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Blue Crab (*Callinectes sapidus*) Population Structure in Southern New England Tidal Rivers: Patterns of Shallow-Water, Unvegetated Habitat Use and Quality

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Abstract

The blue crab, *Callinectes sapidus*, has a broad geographic distribution encompassing coastal waters of the eastern USA and Gulf of Mexico, but intraspecific patterns of habitat use and quality are lacking at northern latitudes. This study examined the population structure of blue crabs in the Seekonk and Taunton Rivers (Rhode Island and Massachusetts, USA): two tidally influenced rivers contiguous with the Narragansett Bay Estuary and dominated by shallow-water, unvegetated habitats. Crabs were collected fortnightly from May through August (2012–2016), and abundance- and growth-based metrics were used to assess riverine habitat use and quality. These metrics were also analyzed with respect to crab life history traits and in situ abiotic conditions to elucidate patterns of habitat selection throughout ontogeny. Crabs measuring 8 to 185 mm carapace width (CW; $n = 2577$) were collected, and two distinct age classes occupied the rivers during the spring and summer (maximum abundance ~ 5 crabs/10 m^2). The younger age-0+ cohort was numerically dominant (~ 88% of total catch) and comprised of male and juvenile female crabs (mean ± SD abundance = 0.28 ± 0.26 males/10 m^2 and 0.14 ± 0.12 juvenile females/10 m^2). Males accounted for the majority of age-1+ crabs (~ 83% of cohort), yet sexually mature females were also observed (9% of cohort; mean ± SD abundance = 0.04 ± 0.06 adult females/100 m^2; size at 50% maturity ± 95 CI = 129.0 ± 0.2 mm CW). Crabs were spatially segregated along a salinity gradient with males and juvenile females prevalent in oligohaline waters (upper river salinity ~ 5 ppt) and adult females mainly concentrating in higher salinity areas (mid- and lower-river salinity ~ 11–21 ppt). Seasonal and interannual patterns in crab abundance also differed by sex and ontogeny. Peak catches of males and juvenile females occurred during the spring and mid-summer, and annual abundances were positively related to dissolved oxygen (DO) concentrations. In contrast, mature females were most abundant during August and years with elevated water temperatures. The absolute and relative growth rates of juvenile crabs equaled 0.9 ± 0.3 mm CW/day and 1.5 ± 0.6% CW/day, respectively, and were directly related to DO levels. A synoptic examination of crab abundance and growth across a broad geographic range indicated that shallow-water, unvegetated habitats presently serve as functional nurseries in southern New England tidal rivers.

Keywords Blue crab · *Callinectes sapidus* · Abundance · Growth · Maturity · Shallow-water, unvegetated nursery habitat · Tidal river · Salinity · Dissolved oxygen

Introduction

Estuaries are composed of mosaics of interconnected habitats that serve as nurseries for juvenile fishes and invertebrates (Peterson 2003; Sheaves 2009; Fulford et al. 2011). The nursery value of discrete habitat types within an estuarine complex is variable, however, and depends on their respective quality and availability. The overall functioning and quality of a nursery is determined by each habitat's relative contribution of recruits to the adult population (Beck et al. 2001), and formal conceptualizations of nursery habitats have been proposed and empirically examined (Lefcheck et al. 2019 and references therein). There is a general consensus that survival and recruitment success of estuarine fauna are closely associated with rates of somatic growth and development during early ontogeny (Anderson 1988), and the abundance of juvenile fishes and invertebrates is higher in nursery habitats that optimize intraspecific growth performance (Heck Jr. et al.

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2003; Minello et al. 2003; Sheridan and Hays 2003; Igulu et al. 2014). Accordingly, the functional value of nursery habitats is quantifiable through direct estimates of juvenile growth and abundance, operating on the premise that high-quality nurseries are those in which these metrics are maximized (Beck et al. 2001; Lefcheck et al. 2019).

Previous studies that used abundance- and growth-based metrics to evaluate nursery value indicate that structurally complex habitats in coastal environments, e.g., seagrass beds, salt marshes, mangroves, and biogenic reefs, are critical nurseries for juvenile fishes and invertebrates (Nagelkerken et al. 2000; Heck Jr. et al. 2003; Minello et al. 2003; McDevitt-Irwin et al. 2016). These specific habitat types are spatially limited, however (Orth and van Montfrans 1990; Lefcheck et al. 2019), and have further experienced significant declines due to anthropogenic insults (Lotze et al. 2006; Waycott et al. 2009; Polidoro et al. 2010; Ganju et al. 2017; Watson et al. 2017). Shallow-water, unvegetated habitats, in contrast, are spatially and temporally ubiquitous (Rakocinski et al. 2003; Lipcius et al. 2005), and mounting evidence suggests this habitat type functions as a concurrent or alternative nursery for estuarine fauna (Rozas and Hackney 1984; Ruiz et al. 1993; Dittel et al. 1995; Hines and Ruiz 1995; James et al. 2019). Further, oligo-mesohaline estuarine environments, which are typically shallow, non-structured habitats, are particularly valued because of their optimal physicochemical conditions (Ross 2003), reduced predator densities (Currin et al. 1984; Miller et al. 1985; Posey et al. 2005), and abundant prey resources (Burke 1995; Seitz et al. 2005; Taylor and Gervasi 2017), which collectively increase the growth, condition, and survival of juveniles (Ross 2003; Lipcius et al. 2005; Seitz et al. 2005). It is also noteworthy that evaluating nursery quality for singular habitat units is problematic for mobile fauna that undergo ontogenetic shifts in habitat use (Gillanders et al. 2003). As such, compiling data on the functional significance of multiple habitat types, i.e., seascape nursery concept, is necessary for transient species across their biogeographic ranges (Nagelkerken et al. 2015).

The blue crab, *Callinectes sapidus* Rathbun (Family Portunidae), is a decapod crustacean with a broad distribution extending from Cape Cod (Massachusetts, MA, USA) to Argentina (Millikin and Williams 1984; Johnson 2015). Along the eastern and southern USA, blue crabs are primarily concentrated in the Middle and South Atlantic Bight (Delaware to Florida) and Gulf of Mexico, and their complex life history has been extensively studied in these geographic regions (Kennedy and Cronin 2007 and references therein). The blue crab life cycle encompasses numerous larval (zoeae), post-larval (megalopae), and juvenile phases punctuated by an abrupt transition to adults (Millikin and Williams 1984). Throughout this complex life cycle, patterns of habitat use vary by sex and ontogenetic stage. For example, after mating in low-salinity waters, adult female crabs migrate to the polyhaline zones of lower estuaries to produce and incubate eggs prior to spawning (Aguilar et al. 2005). Subsequent to spawning, planktonic larvae are advected offshore to the continental shelf (Epifanio 2007), after which early-stage crabs in the megalopal stage return inshore and ingress into estuaries (Epifanio 2007; Lipcius et al. 2007). Fine-scale habitat selection, i.e., dispersion into shallow-water nurseries, occurs thereafter by directed movements of metamorphosed, juvenile crabs (initially 3 mm carapace width, CW) (Lipcius et al. 2007). Juvenile crabs utilize a diverse array of nurseries throughout ontogeny, including initial residency in structurally complex habitats for individuals < 12 to 25 mm CW (Sogard and Able 1991; Heck et al. 2003; Shervette et al. 2011), followed by juveniles > 25 mm CW migrating to secondary unvegetated nurseries that are low-salinity, soft-bottom habitats (Lipcius et al. 2005; Posey et al. 2005). Blue crabs remain in secondary nurseries until attaining sexual maturity at ~ 100–200 mm CW (age-at-maturity and longevity ~ 1–2 years and 3 years, respectively, depending on phenology and geographic location) (Hines 2007). Mating commences immediately after the female pubertal-terminal molt (Jivoff et al. 2007), after which females undergo the directional reproductive migration described above, and adult male crabs remain dispersed in upper estuarine habitats (Hines 2007).

In contrast to the Middle-South Atlantic and Gulf of Mexico, there is a paucity of bio-ecological information on blue crabs at higher latitudes. Research focused on crab populations at the northern extent of their geographic range is warranted, however, given the species' ecological and economic significance (Hines 2007; Kennedy et al. 2007). The objective of this investigation was to examine the population structure of blue crabs collected from the Seekonk and Taunton Rivers (Rhode Island, RI, and MA, USA): two tidally influenced rivers contiguous with the Narragansett Bay Estuary and dominated by shallow, unvegetated habitats. This report is an extension of ongoing efforts to evaluate the role of tidal rivers as juvenile nursery habitat in southern New England (Taylor et al. 2016; Taylor and Gervasi 2017). Moreover, unvegetated, soft-substrate habitats have been previously ascribed as critical nurseries for juvenile blue crabs in southerly locations, but it is unknown if this habitat type maintains the same functional importance at northern latitudes. The current study, therefore, sought to: (1) measure the abundance, size-structure, and growth of blue crabs in the tidal rivers and use these metrics to assess habitat use and quality; (2) analyze abundance- and growth-based metrics relative to crab life history traits, e.g., sex, maturity, and ontogeny, and in situ abiotic factors to elucidate patterns of habitat selection; and (3) perform a synoptic examination of blue crab abundance and growth across a broad geographic range to ascertain the functional significance of southern New England tidal rivers as juvenile nurseries.

Methods

Study Area and Field Sampling

The Narragansett Bay is a southern New England estuary that adjoins RI Sound at its mouth and extends northward into RI and MA (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. Two tidal rivers, the Seekonk River (SR) and Taunton River (TR), were the subject of this investigation (Fig. 1). The SR and TR are located in the northwest and northeast portions of the main estuary with total areas equal to 2.7 and 10.2 km^2, respectively, and the mean depth of each river is ~ 1.3 m (maximum depths in narrow channels ~ 3–4 m). The tidal rivers have salinities ranging from < 2 to 28 ppt in upper and lower reaches, respectively, and annual water temperatures range from 2 to 29 °C (Kremer and Nixon 1978; Taylor and Gervasi 2017). The rivers are further characterized by fine-grain substrates with high organic content (% silt-clay content ~ 48%; total organic content ~ 2–3% dry weight; Taylor et al. 2016) and the waters are prone to episodic hypoxia during the summer (Deacutis et al. 2006; Desbonnet and Costa-Pierce 2008; this study). The riverine habitats are unvegetated with only limited occurrences of terrestrially derived plant material in the upper- and mid-reaches and unattached macroalgae, e.g., *Ulva* spp., in the lower portions. The rivers are also intermittently bordered by fringing salt marshes comprised of *Spartina alterniflora* and *S. patens* (total salt marsh area in SR and TR = 0.02 and 0.36 km^2, respectively; NBEP 2017). For a more detailed description of marsh characteristics in the SR and TR, including spatial coverage, refer to NBEP (2017).

Blue crabs were surveyed in the SR and TR from May through August over a 5-year period (2012–2016). Three fixed sites per river (SR1-3 and TR1-3; Fig. 1) were sampled fortnightly with a 15 × 1.8 m beach-seine set (0.64 cm mesh size and 0.48 cm bunt), and previous research indicates catches from seine nets are representative of portunid crab populations (Bellchambers and De Lestang 2005). A fixed-site sampling design was chosen for this study to ensure sampling occurred across a salinity gradient, which was further constrained by the number of sites accessible to boats and seining gear. Moreover, a key objective of this research was to assess temporal patterns in crab abundance and size-structure, including growth, which is optimally achieved through a fixed-site design (Quist et al. 2006; Boone et al. 2019). Consequently, statistical comparisons between the SR and TR described hereafter are limited to the three fixed sites per river and do not necessarily reflect conditions throughout the entirety of each riverine system. Sampling occurred during daylight (~ 0800–1400; ± 2 h 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 (one haul per site per date; water depth sampled ~ 0–1.5 m). The area swept by each seine effort was recorded and varied due to tidal stage and beach profiles (mean ~ 850 m^2; range = 243 to 1774 m^2). Crabs collected during field sampling were immediately preserved in 95% ethanol for subsequent laboratory analyses. Surface water temperature (°C), salinity (‰), and dissolved oxygen (mg/L) were also measured at each site per date with YSI meters (YSI Incorporated, 1700/1725 Brannum Lane Yellow Springs, OH). Further, substrate characteristics at sites SR1-3 and TR1-3, including sediment grain size and total organic carbon, are reported in Murray et al. (2007) and Taylor et al. (2016).

Blue Crab Abundance and Maturity

In the laboratory, field-collected blue crabs were enumerated, measured to the nearest millimeter for CW, and identified by sex. Life stage (juvenile or adult) was also determined for female crabs by inspection of their external abdomen morphology (Jivoff et al. 2007). Crab enumeration data were converted to abundance estimates using the known area sampled by each seine effort (# crabs/10 m^2) and assuming 50% seine efficiency; the latter was reported for seines (0.7 cm mesh size) sampling blue crabs > 25 mm CW in soft substrates (Hines 2007). Specific to a site (SR1-3 and TR1-3) and year (2012–2016), crab abundances estimated from multiple seine efforts were averaged within a month (May–August); hereafter referred to as monthly abundance. Mean differences in crab monthly abundance between rivers were analyzed with a one-way analysis of variance (ANOVA) model with river site as a fixed explanatory factor (SR1-3 vs. TR1-3). Within each river, variations in crab abundance were examined as a function of sex (male vs. female), month (May–August), and year (2012–2016) using three-way ANOVA models. Mean values of abundance across four levels of month and five levels of year were analyzed with Ryan-Einot-Gabriel-Welsch (Ryan's Q) multiple comparison tests. Prior to the ANOVA and Ryan's Q tests, abundance data were $\log(x + 1)$-transformed to meet assumptions of normality and homogeneity of variance. Lastly, stepwise multiple linear regression analyses were used to assess the effects of water temperature (°C), salinity (ppt), and dissolved oxygen (mg/L) on male, juvenile female, and adult female crab abundances. Here, crab abundance and environmental data were expressed as monthly means averaged across years at each site ($n = 29$), and abundance data were $\log(x + 1)$-transformed prior to analysis. The significance level for each response variable's entry and retention into the regression models was set at $p < 0.05$.

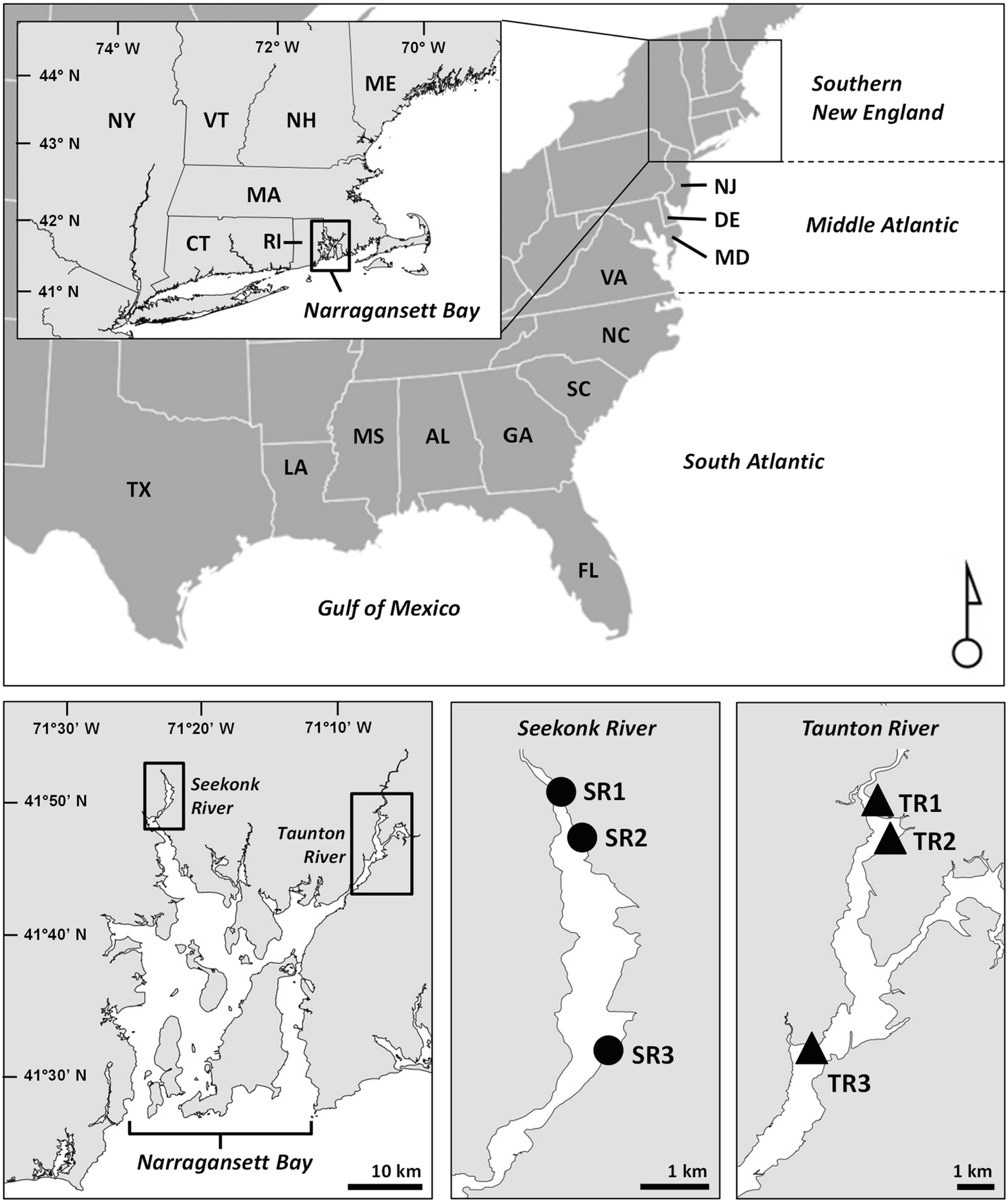


Fig. 1 Map of the coastal USA showing southern New England, Middle Atlantic, South Atlantic, and Gulf of Mexico. Inset maps illustrate the Narragansett Bay Estuary, Seekonk River (SR), Rhode Island, and Taunton River (TR), Massachusetts. Solid points demarcate collection sites of blue crabs. Three sites were sampled fortnightly in each river (SR1-3 and TR1-3) from May to August 2012–2016, with the exception of SR1, which was not surveyed in 2014

The size at maturity for female blue crabs was determined by calculating the proportion of individuals mature at 1-mm CW intervals and fitting a linearized logistic function to the resulting data:

$$Ln[(1-P_i)/P_i] = rCW_m - rCW_i \quad (1)$$

where P_i is the proportion of crabs mature at size i (mm CW_i), r is the slope of the equation, and CW_m is the size at which 50% of females attain sexual maturity. Size at 50% maturity (CW_m) was calculated as $-(a/r)$, where a is the estimated y-intercept parameter of the logistic function (Sumer et al. 2013).

Blue Crab Size-Structure and Growth

Size-frequency distributions were created for blue crabs collected from each seine effort using class intervals of 10 mm CW. From these size-frequency distributions, the modal progression routine of FiSAT II was used to identify distinct cohorts, i.e., age-classes (Food and Agriculture Organization–International Center for Living Aquatic Resources Management stock assessment tools; Gayanilo Jr. et al. 2002). The FiSAT II software uses the Bhattacharya's (1967) method to fit normal components to mode means in the size-frequency distributions. The procedure NORMSEP then refines parameter estimates by using an iterative process of the maximum likelihood concept, which decomposes size-frequency distributions into a series of normal curves that represent each cohort within the data set. Modes were only accepted as distinct cohorts when differentiated by a separation index above a critical value of 2.0 (Gayanilo Jr. et al. 2002).

The absolute growth rates of blue crabs (G_A) at each site and year were analyzed by fitting least-squares linear regression models to the mean CW data over time (G_A = slope of linear regression; mm CW/day). Linear regression models were only applied to the numerically dominant cohort at a specific site and year, as identified by FiSAT II (i.e., one growth estimate per site per year), and these cohorts were comprised exclusively of male and juvenile female crabs (see below). Relative growth rates for each dominant cohort (G_R; % CW/day) were calculated as:

$$G_R = \frac{[\ln(\mathrm{CW}_F) - \ln(\mathrm{CW}_I)]}{T_F - T_I} \quad (2)$$

where, T_F and T_I are the final and initial dates (day of year) when the dominant cohort was observed, and CW_F and CW_I represent the mean body size of crabs on these respective days. This instantaneous rate of growth per unit width minimizes biases associated with size-dependent effects on blue crab growth (Hines 2007), and this approach is valid for organisms with discontinuous growth (e.g., crustaceans) when the evaluation period is sufficiently narrow (Chang et al. 2012), i.e., juvenile crab growth from late May to early August. Mean differences in crab growth rates [G_A and G_R; log(x)-transformed] as a function of river (SR1-3 vs. TR1-3) and year (2012–2016) were analyzed using two-way ANOVA models, as described above, with river site and year as fixed factors. Further, stepwise multiple linear regression models were used to examine the effect of water temperature, salinity, dissolved oxygen, and conspecific abundance (# crabs/10 m^2) on crab growth rates, expressed as annual growth rate at each riverine site ($n = 29$). For this analysis, the explanatory variables included in the regression model were averages calculated over the determined growth period and growth rates were log(x)-transformed.

Geographic Analysis of Blue Crab Abundance and Growth

The abundance and juvenile growth rates of blue crabs from the Seekonk and Taunton Rivers were compared to conspecifics from other geographic locations to evaluate the relative importance of these tidal rivers as nursery habitat. The focal areas were shallow-water (typically < 2 m), unvegetated, soft-bottom habitats previously described as crab nurseries in the Middle Atlantic, South Atlantic, and Gulf of Mexico (Fig. 1). The selected areas were the Great Bay-Little Egg Harbor Estuary, New Jersey (Wilson et al. 1990; Rountree and Able 1992), Delaware Bay Estuary, Delaware (Boutin and Targett 2013), upper and lower Chesapeake Bay, Maryland-Virginia (Hines et al. 1987; Seitz et al. 2003a, 2005; Puckett 2006), Newport River Estuary, New River, and Cape Fear River, North Carolina (Posey et al. 2005; Johnson and Eggleston 2010), Charleston Harbor Estuary, South Carolina (Mense and Wenner 1989), Duplin River, Georgia (Fitz and Wiegert 1992), and estuarine complexes in Alabama (Tatum 1980; McClintock et al. 1993), Mississippi (Perry 1975), Louisiana (Darnell 1959; Adkins 1972), and Texas (Hammerschmidt 1982; Zimmerman and Minello 1984; Thomas et al. 1990).

One-sample t tests were used to compare annual monthly peak abundances (# crabs/10 m^2) and annual growth rates (mm CW/day) of blue crabs from the Seekonk and Taunton Rivers (combined) to southerly locations averaged separately for the Middle Atlantic, South Atlantic, and Gulf of Mexico. Crab abundance data were adjusted to account for differences in sampling gear efficiencies, as reported for beach seines (50% efficiency; Hines 2007; exception = Boutin and Targett 2013 that reported 95% efficiency with replicated seines), suction and drop samplers (88%; Orth and van Montfrans 1987), sweeps (15–25%; Posey et al. 2005, sweep = $-0.138 + 0.294 \times$ drop), otter trawls (22%; Homer et al. 1980), and beam trawls (50% across collected decapods;

Reiss et al. 2006). Growth rates of juvenile blue crabs were assessed in previous studies using field enclosure experiments (Seitz et al. 2005) and the progression of size-frequency means or modes over time (Darnell 1959; Adkins 1972; Perry 1975; Tatum 1980; Hammerschmidt 1982; Puckett 2006). When previous studies only reported ranges in peak crab abundances or growth rates, the means within the ranges were used for statistical comparisons.

Results

Environmental Conditions

Mean monthly water temperatures were generally consistent between the Seekonk and Taunton Rivers (mean ± SD = 23.2 ± 2.9 and 23.9 ± 3.2 °C, respectively), with moderate variation among sites (range = 17.9–29.5 °C; Table 1). In contrast, temperatures varied considerably across months, steadily increasing from May through July and declining modestly thereafter (mean May, July, and August temperatures = 20.1 ± 1.7, 26.2 ± 1.3, and 25.9 ± 1.7 °C, respectively; Fig. 2a, b). Mean annual temperatures were also higher in 2016 relative to other years (24.7 ± 3.5 and 23.3 ± 2.8 °C, respectively).

Monthly salinity values differed markedly among the Seekonk and Taunton River sites (Table 1). Specifically, the lower portion of the Taunton River (TR3) was characterized as polyhaline with a mean salinity of 21.1 ± 4.1 ppt. Conversely, the mid- and lower Seekonk River and mid-Taunton River were defined as mesohaline waters (mean SR2, SR3, and TR2 salinity = 9.5 ± 5.3 ppt), whereas the upper reaches of both rivers were consistently oligohaline (mean SR1 and TR1 salinity = 4.7 ± 3.5 ppt). Further, salinities gradually increased throughout the seasonal survey irrespective of river and site (mean May and August salinity = 6.8 ± 5.6 and 15.0 ± 7.0 ppt, respectively; Fig. 2 c, d) and varied annually (range = 5.9 ± 5.7 in 2013 and 12.7 ± 6.9 in 2016).

Dissolved oxygen (DO) levels measured across river sites ranged between 1.9 and 13.3 mg/L, and concentrations were greater at the Seekonk River relative to the Taunton River sites (means = 7.7 ± 2.2 and 6.7 ± 1.8 mg/L, respectively; Table 1). Mean monthly DO concentrations also differed temporally, decreasing from spring to late summer (mean May and August DO = 8.8 ± 1.4 and 6.6 ± 2.2 mg/L, respectively; Fig. 2e, f) and lower in 2014 relative to other years (5.5 ± 2.3 and 7.7 ± 1.8 mg/L, respectively). Episodic hypoxia (DO < 3.0 mg/L, as defined by Deacutis et al. 2006 for the Narragansett Bay estuarine complex) was also prevalent at river sites, with low DO events occurring in 6.8% of independent measurements (range across sites = 3.6 to 10.7% occurrence). Moreover, hypoxic events occurred between early July and mid-August but were most common in late July (mean and range of day of year of occurrence = 207 ± 11; 190–224).

Table 1 Summary of environmental conditions and biological characteristics across rivers and sites

	Seekonk River			Taunton River		
	SR1	SR2	SR3	TR1	TR2	TR3
Environmental conditions						
Temperature	23.0 (18.2–27.7)	23.8 (19.4–29.0)	22.7 (17.9–27.5)	24.0 (18.6–28.8)	24.6 (20.1–29.5)	23.3 (18.4–28.4)
Salinity	5.1 (1.2–12.6)	7.8 (2.3–18.9)	10.9 (2.2–24.0)	4.4 (0.1–12.8)	10.8 (0.3–21.5)	21.1 (8.0–27.8)
Dissolved oxygen	7.0 (2.9–9.5)	7.6 (1.9–12.9)	8.3 (5.0–13.3)	6.4 (2.7–9.2)	7.2 (2.6–9.8)	6.5 (2.6–8.5)
Occurrence of hypoxia	8.7 (207 ± 24)	10.7 (190 ± 13)	3.6 (203)	7.4 (208 ± 23)	3.8 (224)	7.4 (208 ± 23)
Biological characteristics						
Abundance (male)	0.67 (0.06–1.39)	0.38 (0–2.39)	0.23 (0.04–1.26)	0.09 (0–0.24)	0.26 (0–0.78)	0.07 (0–0.17)
Abundance (juvenile female)	0.21 (0–0.51)	0.20 (0–1.15)	0.14 (0–0.72)	0.06 (0–0.42)	0.20 (0–0.54)	0.08 (0–0.30)
Abundance (adult female)	0.01 (0–0.21)	0.02 (0–0.18)	0.04 (0–0.23)	0.02 (0–0.18)	0.09 (0–0.77)	0.06 (0–0.28)
Size (male)	65.1 (8–155)	52.0 (13–153)	87.9 (12–171)	71.9 (12–170)	53.1 (14–173)	79.9 (12–185)
Size (juvenile female)	57.8 (11–140)	45.4 (11–125)	63.4 (13–125)	57.9 (14–132)	50.3 (12–114)	63.9 (14–121)
Size (adult female)	144	141.3 (135–153)	145.0 (123–164)	149.0 (138–160)	144.5 (135–157)	142.7 (127–172)
Absolute growth rate	0.96 (0.72–1.34)	0.92 (0.77–1.14)	1.05 (0.74–1.64)	0.92 (0.58–1.56)	0.74 (0.52–1.25)	0.83 (0.48–1.20)
Relative growth rate	1.55 (0.86–2.36)	1.81 (1.01–2.34)	1.72 (1.00–2.58)	1.58 (0.78–2.72)	1.18 (0.48–1.85)	1.24 (0.79–1.85)

Environmental conditions include water temperature (°C), salinity (ppt), dissolved oxygen (DO; mg/L), and the occurrence of hypoxic conditions (DO < 3.0 mg/L, as defined in Deacutis et al. 2006). Biological characteristics include blue crab abundance (male and juvenile female: #/10 m^2; adult female: #/100 m^2), body size (mm carapace width, CW), and absolute and relative growth rates (mm CW/day and % CW/day, respectively). Temperature, salinity, DO, size, and abundance data are monthly means averaged across years and ranges are reported in parentheses. Hypoxia data are the percent of DO measurements < 3.0 mg/L, with the mean ±1 standard deviation of the occurrence date (day of year) reported in parentheses. Growth data are averages across years and ranges are reported in parentheses. Sites are defined in Fig. 1

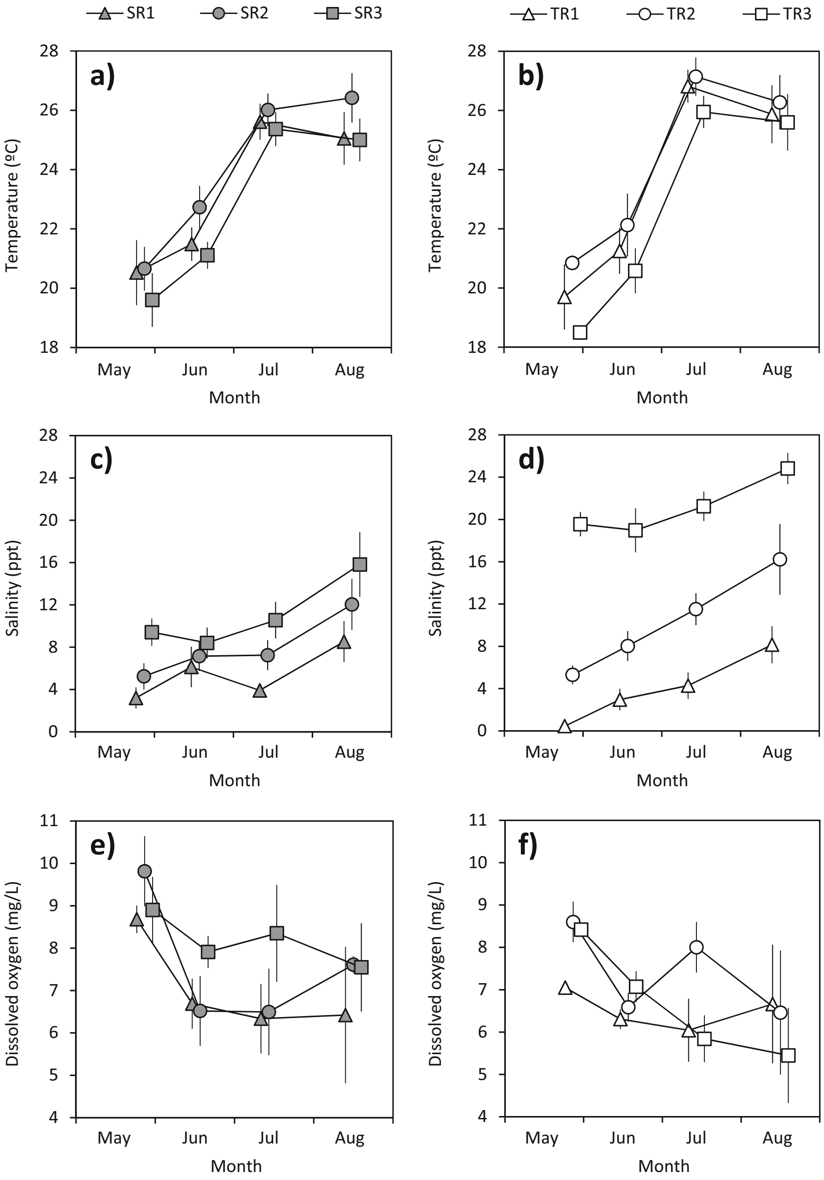


Fig. 2 Water temperature (°C; **a**–**b**), salinity (ppt; **c**–**d**), and dissolved oxygen (mg/L; **e**–**f**) in the Seekonk River (SR) and Taunton River (TR). Data points are monthly means at each site (SR1-3 and TR1-3; Fig. 1) and averaged across years (2012–2016). Error bars denote ± 1 standard error

Blue Crab Abundance and Maturity

In this study, 2577 blue crabs were collected from the Seekonk and Taunton Rivers between 2012 and 2016. Crabs were observed in 95.7% of the seine hauls (161 total hauls), and the occurrence of crabs was similar between rivers (96.3% and 95.0% of 81 and 80 hauls in SR and TR, respectively). However, the mean monthly abundance of crabs was greater at the Seekonk River sites compared to the Taunton River sites (SR1-3 = 0.60 ± 0.72; TR1-3 = 0.23 ± 0.32 crabs/10 m^2; one-way ANOVA: $F_{(df)} = 6.18_{(1,\ 100)}$, $p = 0.015$), although catch differences were inconsistent across sex, months, and years. At the Seekonk River sites, male crabs were more abundant than females, and irrespective of sex, crab catches were highest in 2013 relative to all other years (Tables 1 and 2; Fig. 3a). In contrast, crab abundance at the Taunton River sites did not differ by sex, and catches were notably lower in 2014 and 2015 (Tables 1 and 2; Fig. 3b).

Blue crab abundances varied spatially and seasonally within each river, and these patterns differed by sex and ontogeny (Table 1; Fig. 4). Irrespective of sex, crab abundances were maximal in the upper reaches of the Seekonk River and were typically highest during mid-summer months (SR1; Fig. 4a; maximum abundance = 4.7 crabs/10 m^2). Conversely, in the mid- and lower regions of the Seekonk River, male and juvenile female crabs reached peak abundances in May with numbers declining thereafter, whereas the abundance of adult female crabs continually increased throughout the season (SR2 and SR3; Fig. 4c, e). Crab abundances were highest in the mid-region of the Taunton River (TR2; Table 1; Fig. 4d; maximum abundance = 2.0 crabs/10 m^2), followed by the upper and lower reaches, respectively (TR1 and TR3; Fig. 4b, f).

Table 2 Summary statistics for three-way and two-way analysis of variance (ANOVA) models

Factor	*F* (df)	*p*	*F* (df)	*p*
	Abundance: Seekonk River ($n = 106$)		Abundance: Taunton River ($n = 96$)	
Sex	8.76 (1)	0.0042	0.40 (1)	0.531
Month	0.44 (3)	0.724	1.96 (3)	0.130
Year	6.09 (4)	0.0003	6.59 (4)	0.0002
Sex × month	0.06 (3)	0.983	0.12 (3)	0.951
Sex × year	0.30 (4)	0.875	0.27 (4)	0.893
Month × year	0.60 (11)	0.823	0.53 (8)	0.826
Sex × month × year	0.08 (11)	1.00	0.12 (8)	0.998
	Absolute growth ($n = 29$)		Relative growth ($n = 29$)	
River	5.35 (1)	0.032	4.8 (1)	0.041
Year	7.98 (4)	0.0006	5.4 (4)	0.0046
River × year	0.72 (4)	0.587	1.8 (4)	0.176

ANOVA models were used to examine differences in monthly mean blue crab abundance (#/10 m^2), absolute growth rates [mm carapace width (CW)/day], and relative growth rates (% CW/day) as a function of sex (male and female), month (May–August), year (2012–2016), and river (Seekonk River = SR1–3 vs. Taunton River = TR1–3; Fig. 1)

Seasonal patterns in crab abundance in the Taunton River were generally consistent with observations from the Seekonk River, i.e., the abundances of male and juvenile female crabs were maximal in spring or mid-summer, and adult female crabs were more prominent in later months (Fig. 4b, d). An exception to this trend occurred in the lower Taunton River, where adult female crabs were more abundant in May (2013 only) and June (Fig. 4f).

Spatial and interannual variations in blue crab abundance were related to several environmental parameters (Table 3; Fig. 5); however, the responsiveness of crabs to these factors differed by sex and life stage. The abundances of male and juvenile female crabs were related to salinity and dissolved oxygen (Fig. 5a–d), and these parameters accounted for 22 to 25% of the total variation in the response variables (Table 3). The estimated coefficients for salinity were negative (slope coefficients = − 5.59E^{-3} and − 1.35E^{-3} for male and juvenile female, respectively) and positive for dissolved oxygen (slopes = 1.58E^{-2} and 1.58E^{-2}, respectively), indicating that male and juvenile female crab abundances were maximal in low-salinity, highly oxygenated waters. In contrast, the abundance of adult female crabs was greatest in high-salinity, warm waters (Table 3; Fig. 5e, f). Specifically, salinity and temperature accounted for 28% of spatiotemporal variation in adult female catches, and the coefficients for both explanatory variables were positive (slopes = 1.26E^{-3} and 7.27E^{-3}, respectively) (Table 3).

A total of 955 female blue crabs, ranging from 11 to 172 mm CW, were evaluated for sexual maturity based on their abdomen morphology. The estimated size (± 95% CI) at which 50% of the females attained maturity (CW_m) was 129.0 ± 0.2 mm. The minimum size for an adult female crab was 123 mm CW, and the largest juvenile female was 132 mm CW.

Blue Crab Size-Structure and Growth

A broad size range of blue crabs was collected from the Seekonk and Taunton Rivers (8–185 mm CW; Table 1), and the decomposition of monthly size-frequency distributions revealed a bimodal size-structure and presence of two distinct cohorts (Fig. 6). The younger age-class, hereafter referred to as age-0+ (Hines 2007), overwhelmingly dominated total catches (87.9% of catch). The age-0+ cohort was comprised exclusively of male and juvenile female crabs (60.3 and 39.7% of catch, respectively). In late May, the mean body size of age-0+ crabs equaled 31.0 ± 3.5 mm CW (monthly mean averaged across rivers and years; Figs. 6 and 7) with a maximum size of ~ 75 mm CW. The age-0+ cohort persisted in subsequent months with pronounced shifts in their size-frequency distributions over time. Between May and early August, for example, the mean CW of age-0+ crabs increased by 64.5 mm (mean August CW = 95.5 ± 5.8 mm; Figs. 6 and 7), and by late summer these crabs attained a maximum size of ~ 135 mm CW.

Relative to younger blue crabs, the age-1+ cohort exhibited greater spatial and seasonal variations in their occurrence during field sampling (Figs. 6 and 7). During the late spring and early summer, for example, age-1+ crabs were scarce in the upper and mid-regions of the Seekonk and Taunton Rivers, accounting for only 7.6% of the total catch. Conversely, across all months, proportional catches of age-1+ crabs were

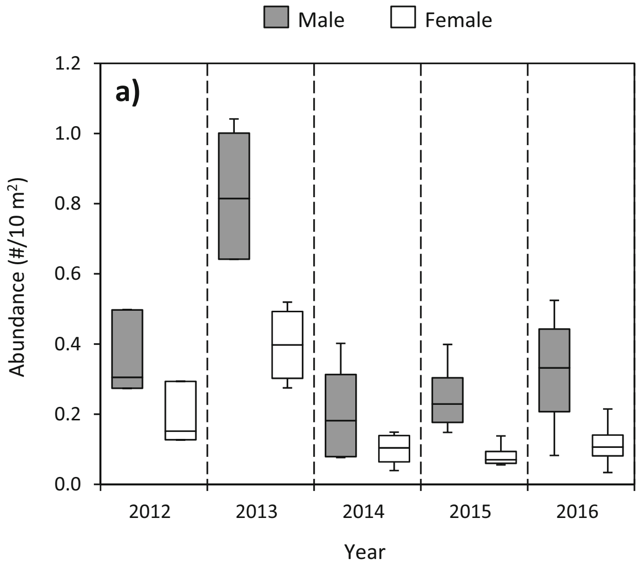


Fig. 3 Blue crab abundance (#/10 m^2) in the Seekonk River (**a**) and Taunton River (**b**) as a function of sex and year. Box plots illustrate the median, first and third quartiles, and maximum and minimum values. Data were pooled across sites (SR1-3 or TR1-3; Fig. 1) and months (May–August). Note: *y* axes are scaled differently between figures

relatively high in the lower reaches of both rivers (18.4% of catch). Also, in comparison to younger crabs, the age-1+ cohort differed by sex and ontogenetic composition. Specifically, a larger percentage of age-1+ crabs were male (83.2% of catch), and adult, sexually mature females accounted for 8.8% of this older age-class.

Age-0+ blue crabs were analyzed for growth performance because of their numerical dominance and monthly persistence in this study (Fig. 7). Further, it was necessary to exclude adult female crabs from growth analyses because these individuals cease molting after reaching sexual maturity (Hines 2007). The absolute growth rate (G_A) of juvenile crabs ranged between 0.5 and 1.6 mm CW/day (mean = 0.9 ± 0.3 mm CW/day), and relative growth rates (G_R) ranged between 0.5 and 2.7% CW/day (mean 1.5 ± 0.6% CW/day) (Table 1). Both growth measurements differed between rivers (SR1-3 vs. TR1-3) and among years (Tables 1 and 2; Fig. 8). Specifically, crabs inhabiting Seekonk River sites had faster G_A and G_R in comparison to conspecifics from Taunton River sites (mean G_A and G_R: SR1–3 = 1.0 ± 0.3 mm CW/day and 1.7 ± 0.6% CW/day; TR1–3 = 0.8 ± 0.3 mm CW/day and 1.3 ± 0.6% CW/day). Crabs in 2012 also experienced higher rates of G_A and G_R relative to other years (mean 2012 and 2013–2016 G_A = 1.3 ± 0.3 and 0.8 ± 0.2 mm CW/day; mean 2012 and 2014–2015 G_R = 2.0 ± 0.4 and 1.1 ± 0.5% CW/day). Finally, there was a positive relationship between crab growth and site-specific DO concentrations (slope coefficients = 0.045 and 0.058), and this explanatory variable accounted for ~ 19% and 16% of the variation in G_A and G_R, respectively (Table 3; Fig. 9).

Geographic Analysis of Blue Crab Abundance and Growth

The annual monthly peak abundance of blue crabs in the Seekonk and Taunton Rivers (SR1-3 and TR1-3 = 2.6 ± 1.8 crabs/10 m^2; range = 0.8–4.7 crabs/10 m^2) was ~ 10 to 39% lower than the abundances of conspecifics from similar habitats in the Middle Atlantic (2.9 ± 1.9 crabs/10 m^2; range = 1.0–5.0 crabs/10 m^2), South Atlantic (3.7 ± 1.2 crabs/10 m^2; range = 2.1–5.0 crabs/10 m^2), and Gulf of Mexico (3.6 ± 4.5 crabs/10 m^2; range = 0.3–10.2 crabs/10 m^2), although these values did not differ statistically at $p < 0.05$ (Tables 4 and 5). Although blue crabs were collected using different sampling gears among the abovementioned studies, catches were adjusted to account for gear-specific efficiencies (Table 4). Potential methodological biases in abundance estimates were also minimized because of consistencies in sampled water depths (< 2 m; exception = Hines et al. 1987; Lipcius et al. 2005) and bottom composition (unvegetated, mud-sand substrates).

Despite efforts to minimize sampling biases across studies, direct comparisons of abundance values derived from different sampling methodologies should be interpreted with caution. To that end, an additional *t* test was performed on abundance data derived exclusively from seine surveys, which included the Seekonk and Taunton Rivers (this study), Great Bay-Little Egg Harbor (Rountree and Able 2002), Delaware Bay Estuary (Boutin and Targett 2013), and southeastern Texas Bays (Hammerschmidt 1982). The seine specifications for these studies were as follows: Great Bay-Little Egg Harbor (net dimension = 18.3 × 1.2 m; mesh = 0.64 cm; area sampled per haul = 100 m^2), Delaware Bay (dimension = 7.6 × 1.2 m; mesh = 0.5 cm; area = 45.6 m^2), and Texas bays (dimension = 18.3 × 1.8 m; mesh = 1.3–1.9 cm; area = 300–600 m^2). The seine mesh diameter used in the Texas survey was

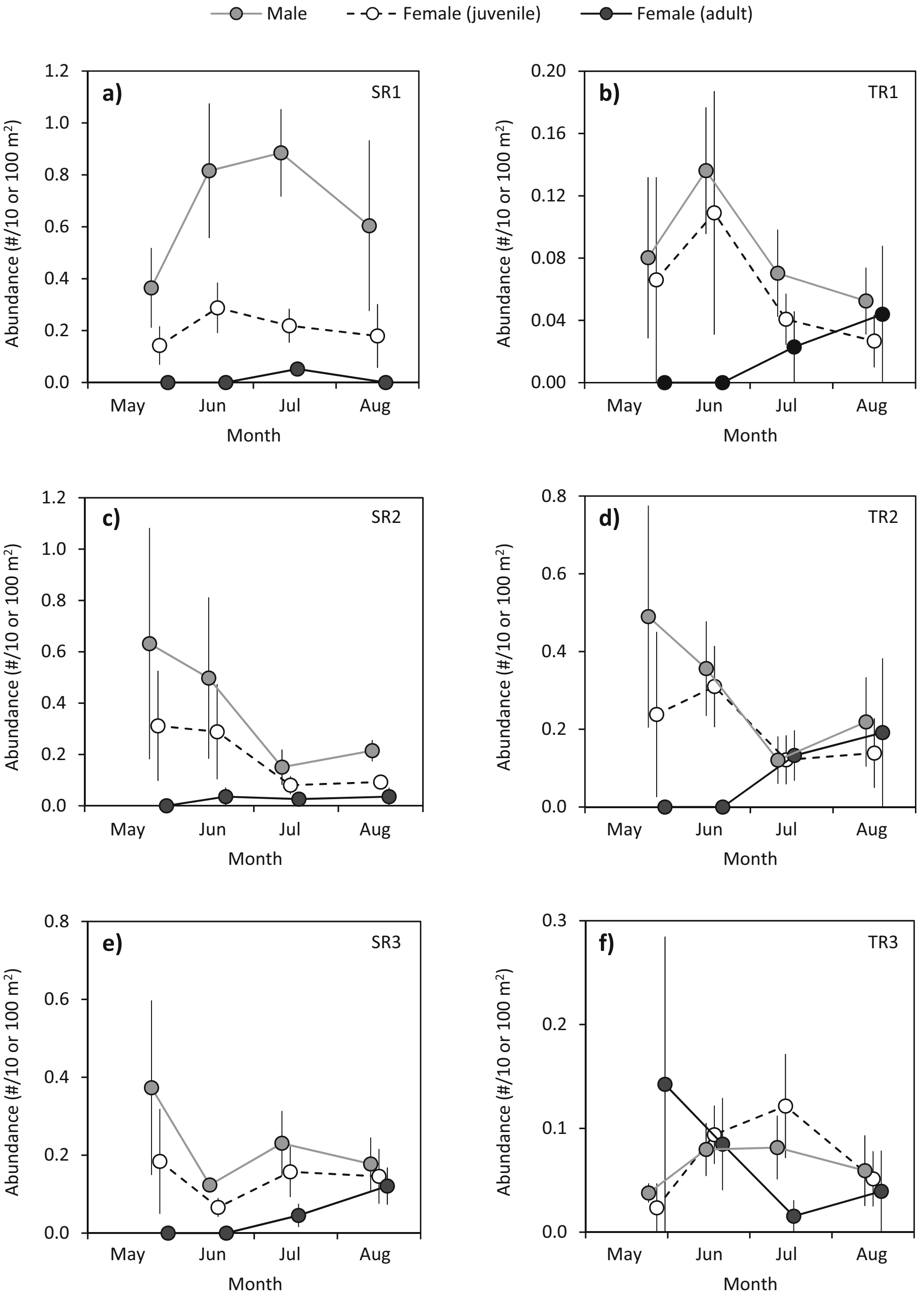


Fig. 4 Blue crab abundance in the Seekonk River (SR) and Taunton River (TR) as a function of site [SR1-3 (**a**, **c**, **e**) and TR1-3 (**b**, **d**, **f**); Fig. 1], sex, and life stage (male and juvenile female = #/10 m^2 and adult female = #/100 m^2). Data points are monthly means averaged across years (2012–2016), and error bars denote ± 1 standard error

greater than meshes reported elsewhere, yet the larger mesh did not ostensibly yield a different size-structure of blue crabs. Hammerschmidt (1982), specifically, documented crab sizes between 6 mm and > 126 mm CW, and crabs measuring 6 to 30 mm CW constituted 38% of the total catch. For comparison, in this study, crabs of 6 to 30 mm CW comprised 25% of the catch. Furthermore, the seine net length in the Delaware survey was considerably shorter than those used in other studies, and smaller seines have reportedly higher catch efficiencies (Steele et al. 2006). Note, however, that crab abundances in Boutin and Targett (2013) were adjusted using 95% efficiency (as opposed to 50%), given that catches were from two immediately replicated seine hauls and this correction factor was verified in their study. Exclusively for the seine survey comparisons, the annual abundance of blue crabs in the Seekonk and Taunton River was ~ 10% greater than values combined for the Middle Atlantic and Gulf coasts (2.0 ± 2.4 crabs/10 m^2; range = 0.3–4.8 crabs/10 m^2), but this difference was not statistically significant (Table 5).

Table 3 Summary statistics for stepwise multiple linear regression analyses

Response variable	Optimal model explanatory variables	*F* (df)	*p*	R^2
Abundance (male)	Salinity (−)/DO (+)	4.40 (2, 28)	0.023	0.253
Abundance (juvenile female)	Salinity (−)/DO (+)	3.72 (2, 28)	0.038	0.222
Abundance (adult female)	Salinity (+)/temperature (+)	4.94 (2, 28)	0.015	0.275
Absolute growth rate	DO (+)	6.46 (1, 28)	0.017	0.193
Relative growth rate	DO (+)	5.02 (1, 28)	0.034	0.157

Regression analyses were used to examine blue crab abundance (male and juvenile female: #/10 m^2 ; adult female: #/100 m^2), absolute growth rate [mm carapace width (CW)/day], and relative growth rate (% CW/day) as a function of salinity (ppt), dissolved oxygen (DO; mg/L), and water temperature (°C). Crab abundance and environmental variables are expressed as monthly means averaged across years. Positive (+) and negative (−) symbols in parentheses after each explanatory variable denote their directional effect on each response variable

Mean annual growth rates of juvenile blue crabs from the Seekonk and Taunton Rivers (SR1-3 and TR1-3 = 0.9 ± 0.1 mm CW/day; range = 0.8–1.1 mm CW/day) exceeded estimates reported in the Middle Atlantic (0.7 ± 0.3 mm CW/day; range = 0.5–0.9 mm CW/day) and Gulf of Mexico (0.6 ± 0.2 mm CW/day; range = 0.4–0.8 mm

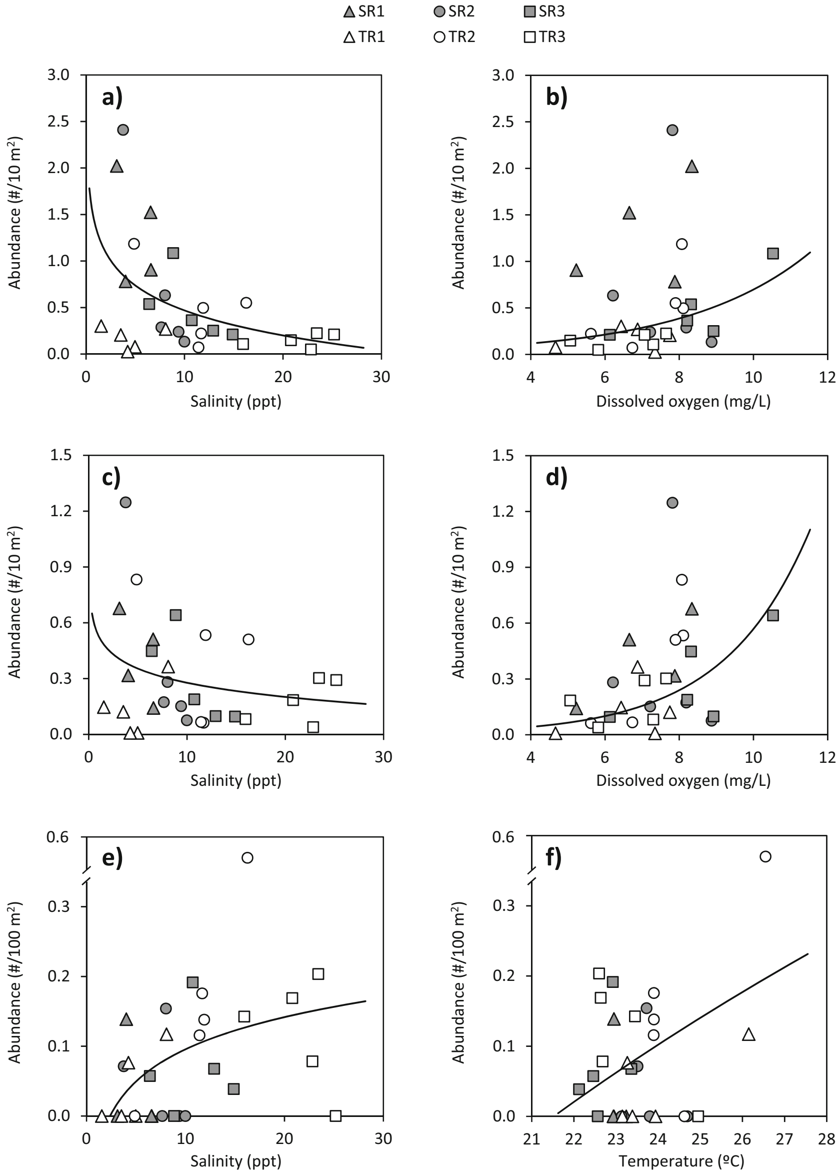


Fig. 5 Blue crab abundance in the Seekonk River (SR) and Taunton River (TR) as a function of salinity (ppt), dissolved oxygen (mg/L), and water temperature (°C) displayed for males (#/10 m^2; **a**–**b**), juvenile females (#/10 m^2; **c**–**d**), and adult females (#/100 m^2; **e**–**f**). Crab abundance and environmental variables are expressed as monthly means averaged across years at each site (SR1-3 and TR1-3; Fig. 1). Least squares logarithmic or exponential regressions were fit to the full data sets ($n = 29$)

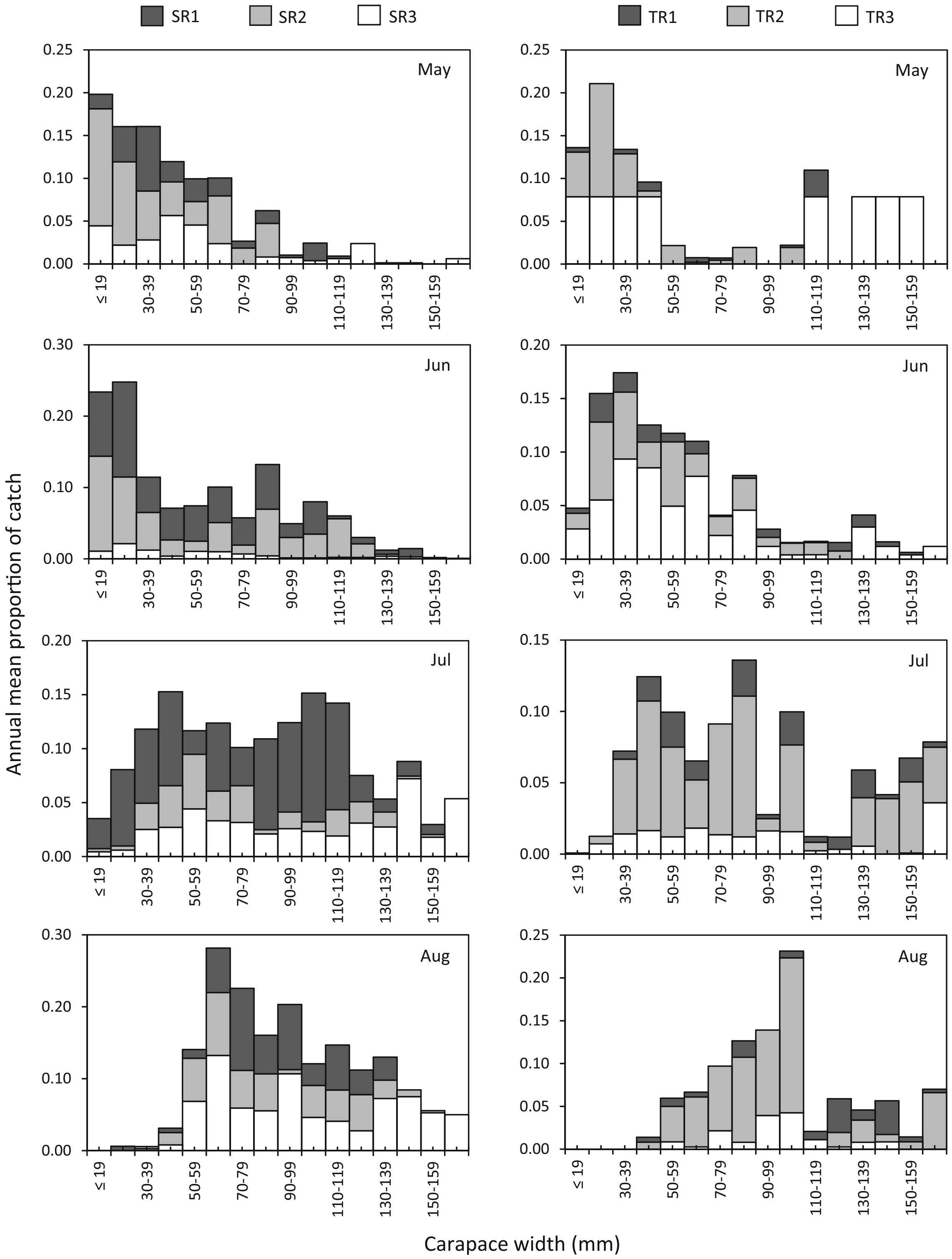
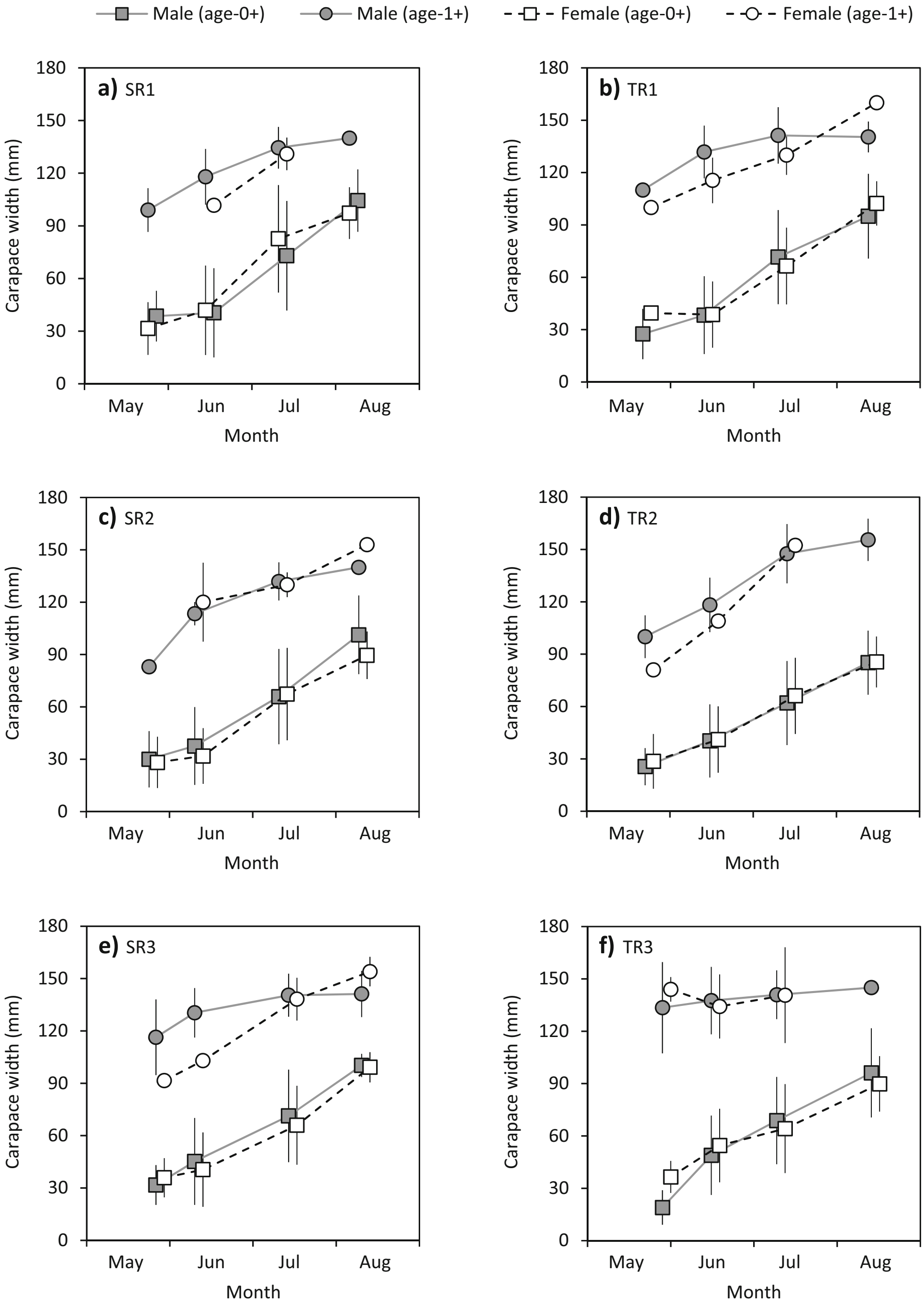


Fig. 6 Blue crab monthly size-frequency distributions (mm carapace width, CW) in the Seekonk River (SR) and Taunton River (TR), displayed in relation to site (SR1-3 and TR1-3; Fig. 1). Frequencies were calculated as the proportion of total monthly catch averaged across years (2012–2016). Note: *y* axes are scaled differently among figures

CW/day) (Tables 4 and 5). Moreover, there were no apparent differences in juvenile growth rates estimated in previous studies that implemented field enclosure experiments versus size-frequency analysis (ranges = 0.3–0.7 and 0.2–1.1 mm CW/day, respectively; Table 4).

Fig. 7 Blue crab carapace width (CW; mm) in the Seekonk River (SR) and Taunton River (TR) as a function of site [SR1-3 (**a**, **c**, **e**) and TR1-3 (**b**, **d**, **f**); Fig. 1], sex, and age class. Data points are monthly means averaged across years (2012–2016), and error bars denote ± 1 standard deviation



Discussion

Blue Crab Abundance and Factors Affecting Habitat Use and Selection

To the knowledge of the authors, this study represents the first detailed description of blue crab population structure at northern latitudes, with a focus on southern New England tidal rivers. Here, blue crabs occupied several unvegetated, shallow-water sites throughout the Seekonk and Taunton Rivers, demonstrating a tolerance to a wide range of physicochemical conditions. From May through August over a 5-year period, crabs were collected in > 95% of the seine hauls conducted in the rivers at temperatures ranging from 18 to 30 °C, salinities from < 1 to 28 ppt, and hypoxic to normoxic conditions (1.9–13.3 mg DO/L). Riverine crabs are therefore aptly characterized as habitat generalists, especially with respect to their euryhaline designation during post-larval stages (Millikin and Williams 1984; Pequeux 1995).

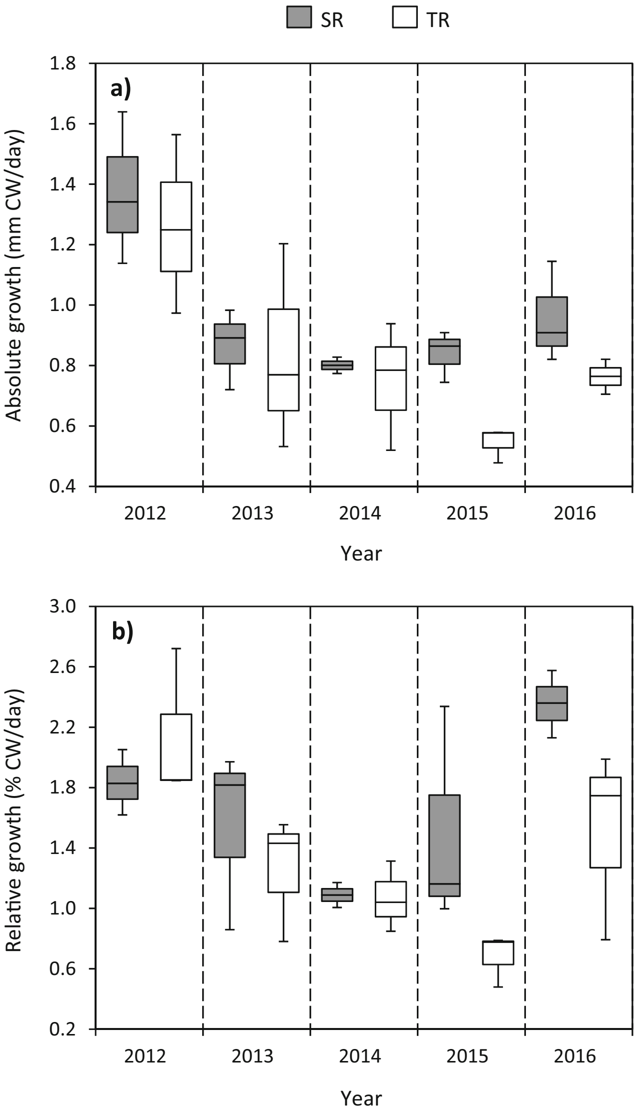


Fig. 8 Age-0+ blue crab absolute growth rate [mm carapace width (CW)/day; **a**) and relative growth rate (% CW/day; **b**) in the Seekonk River (SR) and Taunton River (TR) as a function of year (2012–2016). Box plots illustrate the median, first and third quartiles, and maximum and minimum values. Data were pooled across sites (SR1-3 or TR1-3; Fig. 1)

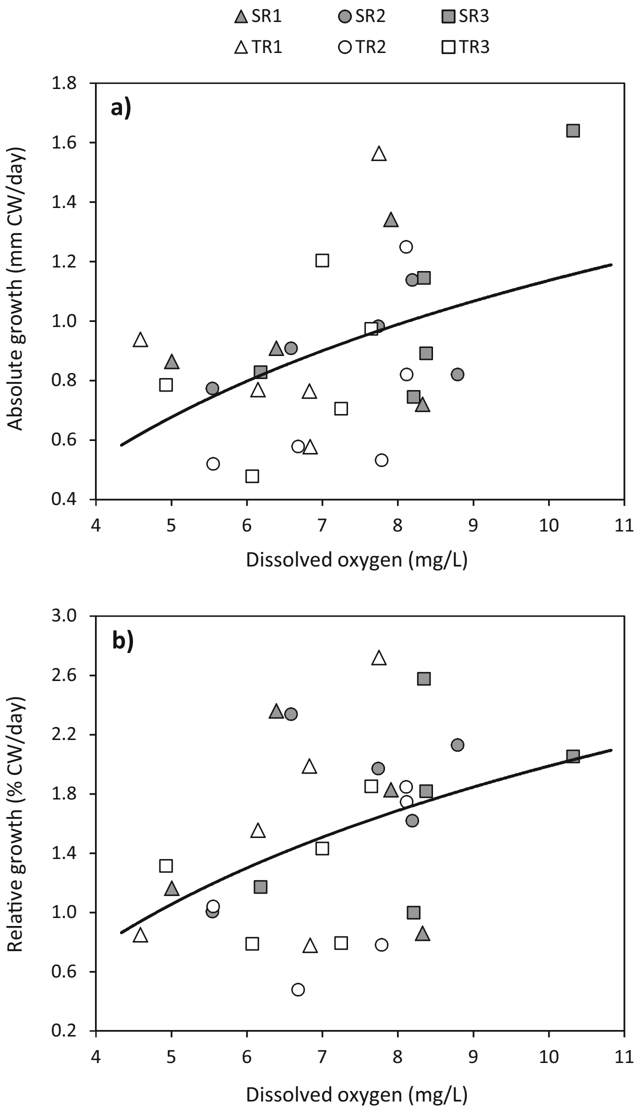


Fig. 9 Age-0+ blue crab absolute growth rate [mm carapace width (CW)/day; **a**) and relative growth rate (% CW/day; **b**) in the Seekonk River (SR) and Taunton River (TR) as a function of dissolved oxygen (mg/L). Data points are annual growth estimates at each site (SR1-3 and TR1-3; Fig. 1), and least-squares logarithmic regressions were fit to the full data sets (*n* = 29)

Despite the evidence for broad habitat usage, blue crabs were spatially segregated along a salinity gradient in accordance with sex and ontogenetic life stage. Male and juvenile female crabs preferentially occupied upriver oligohaline waters, whereas adult females were more frequent at the meso- and polyhaline segments of the rivers. These spatially explicit abundance patterns correspond to the current paradigm of blue crab habitat use in other geographic locations (Kennedy and Cronin 2007; Bromilow and Lipcius 2017). Following a planktonic larval phase in coastal waters, megalopal blue crabs recruit into estuaries and settle in structurally complex habitats that confer a predator refuge for individuals < 12 to 25 mm CW (Posey et al. 2005 and references therein). After reaching ~ 25 mm CW, juvenile crabs then disperse to secondary unvegetated, i.e., non-structured, nurseries that are low-salinity, shallow-water habitats with mud-sand substrates (Lipcius et al. 2005; Posey et al. 2005; Seitz et al. 2005; Bromilow and Lipcius 2017; this study). In this study, peak abundances of age-0+ crabs in the mid- and lower reaches of the Seekonk and Taunton Rivers occurred in May, whereas crab densities were greatest in the upper portion of the rivers during June and July. This seasonal pattern in abundance may reflect the progressive movement of juvenile crabs upriver along a salinity gradient, eventually settling in oligohaline, unvegetated nurseries by mid-summer (Rountree and Able 1992).

Table 4 Literature review of blue crab abundance and juvenile growth rates in shallow-water, unvegetated, soft-bottom habitats from the Middle Atlantic, South Atlantic, and Gulf of Mexico, including the methodology and environmental conditions during field sampling

Location	Sampling methodology			Environmental conditions[a]		Biological characteristics[b]		
	Gear and techniques	Depth	Months	Temperature	Salinity	Abundance	Growth	Size
Middle Atlantic								
Great Bay-Little Egg Harbor, NJ (Rountree and Able 2002)	Seine	0–1.2	Apr–Nov	8–28	23–33	4.8 ± 7.5 (9.8)	–	11–127[f]
Little Egg Harbor, NJ Wilson et al. (1990)[c]	Suction sampler	1	May–Aug	20–25	25–34	5.0 ± 8.9 (20.5)	–	4–103
Miller Creek, DE Boutin and Targett (2013) Boutin (personal communication)	Seine	0–1.2	Apr–Nov	13–33	5–31	1.0 ± 0.2 (1.2)	–	3–153
Rhode River, MD Hines et al. (1987)	Otter trawl	2–4	Apr–Nov	~ 29 (Jul)	4–15	4.1 ± 4.6 (7.3)	–	~ 5–195
Choptank and Patuxent Rivers, MD Puckett (2006)	Size frequency	0–20	Jun–Oct	13–29	< 1–12	–	0.6–1.1	33–49
York River, VA Seitz et al. (2003a)	Otter trawl	1–2	Jul–Aug	nr	12–217	1.5 ± 0.9 (8.3)	–	nr
York River, VA Lipcius et al. (2005)[e]	Suction sampler and otter trawl	< 3	Summer and fall	nr	nr	1.2 ± 1.2 (2.5)[i]	–	< 100
York River, VA Seitz et al. (2005)	Field enclosure	0.25	Jul–Sep 2001	nr	12–21[g]	–	0.3–0.7	25–52
South Atlantic								
Newport River Estuary, NC Johnson and Eggleston (2010)[d]	Beam trawl	nr	Jun–Oct	nr	nr	4.1 ± 5.2 (45.5)	–	22–153
New and Cape Fear Rivers, NC Posey et al. (2005)	Sweep	0.1–0.3	Jun–Aug	27–35	0–36	2.1 ± 0.8 (16.6)	–	> 24
Charleston Harbor Estuary, SC Mense and Wenner (1989)[c]	Suction sampler	1.2	Monthly for 16 months	8–32	5–32	3.6 ± 2.0 (5.2)	–	1–36
Duplin River, GA Fitz and Wiegert (1992)[c]	Otter trawl	1.5	~ Monthly for 2.5 years	10–30[h]	10–30[h]	0.9 (9.1)	–	< 50 to > 125
Gulf of Mexico								
Weeks Bay, AL McClintock et al. (1993)	Otter trawl	1.5	Monthly for 14 months	10–32	0–19	1.5 ± 1.9	–	< 20 to > 120
Mobile Bay, AL Tatum (1980)	Size frequency	nr	Dec–Mar, Mar–Sep	nr	nr	(2.8)	0.2–0.6	10–20

Table 4 (continued)

Location	Sampling methodology			Environmental conditions[a]		Biological characteristics[b]		
	Gear and techniques	Depth	Months	Temperature	Salinity	Abundance	Growth	Size
Mississippi Sound, MS Perry (1975)	Size frequency	0–5	Jul–Jan	10–33	0–32	–	0.8	15–30
Lake Pontchartrain, LA Darnell (1959)	Size frequency	0–1.2	Monthly for ~ 2 years	10–30	3–12	–	0.6	15–25
Terrebonne Bay, LA Guillory et al. (2001) citing Adkins (1972)	Size frequency	nr	nr	nr	nr	–	0.5–0.7	nr
Galveston Bay, TX Zimmerman and Minello (1984)[d]	Suction sampler	< 1	May–Aug	15–32	16–36	2.7 ± 1.7 (1.1–9.1)	–	< 20 to > 60
West Bay, TX Thomas et al. (1990)[c]	Drop sampler	< 1	Monthly for 1 year	11–30	15–30	10.2 ± 12.9 (19.3)	–	5–40
Southeastern Texas bays, TX Hammerschmidt (1982)[e]	Seine	0–1	May–Aug	26–32	2–35	0.26 ± 0.09 (0.35)	–	6 to > 126
Southeastern Texas bays, TX Hammerschmidt (1982)[e]	Size frequency	0–1	May–Aug	18–32	2–35	–	0.7	26–47

[a] Water depth (m), water temperature (°C), and salinity (ppt)

[b] Abundances (#/10 m^2) reported as mean ± 1 SD (maximum value in parentheses) and adjusted for gear efficiencies (see text). Growth [mm carapace width (CW)/day] reported as ranges. Sizes (mm CW) reported for "Abundance" are for duration of field sampling, whereas "Growth" sizes are reported for start of growth period

[c] Abundances reported for unvegetated, sandy-mud, or mud habitats only

[d] Mean abundance for subtidal and intertidal habitats combined and maximum abundance for subtidal habitat only

[e] Bays include Galveston Bay, Matagorda Bay, San Antonio Bay, Aransas Bay, Corpus Christi Bay, and upper-lower Laguna Madre Bay

[f] Crab CW converted from wet weight (g; Cadman and Weinstein 1985)

[g] Salinities reported in Dauer (1993)

[h] Salinities and temperatures reported in Fitz and Wiegert (1991)

[i] Abundances pre-adjusted for gear efficiency (Lipcius et al. 2005)

nr = not reported

Table 5 Summary statistics for one-sample *t* tests

Location	Abundance			Growth		
	Mean ± 1 SD	*t* value (df)	*p* value	Mean ± 1 SD	*t* value (df)	*p* value
Southern New England	2.6 ± 1.8	–	–	0.93 ± 0.11	–	–
Middle Atlantic	2.9 ± 1.9	− 0.77 (4)	0.487	0.67 ± 0.26	5.17 (4)	0.0066
South Atlantic	3.7 ± 1.2	− 1.54 (4)	0.199	–	–	–
Gulf of Mexico	3.6 ± 4.5	− 1.50 (4)	0.207	0.62 ± 0.17	6.05 (4)	0.0038
Middle Atlantic and Gulf of Mexico (seine only)	2.0 ± 2.4	0.36 (4)	0.736	–	–	–

One-sample *t* tests were used to contrast log(x + 1)-transformed annual monthly peak abundances (#/10 m^2) and growth rates (mm carapace width/day) of blue crabs from southern New England tidal rivers (this study) with conspecifics from the Middle Atlantic, South Atlantic, and Gulf of Mexico. A fourth *t* test was performed on abundance data derived exclusively from seine surveys (this study compared to Middle Atlantic and Gulf of Mexico combined; Hammerschmidt 1982; Rountree and Able 2002; Boutin and Targett 2013). A summary of biological data for all geographic locations is provided in Table 4

Several mechanisms may explain the ontogenetic change in blue crab habitat use through sequential juvenile stages (i.e., migration from structured to non-structured nurseries). The predator refuge provided by structured nurseries is lost when juvenile crabs increase in size, such that protective interstices of the complex habitat become obsolete (Bromilow and Lipcius 2017). Larger juveniles that disperse into secondary nurseries may also benefit from reduced predation pressure in oligohaline waters owing to fewer predators and decreased size-dependent cannibalism (Moksnes et al. 1997; Reyns and Eggleston 2004; Lipcius et al. 2005). Moreover, relative to seagrass and high-salinity unvegetated habitats, juvenile crab growth rates are higher in oligohaline, soft-bottom environments due to the exploitation of ample prey resources (Seitz et al. 2003a; Seitz et al. 2005). Maximal abundances of age-0+ crabs in this study occurred in the upper Seekonk River, a site characterized as low-salinity with fine-grain, organically enriched substrates (% silt-clay content ~ 44%; total organic content ~ 6% dry weight; Murray et al. 2007; Taylor et al. 2016). Sediments rich in organic matter in the Narragansett Bay estuarine complex support high densities of benthic infauna and epifauna (Rudnick et al. 1985; Calabretta and Oviatt 2008), including important prey for blue crabs, e.g., bivalves, polychaetes, amphipods, and shrimp (Lipcius et al. 2007). It is also noteworthy that peak catches of age-0+ crabs at the six tidal river sites occurred in 2013, corresponding to the lowest annual salinity. Prior investigations purport that elevated freshwater discharge into estuaries, and thus reduced salinities, correspond to increased blue crab post-larval survival and abundance (Posey et al. 2005; Guillory 2000; Bishop et al. 2010; Sanchez-Rubio et al. 2011), fishery landings (More 1969; Wilber 1994), and decreased prevalence of disease-induced mortality (Lee and Frischer 2004).

Blue crabs often remain in secondary unvegetated nurseries until reaching sexual maturity, after which mating occurs in estuarine basins and river mouths coinciding with the female terminal molt (Hines et al. 1987; Jivoff et al. 2017). Specific to this study, female crabs achieved sexual maturity at ~ 129 mm CW, which is consistent with previous reports (Jivoff et al. 2007). Further, the majority of adult female crabs and sexually mature male crabs (≥ 107 mm CW; Jivoff et al. 2017) occupied the lower Seekonk and Taunton Rivers, in close proximity to riverine mouths. Mating was apparent during July and August when > 75% of the mature crabs were collected and several occurrences of pre-copulatory embraces were observed (D. Taylor, personal observation). Although field sampling concluded in August, it is probable that mating continued into the early fall, similar to the reproductive behavior of crabs in the mid-Atlantic region (Tankersley et al. 1998; Medici et al. 2006).

Spatial and annual variations in blue crab habitat use in the tidal rivers were related to dissolved oxygen (DO) concentrations. First, crab abundances were reduced at the Taunton River sites, and DO concentrations at these sampling locations were ~ 15% lower compared to the Seekonk River sites. Second, cumulative crab abundances at the Taunton River sites declined significantly in 2014, corresponding to the lowest annual DO levels. Third, hypoxia was relatively frequent at all river sites during July (12% of July DO recordings < 3 mg/L), and the abundance of male and juvenile female crabs declined ~ 63 to 114%, respectively, during these oxygen-stressed conditions. It is also notable that environmental parameters assessed in this study were diurnal measurements; hence, DO concentrations reported herein likely overestimate conditions crabs experienced over a complete diel cycle, i.e., lower DO levels are expected at night due to the absence of photosynthetic activity (Deacutis et al. 2006; Saarman et al. 2008). Previous studies report that deficiencies in DO adversely affect numerous estuarine biota and alter faunal assemblages in the affected environments (Diaz et al. 2004; Boutin and Targett 2013). Blue crabs, in particular, are highly sensitive to oxygen stress (Tankersley and Forward 2007; Stover et al. 2013), although recent research contends that blue crabs are more hypoxia-tolerant than previously recognized (Brill et al. 2015). Field survey and telemetry data indicate that DO concentrations < 2–4 mg/L initiate an avoidance response in blue crabs (Phil et al. 1991; Eby and Crowder 2002; Bell et al. 2003a), and exposure to < 1.2 mg/L causes acute mortality in the laboratory (Das and Stickle 1993). This study corroborates the supposition that low DO negatively affects blue crab abundance and growth (see below), but there was no evidence of hypoxia-induced mortality.

Blue Crab Growth and Factors Affecting Habitat Quality

Juvenile blue crab absolute and relative growth rates equaled 0.5–1.6 mm CW/day and 0.5–2.7% CW/day, respectively, and were significantly higher for crabs at the Seekonk River sites compared to the Taunton River sites. Spatially explicit growth estimates for mobile fauna are arguably confounded by large-scale movements and exchange across select habitats. These concerns are mostly alleviated for blue crabs, however, owing to their high site fidelity during the late spring and summer (Taylor and Calabrese 2018). For example, numerous tagging studies confirmed that juvenile blue crabs (20–85 mm CW) have limited movements (< 100 m) within post-dispersal nurseries during the spring and summer (Fitz and Wiegert 1991, 1992; van Montfrans et al. 1991; Davis et al. 2005; Johnson and Eggleston 2010). Similarly, adult male blue crabs typically remain in residential summer habitats with movements rarely exceeding 10 km (Oesterling and Adams 1982; Hines 2007). Conversely, post-mating females are highly migratory, initiating large-scale directional movements toward saline spawning areas in the late summer and fall (Aguilar et al. 2005; Eggleston et al. 2015). In this study, it is important to reiterate that growth estimates were limited to age-0+ crabs comprised exclusively of juvenile females and males. Therefore, given the seasonality (May–August) and crab life history traits (juvenile and/or male) relevant to the present study, distances between the Seekonk and Taunton River were sufficient to negate crab exchange among sites, therefore enabling a spatially explicit analysis of growth.

Differences in blue crab growth rates between river sites (SR1-3 vs. TR1-3) were partly attributed to spatial variations in DO concentrations. The absolute and relative growth rates of age-0+ crabs from the Taunton River sites were ~ 18 to 28% lower, respectively, than conspecifics from the Seekonk River, and this suboptimal growth performance may be caused by depressed DO levels, as noted above. Biotelemetry and laboratory-exposure studies revealed that moderate hypoxia (< 2–3 mg/L) resulted in suppressed feeding rates and reduced growth in blue crabs (Nestlerode and Diaz 1998; Bell et al. 2003b; Seitz et al. 2003b), the latter quantified by less frequent molts and decreased percent weight gain over time (Das and Stickle 1993). However, a concurrent dietary study in the Seekonk and Taunton Rivers determined that there was no habitat effect on the amount of prey in blue crab stomachs (D. Taylor, unpublished data); hence, the ostensive effect of oxygen stress on crab growth was not related to impaired feeding.

Spatial differences in the abundance and availability of food resources may alternatively explain the site-specific growth rates of blue crabs. Although prey densities were not quantified in this investigation, blue crabs in the Seekonk River consumed more bivalves, a dominant food resource that included *Mya arenaria*, *Modiolus modiolus*, and *Geukensia demissa*, as compared to crabs from the Taunton River (D. Taylor, unpublished data). In the York River, Virginia (VA), a Chesapeake Bay tributary, blue crab growth rates were maximal at upriver locations, where densities of clams *Macoma balthica* and *M. arenaria* were highest. Moreover, across a broad range of habitat types, i.e., seagrasses and unvegetated soft-substrates, blue crab growth rates were positively related to the abundance of *M. balthica* (Seitz et al. 2005).

Blue crab growth rates were unrelated to the other abiotic and biotic factors evaluated in this study, including water temperature, salinity, and conspecific abundance. Previous research purports that temperature is a key determinant in crab growth, including the duration of interecdysial periods and body size increases per molt (Cadman and Weinstein 1988; Brylawski and Miller 2006; Cunningham and Darnell 2015). In the present study, insufficient interannual and spatial variation in temperature among riverine sites may have contributed to the absence of a temperature-dependent growth response. Further, the monthly water temperatures reported herein (mean ~ 23 °C; maximum ~ 29 °C) closely correspond to the conditions at which blue crab growth is maximized (23–27 °C; Cadman and Weinstein 1988; Hines et al. 2010), signifying that New England tidal rivers provide an optimal thermal regime during the summer growth period. In contrast to temperature, salinity varied spatially and was an important factor underlying blue crab abundance patterns, but salinity had no apparent effect on growth performance. Prior investigations that examined the relationship between salinity and blue crab growth are often inconclusive or contradictory (Cadman and Weinstein 1988; Cunningham and Darnell 2015). Agonistic interactions among blue crabs hinders foraging efficiency (Taylor and Eggleston 2000; Seitz et al. 2017), possibly to the determinant of crab growth (Moksnes 2004), but mutual interference occurs at crab densities above those typically observed in this study (2–4 crabs/m^2; Mansour and Lipcius 1991; Clark et al. 1999).

Southern New England Tidal Rivers as Blue Crab Nurseries

The functional significance of nurseries is determined by the habitat's relative contribution of recruits to adult populations, and it is widely accepted that high-quality nurseries maximize the abundance and growth of resident biota (Beck et al. 2001). Shallow, unvegetated habitats in low-salinity waters are important nurseries for juvenile blue crabs > 25 mm CW because of the habitat's expansive areal coverage (Rakocinski et al. 2003; Lipcius et al. 2005), high prey densities (Seitz et al. 2005), and reduced predator abundances (Posey et al. 2005). Moreover, accelerated growth and the attainment of large body sizes increase the survival of blue crabs, especially during early life stages (Lipcius et al. 2007). Estimates of juvenile crab growth, therefore, are frequently used as indicators of nursery quality, such that valued nurseries are habitats that maximize growth potential (Perkins-Visser et al. 1996; Heck et al. 2003; Minello et al. 2003; Seitz et al. 2005). To evaluate the importance of southern New England tidal rivers as blue crab nurseries, the results herein were compared to conspecifics from the same habitat type at southerly locations. Accordingly, blue crab abundances and age-0+ growth rates in this study were consistent with or exceeded estimates from the Middle Atlantic, South Atlantic, and Gulf of Mexico. The corresponding crab abundances among estuarine systems show a consistent pattern in habitat use during the juvenile life stage, and further indicates that tidal rivers at the northern extent of the crab's geographic range may likewise function as valuable nurseries. Moreover, the high growth performance of crabs herein was attributed to optimal thermal conditions and abundant prey resources (e.g., bivalves; Rudnick et al. 1985; Calabretta and Oviatt 2008; D. Taylor, personal observation) in the tidal rivers, which reinforce the posit that soft-sediment, unvegetated habitats serve as high quality nurseries for this species (Lipcius et al. 2005; Seitz et al. 2005).

This study represents the first detailed quantitation of the population abundance and size-structure of blue crabs at northern latitudes. Previously, Ropes (1989) analyzed the seasonal abundance patterns of blue crabs in the Pettaquamscutt River, RI, from 1955 to 1957 and collected 190 crabs (20 to 160 mm CW) by towing a scallop dredge over subtidal shoal bars ($n = 104$ total tows; water depth 1–2 m); yet catches were sporadic in 1955 and 1957 (# crabs/tow = 0 to 12.4), and no crabs were observed in 1956. From August 1985 to July 1986, Able et al. (2002) conducted seasonal seine and trawl surveys in several habitat types of the Nauset Marsh Estuary, MA, including eelgrass, mud-sand sediments, and macroalgae (depth < 1 to 5 m), and collected ten species of decapod crustaceans (> 33,000 individuals), none of which were blue crabs (see also Heck Jr. et al. 1989). Further, from June to August 2001 and 2002, deRivera et al. (2005) performed a latitudinal assessment of blue crab abundance using trap data (depth 0–1.5 m), and detected a progressive decline in crab numbers with increasing latitude between Chesapeake Bay, VA, and Waquoit Bay, MA, and no catches at Nauset Marsh and Casco Bay, Maine. These aforementioned studies indicate that historical populations of blue crabs were ephemeral at the northernmost part of their geographic range. More recently, between 2012 and 2014, Johnson (2015) reported isolated occurrences of blue crabs in the Gulf of Maine, northward of their historical range, and further proposed a poleward expansion of the species due to elevated water temperatures.

Several laboratory investigations have articulated the thermal tolerances of blue crabs across different ontogenetic life stages, which may delineate their northern biogeographical limits. The egg incubation period for blue crabs is prolonged at temperatures < 16–19 °C (Amsler and George 1984), and < 19 °C may compromise hatching success (Sandoz and Rogers 1944). Blue crab survival and developmental rates also decrease at < 20 °C and 15 °C for the zoeal and megalopal stages, respectively (Sandoz and Rogers 1944; Costlow and Brookhout 1959; Costlow 1967). In the upper regions of the Middle-Atlantic Bight, e.g., Delaware Bay, these early life history stages occur primarily from July through October (Epifanio et al. 1984; 1989; Epifanio 1995). Juvenile and adult crabs also endure thermal stress in subsequent months, as feeding and ecdysis are inhibited at temperature < 9–10 °C (Brylawski and Miller 2006). Moreover, small juveniles (< 30 mm CW) and mature females experience high mortality rates at < 3 °C (Rome et al. 2005; Bauer and Miller 2010), and previous studies contend that the intensity and duration of over-wintering periods can drastically affect blue crab population dynamics (Hines et al. 2010; Glandon et al. 2019).

Coastal and inshore waters of northwest Atlantic have significantly increased in temperature over the last several decades (Belkin 2009), including the Narragansett Bay and adjoining coastal systems (Collie et al. 2008; Smith et al. 2010). Specifically for the Narragansett Bay, water temperatures have increased 1.4 to 1.6 °C over the past 50 years with the most pronounced warming having occurred during winter months (December to February, 1.6–2.0 °C increase) (Fulweiler et al. 2015). Current water temperatures in southern New England, therefore, may exceed levels that induce thermal stress and mortality in blue crabs across distinct ontogenetic stages (Johnson 2015), leading to a concomitant increase in recruitment success and over-wintering survival at northern latitudes. In this context, additional research in southern New England should examine the population dynamics and ecological role of blue crabs in structured and non-structured nurseries, and explore each habitat type's relative contribution of recruits to the adult population.

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