Steele et al. 2006; Isha et al. 2008). Mean differences in WF and SF %*FO* and abundance were analyzed with Chi-square tests of independence and two-way analysis of variance (ANOVA) models, respectively, using habitat (bay, river, lagoon) and year (2009–2013) as explanatory factors. For these statistical tests, data were limited to June–August because these months were consistently sampled among all habitats and years. The post hoc examination of %*FO* across 3 levels of habitat and 5 levels of year was performed using pairwise comparisons with Bonferroni corrections of the *p*-values (MacDonald and Gardner 2000). Mean differences in abundance across habitat and year were also contrasted with independent Ryan-Einot-Gabriel-Welsch (Ryan's Q) multiple comparison tests (Day and Quinn 1989). Prior to these analyses, abundance data were natural log($x+1$)-transformed to meet assumptions of normality and homogeneity of variance. When data transformations were unsuccessful in achieving homoscedasticity, hypotheses were rejected at alpha levels lower than the *p*-values of the Levene's test of homogeneity of variance (Underwood 1981).

Multiple linear regression analyses were used to assess the effects of several abiotic variables on flounder abundance [$\ln(x+1)$ -transformed] (Ives 2015). The variables included in the regression models were day of year, water temperature (°C), salinity (ppt), and dissolved oxygen (mg/L). Small-sample, bias-corrected Akaike's Information Criterion (AIC_c) and Akaike's weights (w_i) were used to evaluate and select the optimal regression model among 15 candidate models (Burnham and Anderson 2002):

$$AIC_c = -2\log[\mathcal{L}(\hat{\theta})] + 2K + \frac{2K(K+1)}{n-K-1} \quad (1)$$

$$w_i = \exp(-0.5\Delta_i) / \sum_{k=1}^5 \exp(-0.5\Delta_k) \quad (2)$$

where, $\mathcal{L}$ is the likelihood function of the model parameters, n is the sample size, K is the number of regression parameters, and Δ_i is equal to $AIC_{c,i} - AIC_{c,min}$. The model with the smallest AIC_c value ($AIC_{c,min}$) had the most support, and the w_i value quantified the probability that model i was the best among the candidate models.

Lastly, multivariate linear regression models were used to examine the effects of sediment composition (% silt-clay and TOC) on site-specific flounder abundance. Note that due to missing data elements for the lagoons and Narrow River, the sediment-abundance analyses were limited to sites in Narragansett Bay and the Seekonk and Taunton Rivers, and thus these analyses were performed separately from the other statistical tests.

Flounder Size-structure and Growth

WF and SF length-frequency distributions were created for each sampling month and habitat-type based on size-class intervals of 10 mm TL (flounder < 100 mm) and 20 mm TL (> 100 mm). Intra-specific cohorts were identified by visually inspecting the length-frequency distributions, and then verified using the modal progression routine of FiSAT II (Food and Agriculture Organization–International Center for Living Aquatic Resources Management stock assessment tools; Gayanilo et al. 2002). Annual growth rates of WF and SF at each site were analyzed by fitting least-squares linear regression models to mean body size data over time (growth = slope of linear regression; mm/d). Linear regression models were only used for datasets that included a minimum of 3 size-day (ordinate-abscissa) data points. Accordingly, based on available data, WF growth was evaluated from May/June to September/October, whereas SF growth was estimated from May/June to August/September. Mean differences in WF and SF growth as a function of habitat and year were analyzed using two-way ANOVA models, as described above. Multiple linear regression models, AIC_c , and w_i were also used to examine the effect of water temperature, salinity, dissolved oxygen, sediment composition, and conspecific abundance (flounder/m²) on WF and SF growth rates. For these analyses, independent variables represent averages calculated over the specified growth period.

Results

Environmental Conditions

Mean monthly water temperatures were comparable across habitats and locations (range = 12.0–29.1 °C; Table 1), with the exception of the Seekonk and Taunton Rivers which had relatively warm waters during the late spring (mean $\pm$ 1 standard deviation for May: SR and TR = 20.5 $\pm$ 1.0 °C; NR and lagoons = 16.9 $\pm$ 1.3 °C) (Fig. 2A–C). Seasonal temperature changes were also similar among sites, with temperatures increasing $\sim$ 0.14 °C per day until reaching a maximum in July and steadily declining thereafter (mean: July = 24.8 $\pm$ 0.9 °C; October = 16.6 $\pm$ 0.7 °C) (Fig. 2A–C).

Mean monthly salinity varied markedly across habitats and, to a lesser extent, locations (Table 1). Coastal lagoons and the lower Narragansett Bay had the most saline conditions (mean = 27.9 $\pm$ 0.5 ppt), followed by the mid-bay, upper bay and Narrow River (24.9 $\pm$ 1.6 ppt), and Taunton and Seekonk Rivers (8.6 $\pm$ 1.9 ppt). Accordingly, the bay, lagoons, and

Narrow River were generally regarded as polyhaline habitats (19–30 ppt), whereas the Seekonk and Taunton Rivers had salinity regimes more consistent with mesohaline (6–18 ppt) and oligohaline (0.1–5 ppt) waters. Note that certain sites in the upper bay and Narrow River also routinely experienced mesohaline conditions. Moreover, salinity gradually increased throughout the duration of each annual survey, irrespective of habitat and location (exception = TR; Fig. 2D–F).

Monthly dissolved oxygen concentrations ranged between 2.4 and 12.9 mg/L and were consistently higher in the lagoons (mean = 8.3 ± 0.8 mg/L), followed by the rivers (7.6 ± 1.2 mg/L) and bay (6.8 ± 0.6 mg/L) (Table 1). Dissolved oxygen varied temporally, such that concentrations decreased from spring to late summer (mean: May = 9.0 ± 1.8 mg/L; September = 6.7 ± 1.6 mg/L), after which levels increased modestly at most locations (exception = SR; Fig. 2G–I). There was also evidence of episodic hypoxia ($DO < 4.0$ mg/L) in the bay, Narrow River, and Seekonk River, albeit to a limited extent. Specifically, 980 independent dissolved oxygen measurements were made during this study, from which 15 and 4 incidences of hypoxia were observed in the bay and rivers, respectively. It is important to reiterate that dissolved oxygen measurements were made during daylight (~ 0800–1600), and thus, may not represent conditions over a complete diel cycle.

Sediment grain size and total organic carbon varied spatially across bay and riverine locations (Table 1). The rivers were characterized by fine-grain substrates with high organic content mean % silt-clay: SR = 47.6 ± 7.6 %, TR = 48.0 ± 5.6 %; mean TOC: SR = 5.5 ± 1.7 % dry weight, TR = 3.0 ± 0.01 % dry weight). Mean grain size and organic content of bay sediments were relatively consistent across locations (range: % silt-clay = 29.6–37.8 %; TOC = 1.3–2.7 % dry weight), but exhibited substantial variation among individual sites. In general, embayments and tributaries of the upper and mid-bay were characterized by silts-clays with high organic content, whereas coarser sediments with low carbon content were more common in the shoal areas of the upper bay and in the lower bay.

Flounder Frequency of Occurrence and Abundance

Juvenile WF and SF were captured in 63.0% and 12.8%, respectively, of the total seine hauls conducted in this study (1107 total hauls). Moreover, the occurrence of flounder differed significantly across habitats and years (Tables 1 and 2). From June to August, WF % *FO* was comparable between tidal rivers (81.8%) and coastal lagoons (82.5%), but was significantly lower in Narragansett Bay (59.6%) (Table 2). SF also demonstrated habitat-specific variation in % *FO*, whereby the presence of SF was significantly higher in the rivers (42.8%) relative to the lagoons (13.0%) and bay (3.0%) (Table 2). The % *FO* of WF and SF were also notably higher in 2012 and 2009, respectively (Table 2). Among locations, % *FO* for both flounder species was greatest in the Seekonk River (WF = 91.9%; SF = 74.4%) and lowest in the southern portions of the bay (WF = 28.0%; SF = 0.0%).

The mean (± 1 standard deviation) monthly abundance of WF across habitats was 0.16 ± 0.39 (range = 0.0–4.9 flounder/m²) (Table 1), with the highest catch in a single seine haul occurring in the Seekonk River and equaling 7.3 flounder/m². The mean monthly abundance of SF was 0.01 ± 0.04 flounder/m² (range = 0.0–0.55 flounder/m²) (Table 1), with a maximum abundance of 1.5 flounder/m², also occurring in the Seekonk River. WF and SF

abundances varied temporally and were typically highest in late May and June (May/June mean: WF = 0.29 ± 0.66 flounder/m²; SF = 0.02 ± 0.07 flounder/m²) (Fig. 3). For WF, however, maximal abundances were observed in July for a subset of the locations, including the upper and middle bay, Narrow River, and the Quonochontaug and Charlestown Ponds (July mean for subset = 0.27 ± 0.46 flounder/m²). Flounder abundances continually declined as the season progressed beyond mid-summer (October mean: WF = 0.03 ± 0.06 flounder/m²; SF = 0.0 ± 0.0 flounder/m²) (Fig. 3).

WF abundance differed significantly across habitats, but not years (Table 2; Figs. 3 and 4A). From June to August, WF abundance was greatest in the rivers, principally in the Seekonk and Narrow Rivers (mean: SR and NR = 0.46 ± 0.41 flounder/m²; TR = 0.03 ± 0.02 flounder/m²), followed by the lagoons (0.14 ± 0.17 flounder/m²) and bay (0.05 ± 0.04 flounder/m²). SF abundance similarly varied among habitats; however, year was also a significant factor (Table 2; Figs. 3 and 4B). The June–August abundance of SF was highest in the rivers, principally in the Seekonk and Taunton Rivers (mean: SR and TR = 0.07 ± 0.05 flounder/m²; NR = 0.001 ± 0.001 flounder/m²), and was comparable between the lagoons (0.003 ± 0.004 flounder/m²) and bay (0.0004 ± 0.0006 flounder/m²). Catches of SF were also significantly higher in 2009 relative to all other years (mean: 2009 = 0.03 ± 0.10 flounder/m²; 2010–2013 = 0.003 ± 0.010 flounder/m²) (Fig. 4B). It is important to note that the habitat-year interaction effect was significant in the SF analysis, thereby precluding contrasts across the main effects (Table 2). The interaction effect between habitat and year was attributed to significantly higher abundances of SF in the lagoons, in comparison to the bay, in 2009 and 2012 (Standard t-tests: $p < 0.05$ and 0.0005 , respectively), but no catch differences in other years (Standard t-tests: $p = 0.053$ – 0.143) (Fig. 4B).

The abundance of WF was significantly related to day of year, salinity, and dissolved oxygen; although these parameters accounted for a small portion of the total variation in the response variable (cumulative $R^2 = 0.061$; Table 3). The estimated coefficients for day of year and salinity were negative (slope estimates = $-8.93E^{-3}$ and $-1.62E^{-3}$) and positive for dissolved oxygen ($7.72E^{-3}$), indicating that WF abundance was maximal in late spring/early summer in low-salinity, highly oxygenated waters (Fig. 5A). Similarly, SF abundance was greatest at the onset of the study in low-salinity, cooler waters (Table 3; Fig. 5B). Specifically, day of year, salinity, and temperature accounted for partial R^2 values of 0.002, 0.102, and 0.010, respectively (cumulative $R^2 = 0.115$), and the coefficients for all explanatory variables were negative (slope estimates = $-4.00E^{-5}$, $-1.46E^{-3}$, and $-1.10E^{-3}$). Examining the effects of salinity on flounder abundances in more detail revealed that habitat usage differed across defined regimes: oligohaline (0.1–5 ppt), mesohaline (6–18 ppt), and polyhaline (19–30 ppt) habitats. The mean abundances of WF across these salinity designations equaled 0.3 ± 1.2 flounder/m² (oligo), 0.2 ± 0.6 flounder/m² (meso), and 0.1 ± 0.3 flounder/m² (poly). Discrepancies in habitat-specific abundances were even greater for juvenile SF, with means equaling 0.07 ± 0.2 flounder/m² (oligo), 0.01 ± 0.06 flounder/m² (meso), and 0.001 ± 0.005 flounder/m² (poly). Sediment characteristics explained 34–40% of the variability in WF and SF abundance for a subset of the sites examined in this study (cumulative $R^2 = 0.160$ and 0.116 , respectively) (Table 3). The ability of sediment composition to predict flounder abundance was mostly attributed to a positive relationship

with total organic carbon (partial $R^2 = 0.101$ and 0.139 ; slope estimates = 1.60E^{-2} and 6.42E^{-2}) (Fig. 5CD).

Flounder Size-structure and Growth

Flounder length-frequency distributions across habitats and years were consistently unimodal in May–June, indicating the presence of one annual cohort per species (Fig. 6). These late spring-early summer cohorts were comprised of post-settlement flounder, with minimum sizes equal to 19 and 25 mm TL for WF and SF, respectively. Intra-specific length-frequency distributions further revealed the persistence of each cohort, which generally broadened in range (particularly for WF) and shifted to larger body sizes (i.e., somatic growth) as the season progressed. However, the rate of increase in WF and SF size was not consistent across months. WF experienced the largest positive shift in length-frequency distributions between May–June (mode increase = 9.0 mm TL), whereas SF had the largest increase in modal length-frequencies between June–July (mode increase = 31.4 mm TL). Conversely, WF maintained relatively consistent sizes between July–August (mode increase = 0.1 mm TL), and the smallest increase in SF lengths occurred in May–June (mode increase = 13.7 mm TL). Inclusively, the size ranges of WF and SF observed in this study were 19–199 TL and 25–250 mm TL, respectively, and all individuals were categorized as age-0 juveniles (Packer et al. 1999; Pereira et al. 1999).

Flounder growth rates ranged between 0.02–0.67 mm/d (WF) and 0.65–2.35 mm/d (SF) (mean: WF = 0.25 ± 0.14 mm/d; SF = 1.39 ± 0.46 mm/d) (Table 1). The growth rates and resulting size-structure of WF were generally consistent across habitats, locations, and years (Table 2; Figs. 4C, 6, and 7). The mean TL of WF in June ranged between 48–51 mm among habitats, and these flounder reached mean body sizes of 66–74 mm by October (Figs. 6 and 7). In contrast, SF growth rates differed significantly as a function of habitat (Table 2; Figs. 4D and 7), such that SF growth was slowest in the rivers (mean = 1.30 ± 0.41 mm/d), and comparable in the lagoons (1.94 ± 0.57 mm/d) and bay (1.77 ± 0.56 mm/d). SF growth rates did not vary annually; however, the habitat-year interaction effect was significant (Table 2). This interaction was due to reduced SF growth in the rivers in 2009 and 2013, and insufficient growth data in the other habitats from 2010–2012 that precluded statistical comparisons (Fig. 4D). Differences in the size-structure of SF among habitats were reflective of their spatially distinct growth rates. In June, for example, the mean size of SF differed markedly across habitats: 58.9 mm (bay), 69.8 mm (river), and 86.3 mm (lagoon) (Figs. 6 and 7). Habitat-specific growth rates of SF subsequently caused further divergences in their mean body sizes by September: 181.5 mm (bay), 128.1 mm (river), and 192.3 mm (lagoon). It is also noteworthy that SF body sizes were relatively consistent among riverine locations, but differed substantially among lagoons (mean TL in September: CP = 250.0 mm, PJ = 197.5 mm, WP = 123.3 mm) (Fig. 7).

WF growth rates varied significantly as function of salinity and conspecific abundance at individual sites (Table 3), with each explanatory variable accounting for a partial R^2 of 0.081 and 0.042, respectively (cumulative $R^2 = 0.123$). Moreover, estimated coefficients for both variables were negative (slope estimates = -5.01E^{-2} and -9.24E^{-2}), indicating that WF growth is optimized in low-salinity waters with reduced numbers of conspecifics (Fig. 5E).

Conversely, SF growth rates were significantly faster in high salinity, warm waters (Table 3; Fig. 5F). Specifically, salinity and temperature accounted for partial R^2 values of 0.250 and 0.103, respectively (cumulative $R^2 = 0.353$), and the coefficients for both explanatory variables were positive (slope estimates = 3.03E^{-2} and 0.138). Lastly, growth rates for both flounder species were independent of localized sediment characteristics (Table 3).

Discussion

Patterns in Flounder Habitat Use

Results from this study affirmed that juvenile (age-0) WF and SF utilize a range of shallow-water habitats, as indicated by their presence in the Narragansett Bay, tidal rivers, and coastal lagoons. These broad habitat associations are mediated by the ability of both flounder species to tolerate extremes in physicochemical conditions. For example, in this study, juvenile WF and SF co-occurred in waters ranging in salinities from < 1 to 32 ppt and temperatures from 12 to 30 °C. Equivalent physiological tolerances and euryhaline/thermal designations have been reported elsewhere for these species (Packer et al. 1999; Pereira et al. 1999). WF and SF are therefore appropriately characterized as habitat generalists during early ontogeny (Able and Kaiser 1994; Able and Fahay 1998).

Despite the evidence for habitat generality, this study revealed that WF and SF were non-uniformly distributed across diverse shallow-water habitats. Most notably, the abundances of both flounder species were significantly higher in the rivers relative to the bay and lagoons. Some inconsistencies in these habitat associations were evident, however, e.g., relatively low WF and SF abundances in the Taunton and Narrow Rivers, respectively. Spatial patterns in WF and SF abundance may reflect location-specific differences in survival rates (Burke et al. 1991; Fairchild et al. 2008), thus resulting in non-uniform habitat distributions. It is more likely, however, that flounder demonstrate active habitat selection during ontogeny. Several field and laboratory investigations indicate that juvenile WF select habitats based on their response to favorable physiochemical water conditions (Meng et al. 2005), substrate composition (Howell et al. 1999; Phelan et al. 2001), presence or absence of macroflora (Goldberg et al. 2002; Meng et al. 2004; Lazzari 2008), predator avoidance (Carlson et al. 2000; Manderson et al. 2004), and abundant prey resources (Stoner et al. 2001, Fairchild et al. 2008). Alternatively, juvenile WF habitat usage may result from adults preferentially spawning in certain locations (e.g., depositional environments; Stoner et al. 2001, Fairchild et al. 2008) and successive early life stages maintaining a high level of site fidelity (Crawford and Carey 1985; Saucerman and Deegan 1991). Conversely, for SF, adult spawning behavior likely has marginal effects on juvenile habitat associations, given that this species broadcast spawns on the continental shelf (Able et al. 1990), after which planktonic eggs and small larvae (< 11 mm TL) passively recruit toward inshore waters (Packer et al. 1999). Instead, transforming SF larvae (11–14 mm TL) in closer proximity to inshore nurseries undergo selective tidal stream transport, such that ingress to preferred habitats results from behaviourally-controlled vertical positioning in the water column (Burke et al. 1998; Hare et al. 2005). Finer-scale habitat selection may occur thereafter by directed movements of post-settlement SF (Burke et al. 1991; Rountree and Able 1992; Szedlmayer and Able 1993).

Discrepancies in flounder abundances among shallow-water habitats may also be an artifact of differing sampling procedures, including variations in water depth and tidal stage. These methodological differences, however, likely have negligible effects on habitat-specific abundances. First, the varying water depths sampled in this study (~1 m difference between bay and rivers/lagoons) are insufficient to alter the size-dependent depth distributions of juvenile WF (Stoner et al. 2001; Taylor 2005). This is affirmed by the consistent size-structure of WF across habitat-types, as determined from monthly length-frequency distributions. Second, a tagging study in Schooner Creek, New Jersey, indicated that juvenile SF (210–254 mm TL) principally moved in the same direction as tidal currents or maintained a high degree of site fidelity, irrespective of the tidal cycle (Szedlmayer and Able 1993). Accordingly, SF abundances measured in the Seekonk and Taunton Rivers ($\pm$ 2 hr of low tide) may be underestimated or unaffected by the timing of the survey. If the former is correct, then discrepancies in SF abundances among habitats may actually be greater than reported here. Third, given the consistency in gear-type used in this study and the general similarities in substrate composition among habitats (silts-clays to sands), seine efficiencies are presumably constant across all the surveys (Steele et al. 2006). These collective arguments imply that spatial patterns in WF and SF abundances in shallow waters are the result of intra-specific habitat selection and not an artifact of sampling methodology.

Maximal WF and SF abundances occurred during the late spring to mid-summer (May–July for rivers and lagoons; June–July for bay), and this temporal pattern was consistent across years. The length-frequency distributions for these initial months were comprised exclusively of age-0, post-settlement flounder, and represented single intra-specific cohorts. The persistence of unimodal size-distributions for both WF and SF throughout the summer and early fall indicated that there were few additional recruits to the population and a continued absence of age-1+ flounder in the shallow-water habitats. The precipitous decline in flounder abundances during this time period also coincided with seasonal decreases in water temperature. Specifically, WF and SF abundances in the late summer and early fall were the lowest measured in this study, and typically occurred when water temperatures were $< 15^{\circ}\text{C}$. The relative absence of juvenile flounder during this time period denotes the onset of seasonal migrations and the subsequent overwintering in deeper estuarine or offshore waters. Previous studies also document temperature-sensitive distributions of juvenile WF and SF, and further indicate that decreasing temperature is a causative factor initiating their seasonal migrations (Pearcy 1962; McCracken 1963; Rountree and Able 1992; Szedlmayer and Able 1993; Able and Kaiser 1994; Bell 2009).

Factors Affecting Flounder Habitat Use

Juvenile WF and SF habitat usage was responsive to several abiotic factors that varied among habitat-types. The abundances of both flounder species were inversely related to salinity, and densities were markedly higher in oligo- relative to meso- and polyhaline habitats. Juvenile WF and SF have broad salinity tolerances (1–35 ppt; Packer et al. 1999; Pereira et al. 1999), yet despite this plasticity, prior research indicates these species are more ubiquitous in polyhaline environments (> 18 ppt; Able and Fahay 1998). In this study, juvenile WF and SF principally occupied lower salinity waters (oligo- and mesohaline waters of rivers), and comparable habitat associations occur for other flatfish species

(Kerstan 1991; Armstrong 1997; Martino and Able 2003; Nñez-James et al. 2009; Lowe et al. 2011; Le Pichon et al. 2014). The usage of low-salinity habitats by juvenile WF and SF may provide effective refugia from predation (Kerstan 1991; Meng et al. 2002; Meng et al. 2005). For example, in the upper reaches of the Navesink River/Sand Hook Bay estuary (< 20 ppt), New Jersey, newly settled WF benefited from reduced predation risk owing to the absence of piscivorous fish, e.g., striped searobin, *Prionotus evolans* (Manderson et al. 2006). Juvenile WF and SF selection of low-salinity environments may also be a strategy to reduce competition with fishes and macro-invertebrates that have similar functional roles in estuarine and marine ecosystems (Burke et al. 1991; Kerstan 1991; Armstrong 1997; Martino and Able 2003).

Spatial and temporal variations in dissolved oxygen concentrations and water temperature independently affected juvenile WF and SF habitat associations. The abundance of WF declined significantly at lower oxygen levels, experiencing a 2- to 13-fold decrease at concentrations < 4 mg/L and < 2 mg/L, respectively. Previous studies document a negative correlation between juvenile WF densities and dissolved oxygen (Meng et al. 2005), and early-stage WF avoid moderately hypoxic waters (< 2.0 mg/L; Stierhoff et al. 2006). Comparatively, in this study, the distribution of juvenile SF was unrelated to dissolved oxygen concentrations, and reportedly this species demonstrates avoidance behavior once conditions approach anoxia (< 1.0 mg/L; Tyler 2004). Laboratory investigations further confirm that juvenile SF are more tolerant to low oxygen concentrations relative to comparatively-sized WF (55–90 mm and 35–67 mm standard length, respectively), as evaluated by intra-specific growth and feeding rates (Stierhoff et al. 2006). The abundance of juvenile SF was negatively correlated with water temperature, and this relationship was predominantly governed by seasonal patterns in the Seekonk River. Specifically, SF catches at this location were greatest in May–June (mean abundance ~ 0.1 flounder/m²), coinciding with relatively low temperatures (21°C). SF abundance then declined throughout July–August (mean abundance ~ 0.01 flounder/m²), concomitant with increasing water temperatures (mean temperature ~ 25°C). Juvenile SF have a broad thermal tolerance range (2–30°C), but juvenile growth performance is maximized at 22°C (Howson 2000). The correlation between maximal SF abundance in the Seekonk River at the onset of this study may be a behavioral response, such that SF selected these higher quality habitats because they afford maximum growth potential. As discussed in the subsequent section, however, other physiochemical properties of the tidal rivers (low salinity) may suppress SF growth.

Sediment composition often affects the spatial distribution and cumulative abundance of flatfish owing to their proximal contact with the substrate. In this study, juvenile WF and SF abundances were positively related to sediment organic content, as reported elsewhere (Phelan et al. 2001; Stoner et al. 2001; Goldberg et al. 2002). Sediments rich in organic carbon typically support an abundance of benthic infauna and epifauna (Lopez and Levinton 1987; Shaw and Jenkins 1992; Snelgrove and Butman 1994), including potentially important prey for post-settlement WF and SF (e.g., polychaetes, nematodes, harpacticoid copepods, amphipods, mysids, crangonid shrimp; Stehlik and Meise 2000; Latour et al. 2008). Moreover, previous field and laboratory studies indicate that both flounder species prefer habitats with sufficiently high food resources (Burke 1995; Stoner et al. 2001; Fairchild et al. 2008). The abundances of juvenile WF and SF in this study were also positively

correlated with sediment grain size (i.e., negative relationship with % silt-clay content). Numerous studies report that juvenile SF preferentially select sandy habitats (Burke et al. 1991; Keefe and Able 1994), although a few contradictory studies exist (Able and Kaiser 1994). Substrate preferences for post-settlement WF are size-dependent, with larger juveniles (> 40 mm standard length) selecting coarser-grain sediments (Phelan et al. 2001). The affinity of WF and SF for coarser sands is attributed to their improved burying capabilities in this substrate-type (Burke et al. 1991; Phelan et al. 2001), which may be an effective strategy to minimize predation risk (Tanda 1990).

Flounder Growth and Factors Affecting Habitat Quality

There is a general consensus that rapid growth and the attainment of larger body sizes increases the survival of early-stage fish. To this end, estimates of juvenile fish growth are often used as an indicator of habitat quality, such that valued habitats are those that maximize growth potential (Phelan et al. 2000; Sogard 1992; Le Pape et al. 2003; Gilliers et al. 2006). Defining habitat quality on the basis of growth, however, is complicated by fish movement and the possibility of exchange among different habitats (Le Pape et al. 2003; Gilliers et al. 2006; Taylor et al. 2007). In this regard, juvenile flatfish are an ideal subject because most species exhibit high site fidelity immediately following settlement (e.g., WF; Saucerman and Deegan 1991; Curran and Able 2002) or after movements into first-year nurseries (e.g., SF; Rountree and Able 1992; Szedlmayer and Able 1993). In Waquoit Bay, Massachusetts, for example, Saucerman and Deegan (1991) verified that 90–98% of marked juvenile WF (29–80 mm TL) were recaptured within 100 m of their release site ($n = 329$; days at liberty = 2–39 days). Moreover, in the Great Bay-Little Egg Harbor estuarine system, New Jersey, Rountree and Able (1992) determined that 98% of post-settlement SF (188–299 mm TL) were recaptured in the same marsh creek in which they were released ($n = 63$; days at liberty = 12–63 days). Therefore, in this study, it was concluded that the spatial distances among bay, riverine, and lagoon locations were adequate to minimize or negate flounder exchange across habitats, thus enabling a comparative assessment of growth rates.

Juvenile SF growth rates, assessed from May/June to September, were significantly reduced in the tidal rivers relative to the bay and lagoons. It is possible that SF growth was underestimated in the rivers if larger individuals (> 200 mm TL) emigrated from this habitat during the late summer and early fall (September and October), as reported elsewhere for this species (Rountree and Able 1992; Szedlmayer et al. 1992). Accordingly, for each habitat-type, SF growth rates were reevaluated only through August; presumably before the onset of juvenile SF seasonal migrations (Szedlmayer et al. 1992). This reanalysis yielded similar growth trends, such that SF growth rates were lower in the tidal rivers (1.00 ± 0.24 mm/d), and comparable between the lagoons and bay (1.39 ± 0.54 mm/d and 1.68 ± 0.77 mm/d, respectively). Habitat-related differences in growth were mostly attributed to the lower salinities in the Seekonk and Taunton Rivers. Specifically, juvenile SF inhabiting oligohaline waters have increased osmoregulatory metabolic expenditures, thereby reducing energy for somatic development (Howson 2000; Boeuf and Payan 2001; Stierhoff et al. 2006). Moreover, exposure to low salinities may adversely affect SF condition due to its simultaneous effect on swimming behavior and feeding, digestion, and absorption efficiencies of consumed prey (Boeuf and Payan 2001). Previous studies document the

reduced growth of paralichthid flatfish in low salinities, including SF (Howson 2000; Stierhoff et al. 2006) and the Brazilian flounder *Paralichthys orbignyanus* (Sampaio and Bianchini 2002), and optimal growth for juvenile SF occurs at 24.5 ppt (Howson 2000). Results from this study further revealed the SF growth rates were positively related to temperature, which is consistent with prior studies (Peters and Angelovic 1971; Klein-MacPhee 1979); although exceedingly high temperatures ($> 30^{\circ}\text{C}$) may depress SF growth because a disproportionate amount of energy is devoted to elevated metabolism (Howson 2000; Stierhoff et al. 2006).

Juvenile WF growth rates were consistent across habitat-types and further demonstrated a slight inverse relationship with salinity, i.e., higher growth in oligohaline habitats. Prior studies also purport that the growth of WF and a congener species, European plaice, *Pleuronectes platessa*, increased at lower salinities (Manderson et al. 2002; Meise et al. 2003; Augley et al. 2008); however, these studies only monitored flounder growth within a narrow salinity range ($\sim 20\text{--}35$ ppt). More likely, WF growth is maximized at intermediary salinities that correspond to osmotic equilibrium and reduced standard metabolic rates ($10\text{--}20$ ppt; Frame 1973; Boeuf and Payan 2001). In this study, the accelerated growth of WF in low salinities may involve the interactive effects of numerous physiochemical and biotic variables that affect fish behavior and physiology (Boeuf and Payan 2001), e.g., optimal temperatures and prey resources in some oligohaline habitats may enhance flounder growth, and thus, compensate for osmoregulatory stresses imposed by lower salinities (Burke et al. 1991; Howson 2000).

Juvenile WF growth rates were also inversely related to the density of conspecifics. There is evidence supporting (Shaw and Jenkins 1992; Nash et al. 1994) and refuting (Hagen and Quinn 1991; Rijnsdrop and Van Beek 1991; Van der Veer and Witte 1993; Rogers 1994) the existence of density-dependent growth for several species of flatfish. Specific to WF, density-dependent growth was detected in populations in Narragansett Bay (DeLong et al. 2001) and the Niantic River, Connecticut (DNC 2003). Conversely, there was no significant relationship between growth rate and WF abundance in several New Jersey estuaries (Sogard et al. 2001; Meise et al. 2003). In most situations, it is unlikely that flounder densities reach levels whereby interference or exploitative competition causes the limitation of food resources; hence negatively affecting growth of conspecifics. The feeding ecology of most flatfish is generally regarded as insufficient to reduce prey abundance to levels that are limiting to fish growth (Kuipers 1977; Shaw and Jenkins 1992). However, Modin and Pihl (1994) determined that competitive interactions underlying density-dependent growth in juvenile plaice occurred when extremely high densities were attained (~ 10 flounder/ m^2), and comparable peak abundances of WF were observed in this study, albeit infrequently.

In this study, juvenile WF and SF abundances were significantly higher in certain rivers, despite these habitats not providing any detectable advantage in intra-specific growth rates. It follows that the preference of both flounder species for these riverine habitats was not a function of their respective growth performance, but rather some alternative habitat-specific factor. As previously discussed, the low saline conditions of the rivers (particularly SR and TR) exert a metabolic cost to juvenile flounder to the detriment of their somatic growth (Howson 2000; Boeuf and Payan 2001; Stierhoff et al. 2006). Occupying these oligo- and

mesohaline waters, however, may afford the flounder effective refugia from predation (Le Pape et al. 2003; Martino and Able 2003); thus, increasing survival rates during sensitive early life history stages. Prior studies also purport that habitat selection by juvenile fishes is affected by their intrinsic risk to predation, such that the degree of habitat use is directly correlated with the availability of predator refuge, irrespective of site-specific growth rates (Halpin 2000; Laegdsgaard and Johnson 2001; Taylor et al. 2007).

Functional Significance of Southern New England Nurseries

The functional significance of nurseries is predicated on the habitat's relative contribution of recruits to adult populations. This "nursery-role concept", in turn, is affected by four principal aspects of the habitat, as it relates to the species of interest: (1) abundance, (2) growth, (3) juvenile survival, and (4) migrations to adult habitats (Beck et al. 2001). This study evaluated the abundance and growth of juvenile WF and SF in southern New England shallow-water habitats in an effort to better understand their inherent use and quality. To effectively assess the functional significance of these habitats as WF and SF nurseries, a synoptic examination of the biological indicators is warranted.

The peak abundance of WF in this study, reported as a maximum monthly mean (4.9 flounder/m²), was consistent with, or exceeded, other estimates within the species geographic distribution. This includes nurseries in New Hampshire (maximum abundance = 0.03 flounder/m²; Fairchild et al. 2008), Connecticut (0.03–2.6 flounder/m²; Pearcy 1962; Carlson et al. 2000; Goldberg et al. 2002), and New Jersey (0.06–2.5 flounder/m²; Curran and Able 2002; Goldberg et al. 2002; Taylor 2005). Estimates of juvenile SF abundance (maximum monthly mean = 0.55 flounder/m²) also agreed with or exceeded the densities of conspecifics in southerly-located Middle and South Atlantic Bight nurseries, including New Jersey (maximum abundance = 0.7 flounder/m²; Rountree and Able 1992), Virginia (0.21 flounder/m²; Weinstein and Brooks 1983), and North Carolina (0.01 flounder/m²; Walsh et al. 1999). These cumulative results strongly suggest that southern New England inshore areas currently serve as important nursery habitat for juvenile WF and SF.

Estimated growth rates of WF in this study (0.02–0.67 mm/d) were consistent with previous measurements from several mid-Atlantic and southern New England estuaries. A series of short-term field caging experiments in Narragansett Bay revealed that juvenile WF grew at rates between 0.22 and 0.60 mm/d during the early- to mid-summer (Meng et al. 2001). Field enclosure studies estimated WF growth rates of –0.03–0.21 mm/d and 0.00–0.88 mm/d in the Hammonasset River, Connecticut (Phelan et al. 2000) and Navesink River/Sandy Hook Bay (Manderson et al. 2002), respectively. Also in the Navesink River/Sandy Hook Bay system, otolith increment analysis revealed that juvenile WF grew at highly variable rates (0.25–1.91 mm/d; Meise et al. 2003). Juvenile SF growth rates in this study (0.65–2.35 mm/d) were similar to conspecifics in New Jersey estuaries (1.3–1.9 mm/d; Rountree and Able 1992; Szedlmayer et al. 1992), and exceeded the growth of post-settlement SF in North Carolina waters (0.21–0.50 mm/d; Necaie et al. 2005), as determined from the decomposition of length-frequency distributions, tag recaptures, and field enclosure experiments. The growth performance of juvenile WF and SF in this study,

coupled with abundance estimates, reinforces the supposition that southern New England nurseries may be functionally important to both flounder species.

Finally, to the knowledge of the authors, there are no prior, definitive records of age-0, post-settlement SF in southern New England inshore waters. Extensive spawning and the development of early-stage SF larvae (1–10 mm TL) occur in contiguous continental shelf waters (Able et al. 1990), yet historically juvenile SF failed to recruit to the immediate nurseries. From 1989–1990, Keller et al. (1999) conducted a seasonal ichthyoplankton survey in Narragansett Bay and collected SF eggs and larvae from February–June and September–December, respectively; although both early life stages had low maximum densities (19.5 and 1.4 eggs and larvae/100 m³, respectively) and comprised a minor component of the total catch (< 0.01%). In June–July 2002, Meng et al. (2005) documented the rare occurrence of SF in a beam-trawl survey conducted in Narragansett Bay (0.2% of total catch), but the absence of length information for these flounder precluded age-class estimates. Thus, prior to this study, the northern extent of the juvenile SF distribution was presumably New Jersey, with few occurrences in Connecticut estuaries and Long Island Sound (Able and Kaiser 1994).

Several hypotheses may explain the recent abundance of juvenile SF in southern New England inshore habitats. First, the adult spawning stock of SF has shifted its distribution northward over the past four decades in response to climate change (Nye et al. 2009) and/or a reduction in local fishing pressure (Bell et al. 2014). A larger reproductive population of SF in New England shelf waters potentially augments the supply of larvae to proximate nursery areas. Second, early-stage SF experience intense mortality when water temperatures decrease below 2 °C (Malloy and Targett 1991; Szedlmayer et al. 1992); and this thermal sensitivity may delineate the northern geographical limit of the juveniles (Able et al. 1990). Northwest Atlantic coastal waters have significantly increased in temperature over the last several decades (Collie et al. 2008; Smith et al. 2010), and current winter temperatures in the Narragansett Bay and adjacent waters may no longer decrease below the lower thermal tolerance limit of early-stage SF (Taylor 2003; Bell 2012). Accordingly, warmer winter temperatures at northern latitudes have likely caused a concomitant increase in the over-wintering survival of age-0 SF spawned the previous fall. Future research should focus on the ecological role of juvenile SF in southern New England inshore habitats (e.g., putative biotic interactions with other fish and invertebrates species), and further explore the potential contributions of these nurseries to year-class strength and recruitment to the adult population.

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Fig. 1.

Map of the three “habitats” examined in this study, including the Narragansett Bay, tidal rivers and coastal lagoons. For analysis purposes, Narragansett Bay was partitioned into three “locations”: upper Bay (UB), mid-Bay (MB), and lower Bay (LB). Tidal river “locations” include the Seekonk River (SR), Taunton River (TR), and Narrow River (NR), and coastal lagoon “locations” include the Winnapaug Pond (WP), Quonochontaug Pond (QP), Charlestown Pond (CP), and Point Judith Pond (PJ). Individual points demarcate sampling “sites” within each location

Fig. 2. Monthly water temperature (°C) (A–C), salinity (ppt) (D–F), and dissolved oxygen (mg/L) (G–I) in the Narragansett Bay, tidal rivers, and coastal lagoons. Data points represent location averages across years (2009–2013), and error bars denote +1 standard error. Location abbreviations are defined in Fig. 1. Note that the y-axis is scaled differently for salinity data

Fig. 3. Monthly abundance (flounder/m²) of winter flounder (WF) and summer flounder (SF) in the Narragansett Bay (A–B), tidal rivers (C–D), and coastal lagoons (E–F). Data points represent location averages across years (2009–2013), and error bars denote +1 standard error. Location abbreviations are defined in Fig. 1

Fig. 4. Mean abundance (flounder/m²) (A–B) and growth rate (mm/d) (C–D) of winter flounder (WF) and summer flounder (SF) in relation to habitat (River, Lagoon, Bay) and year (2009–2013). Error bars denote +1 standard error, and “N” represents no data

Fig. 5. Abundance (flounder/m²) of winter flounder (WF) and summer flounder (SF) in relation to salinity (ppt) (A–B), and total organic carbon (TOC; % dry weight) (C–D). Data points represent monthly means for individual years (A–B) or averages across sites and years, with error bars denoting ± 1 standard error (C–D). WF and SF growth rates (mm/d) in relation to salinity (E–F). Least-squares linear regressions were fit to data sets compiled across habitats

Fig. 6. Length-frequency (mm total length, TL) distributions of winter flounder and summer flounder collected from Narragansett Bay, tidal rivers, and coastal lagoons. Abundances (flounder/m²) were compiled from monthly catch data (May–October) and summed across years (2009–2013). Note that the Bay was not sampled in May

Fig. 7.

Mean total length (TL; mm) of winter flounder (WF) and summer flounder (SF) across months in the Narragansett Bay (A–B), tidal rivers (C–D), and coastal lagoons (E–F). Data points represent location averages across years (2009–2013), and error bars denote +1 standard error. Location abbreviations are defined in Fig. 1

Table 1

Summary of environmental and biological characteristics across habitats and locations. Environmental characteristics include water temperature (°C), salinity (ppt), dissolved oxygen (mg/L), sediment grain size (% silt-clay), and sediment total organic carbon (% dry weight). Biological characteristics include winter flounder (WF) and summer flounder (SF) percent frequency of occurrence (% *FO*) in seine hauls, abundance (flounder/m²), and growth rate (mm/d). Location abbreviations are defined in Fig. 1

	Habitat									
	Narragansett Bay					Tidal Rivers				
	UB	MB	LB	NR	SR	TR	CP	PJ	QP	WP
Environmental characteristics										
Temperature	21.7 (15.1–27.2)	21.5 (15.8–26.9)	20.5 (16.4–24.4)	20.5 (13.3–26.2)	23.3 (18.1–28.0)	23.3 (18.1–28.7)	21.2 (12.0–29.1)	21.0 (14.9–25.9)	20.4 (13.6–27.1)	20.1 (13.2–26.3)
Salinity	24.2 (13.5–28.9)	26.7 (19.0–30.4)	28.3 (25.1–32.4)	23.8 (14.3–31.3)	6.6 (2.4–12.5)	9.3 (2.8–16.0)	27.3 (25.2–30.4)	27.3 (20.4–29.8)	28.4 (22.4–31.4)	28.0 (17.1–31.2)
Dissolved oxygen	6.9 (4.4–9.4)	6.7 (2.4–8.9)	6.8 (5.6–8.7)	7.8 (5.3–10.4)	8.2 (4.7–11.4)	7.2 (5.1–9.5)	8.3 (6.8–11.5)	8.4 (6.6–12.9)	7.9 (6.4–9.9)	8.4 (6.4–11.1)
Grain size	29.6 (12.3–46.6)	37.9 (23.4–57.0)	31.4 (9.1–49.0)	—	47.6 (43.0–56.3)	48.0 (44.3–54.4)	—	—	—	—
Total organic carbon	1.8 (1.3–2.2)	2.7 (0.9–4.5)	1.3 (0.3–2.3)	—	5.5 (3.6–6.9)	3.0 (2.9–3.1)	—	—	—	—
Biological characteristics										
WF % <i>FO</i>	56.8	64.0	28.0	79.3	91.9	61.2	68.4	55.0	86.2	77.0
WF abundance	0.039 ± 0.075	0.050 ± 0.089	0.008 ± 0.033	0.378 ± 0.615	0.536 ± 1.428	0.040 ± 0.099	0.127 ± 0.255	0.057 ± 0.127	0.185 ± 0.281	0.213 ± 0.353
WF growth rate	0.15 ± 0.08	0.14 ± 0.07	0.34 ± 0.08	0.21 ± 0.17	0.27 ± 0.11	0.36 ± 0.19	0.21 ± 0.09	0.26 ± 0.14	0.30 ± 0.11	0.21 ± 0.10
SF % <i>FO</i>	1.8	14.1	0.0	3.8	69.7	49.0	13.2	20.0	5.8	13.0
SF abundance	0.0001 ± 0.002	0.001 ± 0.003	0.0 ± 0.0	0.001 ± 0.005	0.072 ± 0.201	0.014 ± 0.058	0.002 ± 0.006	0.001 ± 0.004	0.001 ± 0.003	0.003 ± 0.014
SF growth rate	—	1.77 ± 0.56	—	—	1.23 ± 0.30	1.49 ± 0.62	2.35 ± 0.0	1.54 ± 0.0	—	—

Note: Environmental and abundance data represent monthly “location” means averaged across years (ranges in parentheses and ±1 standard deviations are also presented). Growth data represent “site” means averaged across years (±1 standard deviation)

Table 2

Summary statistics for Chi-square test of independence and two-way analysis of variance models used to examine winter flounder (WF) and summer flounder (SF) frequency of occurrence (June–August; %FO), mean monthly abundance (June–August; flounder/m²) and growth rates (mm/d) as a function of habitat (Bay, River, Lagoon) and year (2009–2013). Results of Bonferroni corrections and Ryan’s Q multiple comparisons tests that contrast %FO, abundance, and growth values across 3 and 5 levels of habitat and year, respectively, are reported

Factor	Habitat		Year		Habitat × Year		Bonferroni correction/ Ryan's Q
	χ ² or F (df)	p	χ ² or F (df)	p	F (df)	p	
Winter flounder							
% FO	38.4 (2, 663)	< 0.0001	12.2 (4, 663)	< 0.05	—	—	River ~ Lagoon > Bay 2012 > 2010
Abundance	18.6 (2, 663)	< 0.0001	1.33 (4, 663)	0.258	1.60 (8, 663)	0.120	River > Lagoon > Bay
Growth	1.04 (2, 114)	0.359	0.52 (4, 114)	0.720	0.50 (8, 114)	0.857	—
Summer flounder							
% FO	126.1 (2, 663)	< 0.0001	27.7 (4, 663)	< 0.0001	—	—	River > Lagoon > Bay 2009 > 2010–2013
Abundance	13.0 (2, 663)	< 0.0001	7.76 (4, 663)	< 0.0001	6.36 (8, 663)	< 0.0001	River > Lagoon ~ Bay 2009 > 2010–2013
Growth	7.78 (2, 22)	< 0.01	0.88 (4, 22)	0.499	7.91 (2, 22)	< 0.005	Lagoon ~ Bay > River

Note: Significance for abundance analyses was determined by comparing p -values with alpha values obtained from Levene’s Test of Homogeneity of Variance ($p = 0.004$ and 0.04 for WF and SF abundance, respectively)

Table 3

Summary statistics for small-sample, bias-corrected Akaike's Information Criterion (AIC_c) and Akaike's weights (w_i) used to select optimal multivariate regression models. Regression analyses were used to predict winter flounder (WF) and summer flounder abundance (A ; flounder/ m^2) and growth rate (G ; mm/d) as a function of day of year (Day ; abundance analysis only), water temperature ($Temp$; $^{\circ}C$), salinity (Sal ; ppt), dissolved oxygen (DO ; mg/L), sediment percent silt-clay composition ($Silt-clay$), sediment total organic carbon (TOC ; % dry wt), and conspecific abundance ($Abund$; growth analysis only)

Species/ Response variable	Optimal model	F (df)	p	R^2	AIC_c	w_i
Winter flounder						
Abundance	$L\pi(A + 1) = 0.266 - (8.93E^{-4} \times Day) - (1.62E^{-3} \times Sal) + (7.72E^{-3} \times DO)$	20.47 (3, 949)	< 0.0001	0.061	-2980.7	0.34
Abundance (sediment effect)	$L\pi(A + 1) = 1.37E^{-2} - (3.12E^{-3} \times Silt-clay) + (6.42E^{-2} \times TOC)$	58.85 (2, 620)	< 0.0001	0.160	-	-
Growth	$G = 0.381 - (5.01E^{-3} \times Sal) - (9.24E^{-2} \times Abund_{WF})$	7.83 (2, 114)	< 0.001	0.123	-470.8	0.34
Growth (sediment effect)	$G = 0.383 - (4.94E^{-3} \times Silt-clay) + (2.45E^{-2} \times TOC)$	2.91 (2, 41)	0.066	0.130	-	-
Summer flounder						
Abundance	$L\pi(A + 1) = 7.25E^{-2} - (4.00E^{-5} \times Day) - (1.10E^{-3} \times Temp) - (1.46E^{-3} \times Sal)$	40.82 (3, 949)	< 0.0001	0.115	-6391.6	0.32
Abundance (sediment effect)	$L\pi(A + 1) = -2.15E^{-3} - (7.75E^{-4} \times Silt-clay) + (1.60E^{-2} \times TOC)$	40.63 (2, 620)	< 0.0001	0.116	-	-
Growth	$G = -2.071 + (3.03E^{-2} \times Sal) + (0.138 \times Temp)$	5.47 (2, 22)	< 0.05	0.353	-40.0	0.33
Growth (sediment effect)	$G = 1.659 - (1.67E^{-3} \times Silt-clay) + (5.80E^{-2} \times TOC)$	0.96 (2, 20)	0.403	0.096	-	-