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ORIGINAL PAPER

Variability of *Mya arenaria* growth along an environmental gradient in the Plum Island Sound estuary, Massachusetts, USA

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Abstract An understanding of the environmental factors that determine how clam growth varies in space and time improves effective mariculture and shellfish management. We examined the importance of temperature, salinity and chlorophyll-*a* in controlling the spatial pattern of *Mya arenaria* growth, the commercially important soft-shell clam, in the Plum Island Sound estuary in northeastern Massachusetts, USA. We collected clams (>5.08 cm) monthly during the April to November growing season from which we determined growth rate, maximum size (L-infinity), and time to reach a harvestable size. We also surveyed selected sites along the estuary to estimate the relationship between clam size and weight. We collected environmental data along the estuary, and our data were complemented with data collected and maintained by the Plum Island ecosystems long-term ecological research project. Clams reached harvestable size fastest and had the greatest L-infinity at the most oceanic site (Yacht Club) in the estuary. Clams had the smallest L-infinity and were slowest to reach the harvestable size at the least oceanic site (Railroad Meander). The spatial patterns of clam growth were best explained by a positive distribution of salinity. Salinity significantly accounted for 95 % of the spatial variation of clam growth in the estuary. Snow melt in spring increases freshwater input to the estuary and results in the lowest spring salinity during a year, and this explained the upper estuary limit of clam distribution. IPCC-projected climate change will cause sea-level rise and increasing precipitation in the northeastern USA, which will modify the spatial pattern of salinity in the region's estuaries. Our research therefore suggests that future management of *M. arenaria*, an important economic resource for the local economy, should be concerned with the changes of salinity distribution under climate and land-use change.

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Introduction

Recognizing the importance of spatial structure has become increasingly important in ecological studies (Legendre and Legendre 2012). A spatially-ordered environmental gradient accounts for much of the variability we see in ecological processes, and failure to account for such spatial variation can result in misguided management practices and conservation guidelines (Beninger and Boldina 2014). This is true for terrestrial and marine ecosystems, including coastal estuaries with important commercial fisheries. Effective mariculture and shellfish management require an understanding of the ecosystem factors that determine the spatial variation of bivalve distribution, growth and reproduction.

Phytoplankton concentration, water temperature and water salinity have been considered major factors that control growth, reproduction and survival of bivalves (Dame 2011). Research has shown a positive relationship between the phytoplankton concentration in the water column and clam growth. The growth of *Mercenaria mercenaria,* a hard-shell clam (Carmichael et al. 2004; Coutteau et al. 1994; Pratt and Campbell 1956; Weiss et al. 2002), *Macoma balthica,* the Baltic clam (Beukema et al. 2014), and *Mya arenaria,* the soft-shell clam (Carmichael et al. 2004; Weiss et al. 2002), have all been shown to increase with elevated phytoplankton concentrations. The growth of *Corbicula fluminea*, a freshwater clam, also increased under increased phytoplankton concentrations (Petter et al. 2014). Mussels have shown similar responses to increasing phytoplankton concentrations (Smaal and Stralen 1990; Stralen and Dijkema 1994).

Water temperature controls the growth, survival and reproduction of bivalves by regulating their metabolic rates (Beukema et al. 2014; Dame 2011; Gatlin et al. 2013; Jones and Quitmyer 1996). Survival of bivalves was significantly correlated with water temperatures, showing no bivalves surviving above the marginal temperatures (Dame 2011; Gatlin et al. 2013; Weber et al. 2013). Spawning was controlled by temperature conditions and triggered by rapid changes in temperatures (Brousseau 1978; Pfitzenmeyer 1962). Bivalves (poikilotherms) grow fastest under an optimal water temperature, showing convex subsidy-stress growth responses to high and low temperatures (Butler 1953; Vernberg and Vernberg 1972). At the broad geographical scale, the greatest growth of *Crassostrea virginia,* the Virginia or American oyster, has been observed in the central portion of its latitudinal range, declining in more northern and southern portions of the US East coast (Butler 1953). Annual growth of estuarine and marine bivalves has shown a strong correlation with the annual variation of temperature. Such a relationship between growth rates and temperature has been used in climatology to deduce and understand paleotemperature information and climate change (Royer et al. 2013; Scourse et al. 2006; Stephens et al. 2008; Strom et al. 2004).

Water salinity influences the growth and distribution of bivalves through osmoregulatory mechanisms (Sumich and Morrissey 2004). Diversity and density of bivalves change with salinity gradients, and their upstream distribution in estuaries can be limited by low salinity (Tezuka et al. 2013; Wells 1961). For example, maximum shell lengths of *M. arenaria* decreased with decreasing salinity in the southern Baltic Sea (Filippenko and Naumenko 2014). The shell size of *Mytilus edulis*, the blue mussel, also significantly declined with decreased salinity in the north-eastern Baltic Sea (Westerbom et al. 2002).

The soft-shell clam, *M. arenaria*, is widely distributed in coastal, intertidal soft substrates in the eastern and western coasts of North America (Cross et al. 2012). *M. arenaria* is a dominating species in local benthic communities in Nova Scotia, many New England estuaries and on the Pacific coast after dry periods. It is a commercially important species in New England and the middle Atlantic region of the US (Strasser 1998). The normal lifespan of *M. arenaria* is 10–12 years (Brousseau 1978) with a maximum of 28 years on the east coast of North America (MacDonald and Thomas 1980). Spawning, survival and growth are mainly influenced by temperature, salinity and food availability (Belding 1930; Carmichael et al. 2004; Filippenko and Naumenko 2014; Stickney 1964).

Mya arenaria grows well in the sediments of the mesotrophic Plum Island Sound estuary (PIE) in northeastern Massachusetts, USA and is an important economic resource for the local economy. In this region increased suburbanization leads to increased nitrogen inputs to the estuary, which can cause increases in phytoplankton abundance and blooms (Bricker et al. 2008; Driscoll et al. 2003). Phytoplankton blooms are most likely in the upper oligohaline regions of PIE and is of concern because of the negative effects on the structure and function of the entire estuarine food web (Nelson et al. 2015). Combined with marginal habitat conditions in the upper oligohaline regions, increased phytoplankton abundance could either benefit or harm clam growth (Cloern 1982). Therefore, understanding the spatial variation of *M. arenaria* growth according to the gradient of environmental factors in relation to phytoplankton abundance is critical for shellfish management in PIE as well as other river-dominated estuaries under environmental changes.

The objectives of this study were to determine the spatial variations of *M. arenaria* growth along the Plum Island Sound estuary and to identify the dominant factors controlling those variations. We hypothesized that the spatial pattern of *M. arenaria* growth was mainly controlled by physical environmental conditions and secondarily by phytoplankton abundance under appropriate environmental conditions. With this in mind, we investigated the spatial variation of *M. arenaria* growth along the strong gradients of salinity, temperature and phytoplankton abundance in the Plum Island estuary.

Materials and methods

Study sites

This study was conducted in the Plum Island Sound estuary in northeastern Massachusetts, USA (Fig. 1), a productive system for *M. arenaria* that supports a valuable commercial fishery of Ipswich steamer clams (*M. arenaria*) with an average yearly harvest of 176,977 kg (Buchsbaum et al. 2000). This 24 km long estuary (20 km^2 intertidal excluding wetlands) has a vertically well-mixed water column with an along-estuary horizontal gradient and temporal range in salinity of 0–32 psu and water temperature of −1.0 to >28 °C (Vallino and Hopkinson 1998). Annual precipitation of 1180 mm is evenly distributed throughout the year, but river flow is greatest during early spring snowmelt and often several orders of magnitude lower in the summer and fall (Claessens et al. 2006). Salinity varies substantially along the full length of the estuary, but the primary clam beds see annual ranges of about 20–32 psu. The mean tidal range of the estuary is about 2.6 m, and the mean depth is about 1.6 m (Deegan and Garritt 1997). There are vast intertidal flats at low tide, many of which are prime clam habitats. Phytoplankton densities and inorganic nutrient concentrations reflect seasonal cycles and the temporally varying relative importance of freshwater versus seawater inputs to the estuary. During summer, chlorophyll-*a* (Chl-*a*) and nutrient concentrations are highest in the upper estuary (Deegan and Garritt 1997), while in late winter and early spring Chl-*a* levels are highest in the lower estuary, where waters exchange daily with the Gulf of Maine and its spring phytoplankton bloom.

Mya arenaria growth estimates

Internal growth line analysis

Annual growth information on *M. arenaria* has been estimated by visual analysis of external color patterns on shell surfaces and growth lines on shell cross-sections (Brousseau 1979; Feder and Paul 1974; Newcombe 1935; Rhoads and Lutz 1980). Occasionally, growth lines on shell cross-sections are more apparent and easier to interpret than growth lines on the shell surfaces (Rhoads and Lutz 1980). Annual growth lines on shell cross-sections were identified, marked and counted. The internal growth lines were transcribed onto the shell surface and the shell length was measured for each year of age.

We selected six sampling sites along the flanks of the lower 14 km of the estuary where the clams are commonly found—from about 10 to 24 km (the estuary mouth or inlet is at km 24): Yacht Club, Third Creek, Clubhead Creek, Grandkid's Flat, Sweeney Creek, and Railroad Meander (Fig. 1). The 14 km long zone where clams grow in this estuary has a strong gradient in food resource base and availability (Deegan and Garritt 1997), water temperature and salinity. We collected approximately 40 clams (>5.08 cm) monthly from May to November in 2010 and April in 2011.

Approximately 20 shells ≥5.08 cm (=2 inch) with obvious external growth lines and patterns but minimal signs of shell repair were selected at each site for

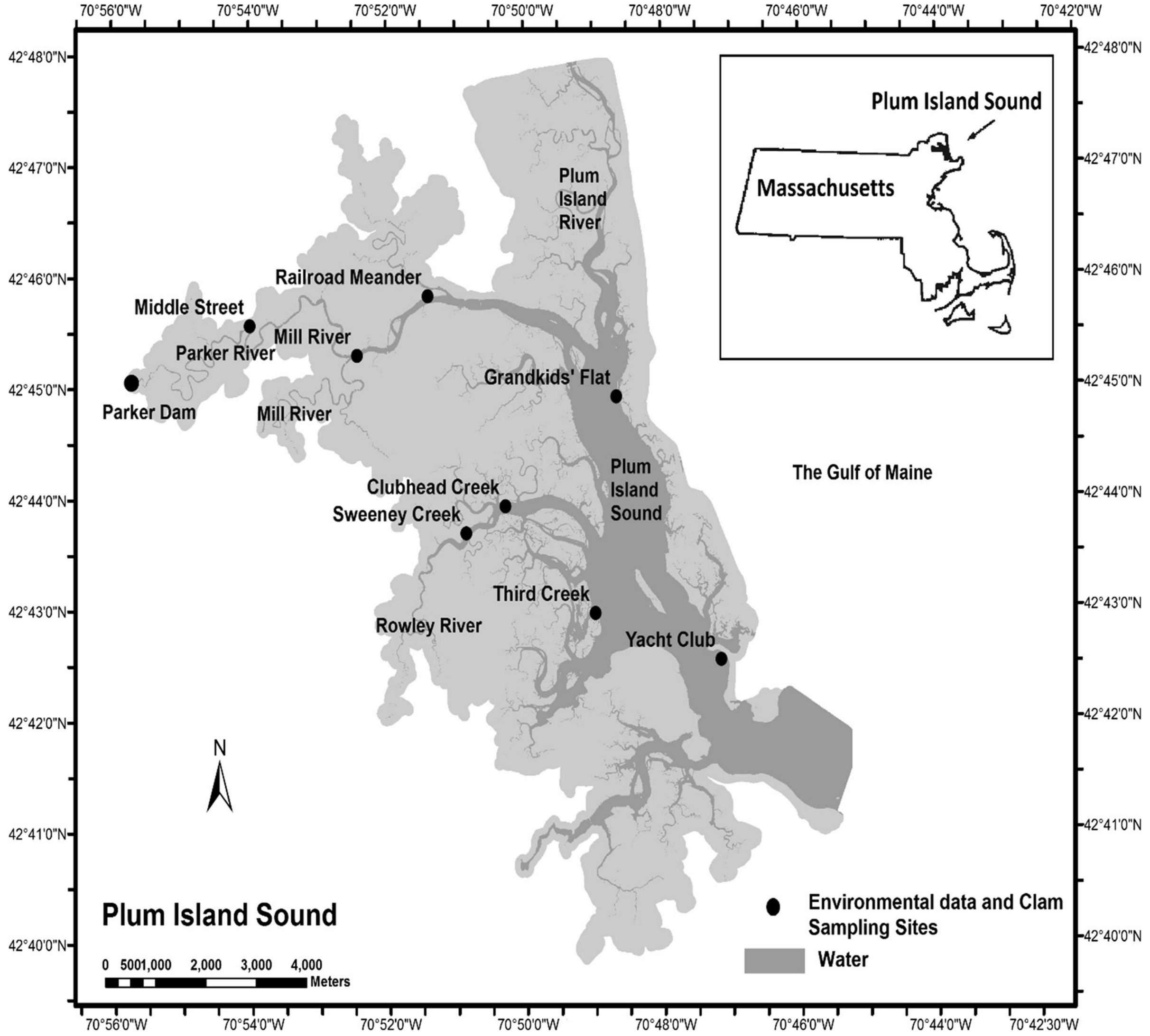


Fig. 1 Map of the Plum Island Sound estuary in northeastern Massachusetts, USA showing locations (*black dots*) where *M. arenaria* and environmental data were collected. The Parker Dam dot (*left-most* position on map) shows the landward end of the estuary, which is labeled as km 0 in Figs. 4 and 6. The *lightly shaded area* denotes intertidal wetlands along the mainstem of the estuary

internal growth line analyses (Fig. 2a). Internal growth line analysis used one valve of each clam for delineation of internal growth lines and the other valve for transcribing internal lines onto the shell surface in order to estimate size for each year of growth. To do this, the valves were first embedded in epoxy resin (Henkel Corp 1365850 Loctite Heavy-Duty Pro Epoxy Extra Time) to prevent shell fracture during sectioning (Ropes 1984). The valves were sectioned from the umbo to the ventral margin using a rock saw (Fig. 2a). The cross-sectional surface was ground with 240, 320 and 600 abrasive papers and polished with Microcloth® PSA of #70–7220 using a Buehler MetaServe® 250 Grinder-Polisher (Ropes 1984). We periodically observed the cross-section under a microscope, Fisher Scientific Stereomaster Stereo Microscope 10X and 30X, during the grinding-polishing process and continued the process until the internal growth lines became apparent. Annual growth lines were identified, marked and counted under the microscope (Fig. 2b). The internal growth lines were transcribed onto the shell surface of the matching

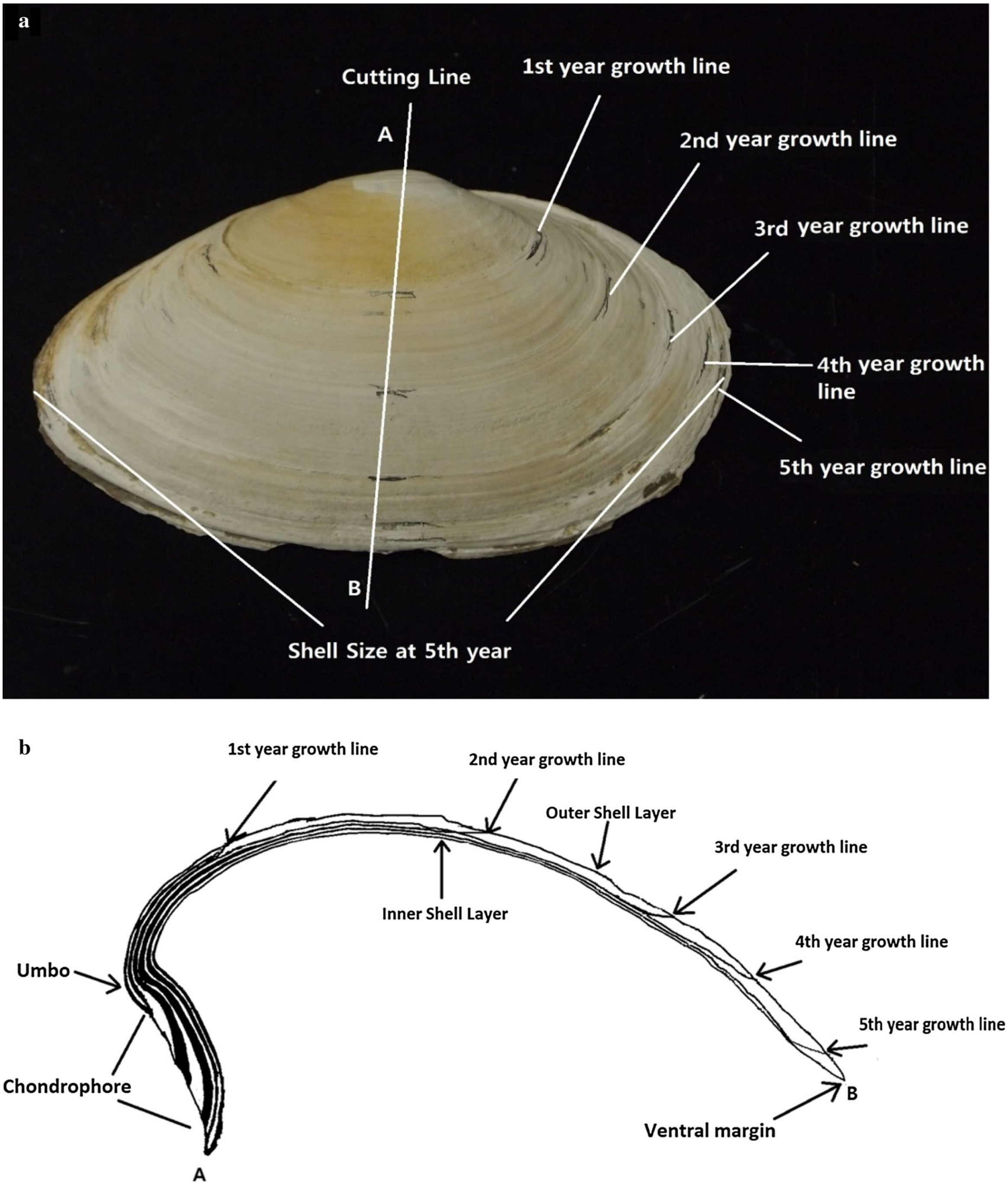


Fig. 2 Pictures and drawings illustrating procedures we followed for identifying internal growth lines and measuring size at various ages in *M. arenaria*. **a** *Step 1* Shell sectioning: shell was sectioned along line *A–B*, followed by sanding and polishing of the cross-sectional edge. *Step 3* Marking growth lines on the shell surface and measuring clam size at different ages: here we show the locations where internal growth lines intersect the shell surface on the uncut shell pair of the clam used in step 2. By tracing the extent of these lines around the shell, clam size (length) was measured for each year of age. **b** *Step 2* Identifying internal growth lines on a polished shell cross-section: Internal growth lines were identified by visual inspection of the shell cross-section. Where growth lines intersect the outer shell surface marks where shell surface growth lines are expected to appear. Here a cross-section with internal growth lines is schematically shown for a 5+ year old clam

valve and then shell length was measured for each year of age (Fig. 2a). Shell length was measured as the maximum distance across the shell surface, typically perpendicular to the cross-sectional cut (A–B in Fig. 2a). The measurements were made to the nearest 0.01 mm using digital vernier calipers.

Mya arenaria can show abnormally small (smaller than 25 percentile) or large (larger than 75 percentile) growth at year . This may be related to the spawning pattern of *M. arenaria* in this region, which is twice a year (Brousseau 1978). The first spawning period begins in spring and the second period in fall (Pfitzenmeyer 1962). Clams spawned in fall have a short growing period the first year and show abnormally small growth at year 1. Alternatively, the short growing period presents a weak first-year growth line, which is not seen in the internal growth line analysis, resulting in a false analysis of abnormally large growth at year 1. Absence of first-year lines on the cross-sections of other marine bivalve species has been reported in the literature previously (Richardson et al. 1993; Richardson et al. 1980; Richardson et al. 1999). Absence of first-year lines on the shell surface of *M. arenaria* has been reported also (Filippenko and Naumenko 2014; Maximovich and Guerassimova 2003). For our analysis we excluded clams with great year 1 variability (smaller than the 25th percentile and larger than the 75th percentile) in order to avoid uncertainty in calculating annual growth.

Maximum growth estimates and its spatial projection

The von Bertalanffy Growth Function (VBGF) model is most commonly used to estimate maximum size *of M. arenaria* (Brousseau 1979; Carmichael et al. 2004; Palacios et al. 1994; Philipp et al. 2005), despite its limitations (Rogers-Bennett et al. 2007). We estimated annual growth of *M. arenaria* by fitting the age-size measurements to a von Bertalanffy growth model:

$$L_t = L_\infty\left(1 - e^{-k(t-t_0)}\right) \tag{1}$$

where L_t is *M. arenaria* length at age t (year); L_∞ (L-infinity) is the mean asymptotic length; k is growth coefficient and determines how fast L_∞ is reached (curvature parameter); t_0 is the theoretical age when a clam's length was 0 ($t_0 = 0$). L-infinity informs the maximum size a clam may reach.

The spatial projection of clam growth

For understanding the spatial patterns of clam growth along the estuary, we simulated the distribution of the maximum size (L-infinity) as a function of longitudinal distance, x, in the estuary. The longitudinal distance presented the distance from the Parker River Dam (0 km), Railroad Meander (~14 km) to the Sound (24 km) (Fig. 1). The spatial pattern of clam growth was fitted to a three parameter sigmoid function [Eq. (2)].

$$\text{Shell length}\,(x) = \frac{a}{1 + e^{-b(x-c)}} \tag{2}$$

We also estimated the relationship between shell length and clam wet and dry weight to determine if changes in shell length reflected the changes of clam weight. The shell length- clam wet weight function was estimated with 85 clams collected from four sites— Yacht Club, Third Creek, Grandkid's Flat and Railroad Meander—during May, 2010. The length-clam dry weight function was estimated with 19 clams collected from Plum Island Sound in the same month. The measurements of shell length were made to the nearest 0.01 mm using digital vernier calipers. The clam wet mass (g) was measured on a precision balance. Clam dry mass (g) was measured similarly but following drying to constant weight at 60 °C. Then, the relationship between clam wet and dry weight and shell length was estimated using a power function.

Acquisition of environmental data and spatial projections

To estimate the quantity of chlorophyll-*a* (Chl-*a*) concentration in the water, water samples were collected monthly from May to November in 2010 and April 2011 at six sites along the length of the estuary. These six sites included Yacht Club, Third Creek, Grandkid's Flat, Railroad Meander, Mill River and Middle Street (Fig. 1). Water samples were collected with 1-L brown Nalgene bottles and filtered using Whatman GFC 25 mm filters. The filters were frozen and the Chl-*a* was extracted in the lab in 90 % acetone. The Chl-*a* extraction was implemented by the method of Arar and Collins (Arar and Collins 1997). Chl-*a* concentrations (µg/L) were measured on a fluorometer. For better understanding of the spatial pattern of Chl-*a* in the estuary, we used the long-term Chl-*a* data obtained from the Plum Island Ecosystems Long-Term Ecological Research (PIE LTER) database (http://ecosystems.mbl.edu/pie/data.htm). The PIE LTER Chl-*a* data include Chl-*a* concentrations collected annually in spring (April 1997–2007) and late summer (September 1996–2007). These data were averaged to illustrate typical spatial patterns of Chl-*a* along the length of the estuary. The distribution of Chl-*a* as a function of longitudinal distance, x, in the estuary was fitted to a second order polynomial function showing the maximum R square value.

Water temperatures were measured along the entire length of the estuary twice a day for 3 days in late summer 2010 as part of the LTER monitoring program. We averaged the water temperatures over time by distance along the estuary to estimate the spatial pattern of temperature for the growing season. The distribution of average water temperatures as a function of longitudinal distance, x, in the estuary was fitted to a second order polynomial function with the maximum R square value. Water temperature at each clam sampling site was then estimated with this function. Water temperatures were measured with YSI 650 XLM water quality datalogging sonde. Salinities were measured simultaneously. We augmented our measurements of salinity with that collected during spring and fall from 1997 to 2007 by the PIE LTER project (http://ecosystems.mbl.edu/pie/data.htm). Salinity data were averaged over time by station to estimate spatial patterns of salinity in the estuary during periods of high (April) and low (September) river flow.

The distribution of salinity at high tide was estimated using a one dimensional, intertidal, advection–dispersion transport model summarized from Vallino and Hopkinson (1998) (Eqs. 3a–3f) (Hopkinson and Vallino 1995; Vallino and Hopkinson 1998).

$$\frac{\partial(A(x)c(x,t))}{\partial t}=\frac{\partial}{\partial x}\left(A(x)D(x)\frac{\partial C(x,t)}{\partial x}-q(x,t)c(x,t)\right)+\sum_{i=1}^{l}\left(cli(t)\frac{\partial qi(x,t)}{\partial x}\right)+A(x)r(t) \tag{3a}$$

$$A(x) = 45 + 0.02x + 4\times10^{-10}x^{3} \tag{3b}$$

$$D(x) = 31.42\left(\frac{x}{24008-x}\right)^{1.055} \tag{3c}$$

where *x* is distance (m), *t* is time (day), c(*x, t*) is salt concentrations (in mg m^{-3}), *A*(*x*) is river cross sectional area at high tide(m^2), *D*(*x*) is the longitudinal dispersion coefficient (m^2 day^{-1}), *q*(*x, t*) is the cumulated freshwater discharge (m^3 day^{-1}), c*li*(t) is the salt concentration in lateral input *i*, r(*t*) is the production rate of salt (mg m^{-3} day^{-1}) and *x* is the location at high tide (m). *A(x)* was calculated by fitting the simple polynomial to the data from the estuary, and *D*(*x*) was estimated from salinity transects and dye release experiments.

The left side boundary condition (*xL*, the Parker Dam) of the model domain was specified by a time dependent flux (Eq. 3d) and right side condition (*xR*, the ocean side) explained by the Dirichlet boundary condition (Eq. 3e). To improve the salinity gradient, $dc_s(x)/dx$, a three parameter sigmoidal function (Eq. 3f) was first fitted to the salinity data and the derivative was calculated at the salinity sampling sites.

$$\left[D(x)A(x)\frac{\partial c(x,t)}{\partial x}-q(x,t)c(x,t)\right]_{x=xL} = -qxL(t)cxL(t) \tag{3d}$$

$$c(x,t)|x = xR = cxR(t) \tag{3e}$$

$$c_s(x) = \frac{a}{1-e^{-b(x-c)}} \tag{3f}$$

where *qxL*(*t*), c*xL*(*t*) and c*xR*(*t*) were the freshwater input and salt concentration in the freshwater and the ocean water at time t, respectively. The freshwater input was calculated using Parker River discharge from the USGS gauge in Byfield, Massachusetts, USA correcting for ungauged portions of the watershed below the gauge (Vallino and Hopkinson 1998).

Relationship between clam growth and environmental factors

For identifying environmental factors that likely control the spatial pattern of *M. arenaria* growth, we simulated the spatial projections of Chl-*a*, water temperature, salinities and clam growth together along the longitudinal distance, x, in the estuary. The simulation enabled the spatial patterns of clam growth and environmental factors to be visually compared and provided information on what environmental factor showed a similar spatial pattern with clam growth.

Polynomial and linear regression analyses were also implemented to find the environmental factors that best explain the spatial pattern of clam growth in PIE. For the regression analyses, we first calculated the estimates of four environmental parameters at 12 sites including six clam sampling sites from Parker Dam to Yacht Club (Fig. 1) using the models developed for Chl-*a*, water temperature, and salinity. Then, we identified the environmental parameters most independent for regression analyses, rejecting the parameters that Pearson's correlation analysis showed to be strongly correlated ($r > 0.7$). Next, we made eight candidate models and applied the regression models to each candidate model. We then determined the environmental factors with the highest R^2 as the dominant factor controlling the spatial pattern of clam growth. The R^2 values of regression models explained what percentage the spatial variation of clam growth in PIE could be attributed to the environmental factors. The p value of 0.05 was used for examining the significance of correlation. Statistical analyses were implemented with R.3.1.2. (Venables and Ripley 2002) and modeling the spatial patterns of salinity, Chl-*a*, water temperature and *M. arenaria* growth were done with Matlab7.8.0. 2009a (Saucez et al. 2009).

Results

Spatial variations of *M. arenaria* growth

Mya arenaria age to size data indicated that the clams we collected throughout the Plum Island Sound estuary ranged in age from 3 to 7 years old. The youngest clam was collected at the site closest to the ocean and the oldest clam was collected from the site furthest from the ocean. The age frequency data, which is shown in the online supplementary information (Fig. S1), presented the clam frequencies at age 5–6 (large clams) are pretty low for most sites (Fig. S1).

Fig. 3 **a** Growth curves of *M. arenaria* clams for six sites in the ▶ Plum Island Sound estuary. Individual growth curves for each site are shown in the online supplementary information (Fig. S1). The individual growth curve figures include data for specific clams at various ages, R^2, p value, and standard deviation of observed clam sizes at each age. The *thin solid horizontal line* shows the legal minimum harvestable size of clams (approximately 50.8 mm or 2 inches). **b** The relation between clam wet weight and shell length. Clam wet weight was fitted to shell length using the second order polynomial equation ($Clam\ wet\ weight = 0.00006L^{3.15}$, $L =$ shell length, $R^2 = 0.96$, $p < 0.01$)

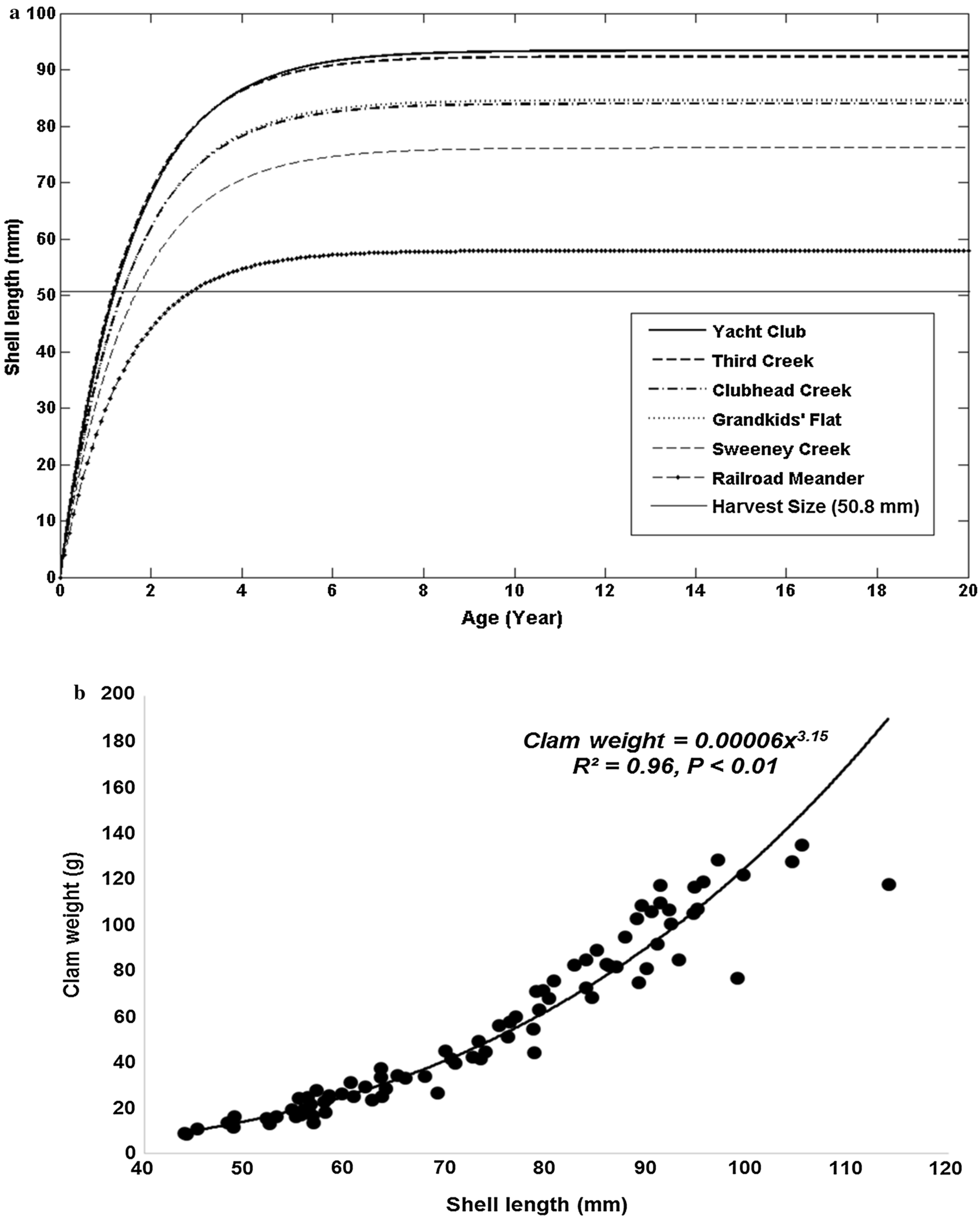
We calculated the growth coefficient (k), the mean maximum size (L-infinity), the age to reach L-infinity and the age to reach the minimal harvest size (5.08 cm) by fitting the VBGF model (Eq. 1) to the age-size data for clams at each site. Growth function estimation was based solely on age 1–4 years data, as there was insufficient data for years 5 and 6 (Table 1; Fig. S1). The growth functions (Table 1) projected the L-infinity of *M. arenaria* for each site (Table 1; Fig. 3a). The individual growth curve with R^2, p value, and standard deviation of observed clam sizes at each age for each site are shown in the online supplementary information (Fig. S1). All growth curves significantly explain clam growth for each site ($R^2 > 0.99$ and $p < 0.01$) (Table 1).

While some aspects of growth as determined from the VBGF showed a continuous spatial pattern, others did not (Table 2). Growth coefficient (k) and the age to

Table 1 Functions describing aspects of *M. arenaria* growth at six sites along the Plum Island Sound estuary

Site	N (# of samples)	VBGF	R^2	P value
Yacht club	10	$L_t = 93.39\ (1–e^{(-0.65t)})$	1.00	<0.01
Third creek	8	$L_t = 92.34\ (1–e^{(-0.68t)})$	1.00	<0.01
Clubhead creek	12	$L_t = 83.99\ (1–e^{(-0.67t)})$	1.00	<0.01
Grandkid's flat	14	$L_t = 84.60\ (1–e^{(-0.66t)})$	1.00	<0.01
Sweeney creek	10	$L_t = 76.15\ (1–e^{(-0.65t)})$	0.99	<0.01
Railroad meander	10	$L_t = 57.92\ (1–e^{(-0.72t)})$	0.99	<0.01

Each function was estimated by fitting the age-size data collected in this study to the VBGF (Eq. 1). L_t indicates *M. arenaria* shell size (mm) at each year (t). Site shows the names of sites where samples were collected and N is the number of clam samples used for estimating the growth function


a
Shell length (mm)
Age (Year)
0
10
20
30
40
50
60
70
80
90
100
0
2
4
6
8
10
12
14
16
18
20
Yacht Club
Third Creek
Clubhead Creek
Grandkids' Flat
Sweeney Creek
Railroad Meander
Harvest Size (50.8 mm)
b
Clam weight (g)
Shell length (mm)
0
20
40
60
80
100
120
140
160
180
200
40
50
60
70
80
90
100
110
120
Clam weight = 0.00006x^3.15
R² = 0.96, P < 0.01

reach L-infinity differed between stations, but not with a consistent along-estuary pattern (Table 2). The Railroad Meander clams grew fastest and reached L-infinity at the youngest age ($k = 0.72$, age to reach L-infinity = 12.7 years) and the Yacht Club and Sweeney Creek clams grew slowest ($k = 0.65$) and reached L-infinity at the oldest age (15.2 years and 14.9 years respectively). The age to reach the minimal harvest size (50.8 mm) and L-infinity showed obvious spatial patterns (Table 2). The age to harvestable size increased from the Yacht Club site (1.2 years), the most oceanic, to the Railroad Meander site (2.9 years), the least oceanic, while L-infinity decreased from the Yacht Club (93.39 mm) to the Railroad Meander (57.92 mm). Overall, we found that clams grew fastest to harvestable size and had the potential for greatest L-infinity at Yacht Club and Third Creek sites, which are sites close to the ocean. The site furthest from the ocean (Railroad Meander) was the slowest to harvestable size and had the smallest potential maximum size (Table 2).

The wet weight of *M. arenaria* is significantly explained by shell length as shown in Fig. 3b ($Clam\ weight = 0.00006L^{3.15}$, L = shell length, $R^2 = 0.96$, $p < 0.01$). Therefore, wet weight decreased up-estuary from the Yacht Club (98.24 g) to the Railroad Meander (21.77 g) site. Dry weight of *M. arenaria* is also significantly explained by shell length as shown in Fig. S3 of the online supplementary ($Clam\ dry\ weight = 0.0001L^{1.99}$, L = shell length, $R^2 = 0.51$, $p < 0.01$), but the relation was not as good as for wet weight. Dry weight per clam at each site was estimated with the clam dry weight-shell length function (Table 4). Dry weight per clam decreased up-estuary from the Yacht Club (0.82 g/clam) to the Railroad Meander (0.32 g/clam) site. Further discussion is limited to wet weights because of the statistically better relation.

Spatial patterns of Chl-*a*, water temperature and salinity

The concentration of Chl-*a* during the primary growing season (June–October in 2010) was much higher at the upper estuarine sites (Middle Street and Mill River) than the ocean sites (Third Creek and Yacht Club) (Fig. 4b–c; Table 3). Chl-*a* concentrations in late fall were almost evenly distributed from Railroad Meander to Yacht Club but lowest in the upper estuary (e.g., 1.4 µg/L at km 11.5 vs. 2.7 µg/L at km 21.3). The PIE LTER long-term average data (September mean and April mean) showed the same trend as our observations from June to October, decreasing from the upper estuary to the ocean (Fig. 4b–c). To estimate the long-term average of growing season Chl-*a* distribution, the September mean was fitted to a second order polynomial equation ($\text{Chl-}a = 0.08x^2 - 3.64x + 40.53$, $R^2 = 0.94$, $p < 0.01$, x = distance from Parker Dam, Fig. 4c). The Chl-*a* function explained 94 % of the Chl-*a* spatial variation along the length of the estuary.

Water temperature averaged over our six observations in August and September 2010 gradually decreased from the upper estuary to the ocean (Table 3; Fig. 4d). The average temperature was fitted to a second order polynomial equation ($Temp_{summer} = -0.0031x^2 - 0.0707x + 24.298$, $R^2 = 0.82$, $p < 0.01$, x = distance from Parker Dam, $Temp_{summer}$ = summer water temperature). The equation significantly explained 82 % of the spatial variation of water temperature in the estuary.

Table 2 Aspects of *M. arenaria* growth at each site where samples were collected in the Plum Island Sound estuary

Site	*K*	Age to reach harvest limit (years)	Age to reach L-infinity (years)	L-infinity (mm)	Clam wet weight (g)	Clam dry weight (g)
Railroad meander	0.72	2.9	12.7	57.92	21.8	0.32
Sweeney creek	0.65	1.7	14.9	76.15	51.6	0.55
Grandkid's flat	0.66	1.4	14.8	84.60	71.9	0.67
Clubhead creek	0.67	1.4	14.6	83.99	70.3	0.67
Third creek	0.68	1.2	14.5	92.34	94.8	0.80
Yacht club	0.65	1.2	15.2	93.39	98.2	0.82

The VBGF growth parameters: growth rate coefficient (k), clam age upon reaching harvestable size (50.8 mm), age of clam if it was to reach L-infinity, and L-infinity, the potential maximum size of clams for each site. k determines how fast L_∞ is reached

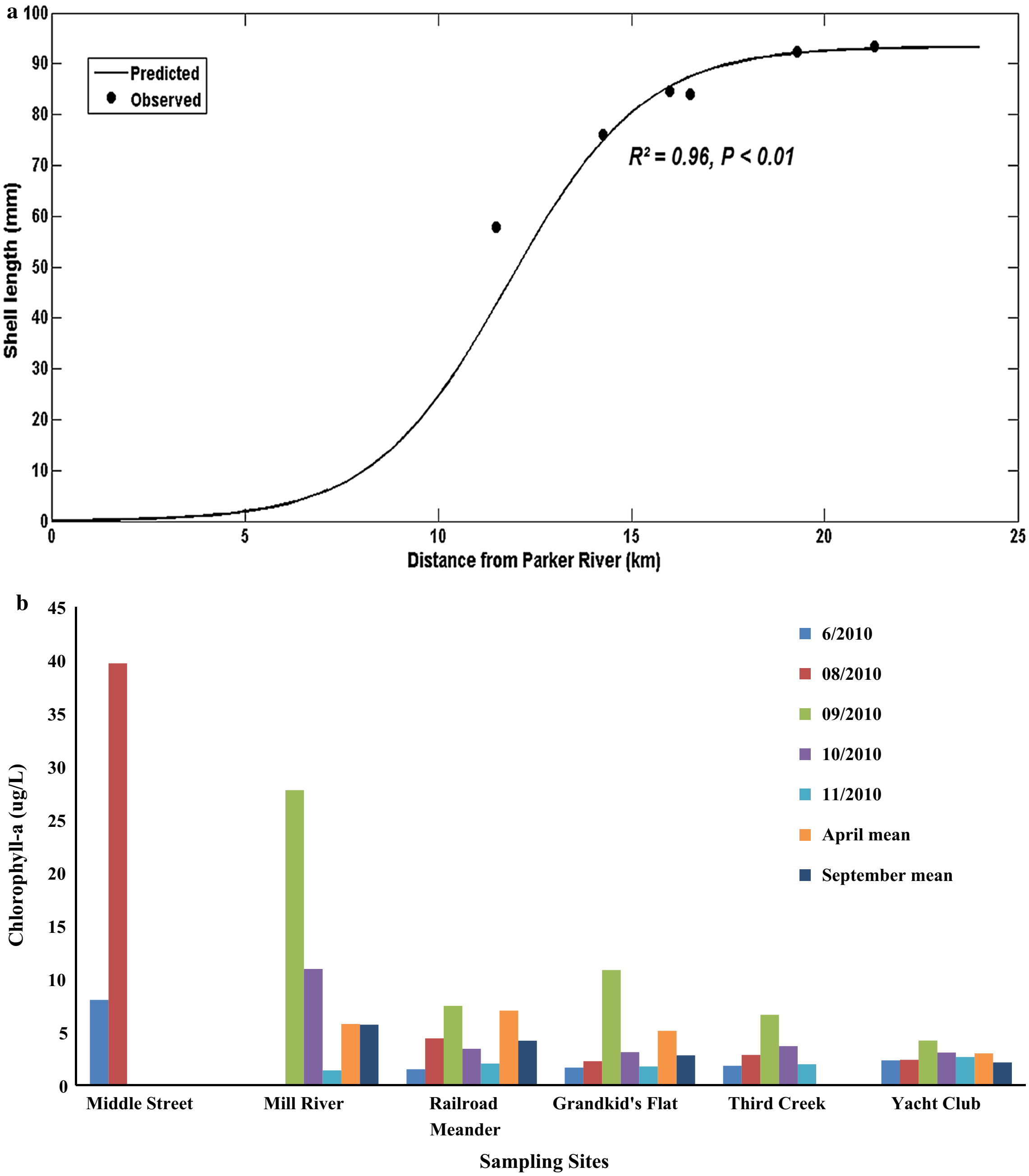


Fig. 4 Spatial variation of environmental factors along the estuary. **a** Spatial pattern of clam growth projected with the three parameter sigmoid function ($\mathit{shell\ length} = 93.39/(1 + e^{-0.57(x-11.8)})$, $R^2 = 0.96$, $P < 0.01$). **b** The field observations of Chl-*a* concentration at each site in the estuary several times during the year of study. **c** Spatial distribution of chlorophyll-*a* concentration (Chl-*a*) estimated with the second order polynomial equation ($\text{Chl-}a = 0.08x^2 - 3.64x + 40.53$, $R^2 = 0.94$, $p < 0.001$). The equation was fitted to the average of PIE LTER September data (not shown). The spatial pattern of Chl-*a* for September was obtained by averaging the data of 1996, 2000, 2001, 2002, 2004, 2005 and 2007. **d** Spatial pattern of summer water temperature estimated with the second order polynomial equation ($\mathit{Temp}_{summer} = -0.0031x^2 - 0.0707x + 24.298$, $R^2 = 0.82$, $p < 0.01$). **e** Spatial patterns of April and September salinity estimated using the 1-D model. *Circle and square dots* indicate observations obtained from the PIE LTER database. x is a distance from Parker Dam

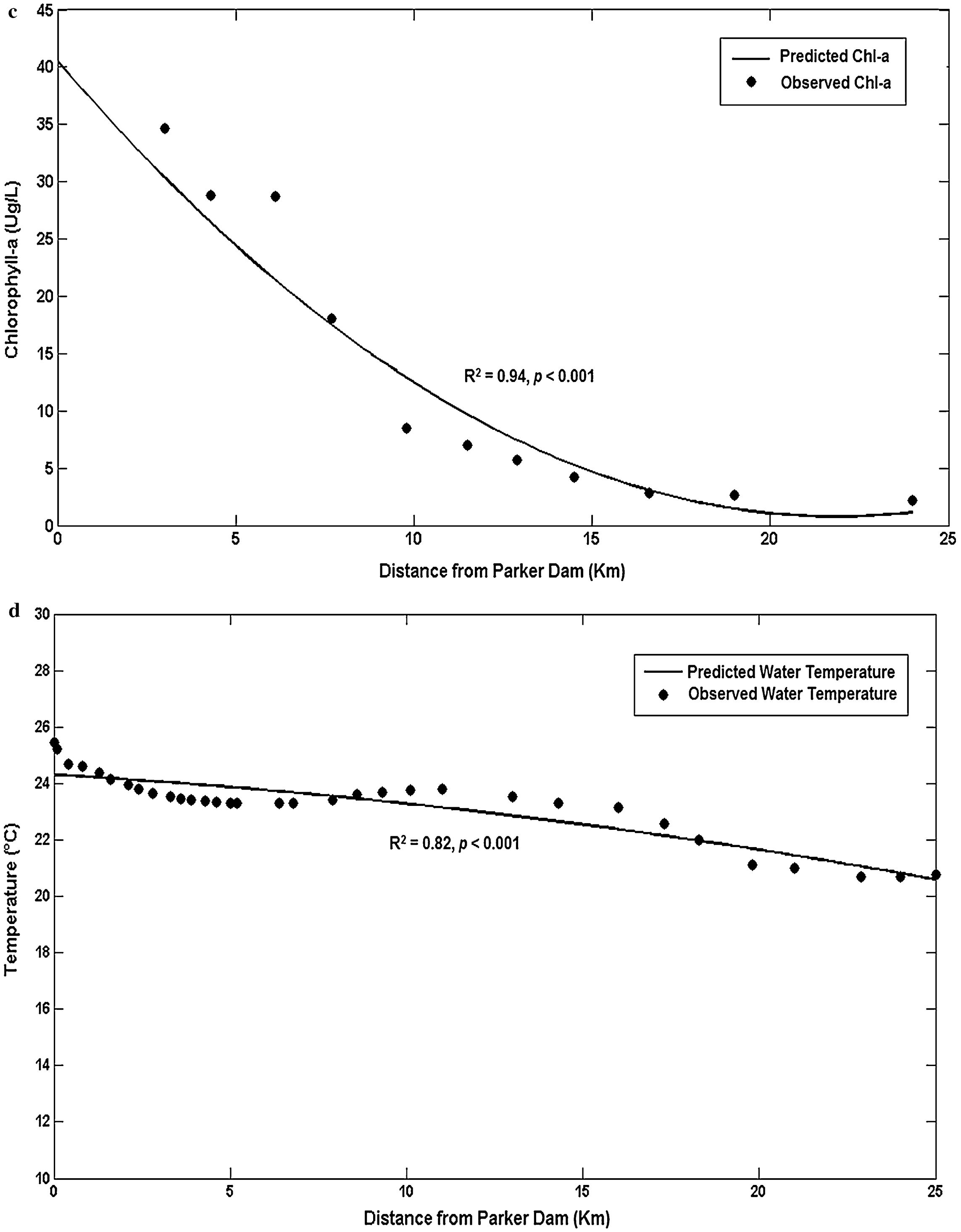


Fig. 4 continued

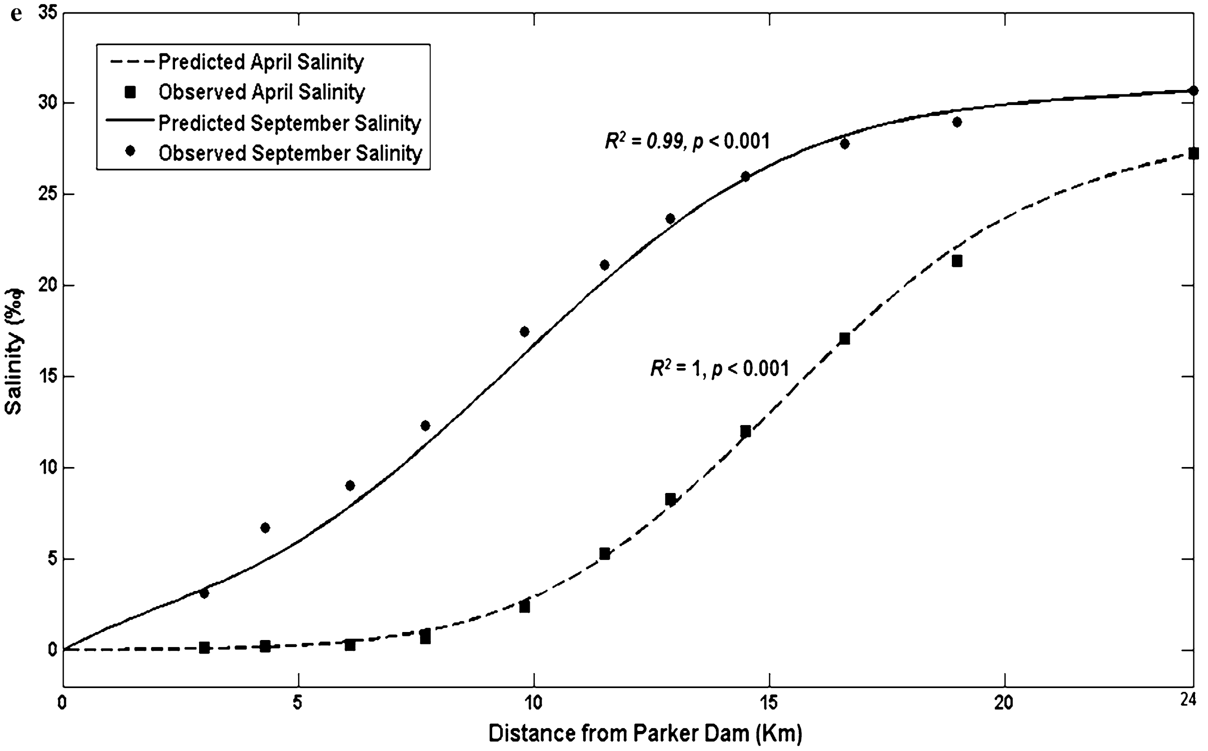


Fig. 4 continued

Table 3 Measures of environmental factors (temperature, salinity and chlorophyll-*a*), maximum shell size of *M. arenaria* in the Plum Island Sound estuary, and the regression results, the data used for the regression analyses

Clam sampling site	Distance from Parker Dam (km)	Maximum shell length (mm)	April salinity (‰)	September salinity (‰)	Chlorophyll-*a* (µg/L)	Summer temperature (°C)
	0.00	0.00	0.00	0.00	40.53	24.30
	3.00	0.00	0.07	3.37	30.37	24.06
	4.30	0.00	0.17	5.01	26.43	23.94
	6.10	0.00	0.45	8.03	21.44	23.75
	7.70	0.00	1.08	11.90	17.45	23.57
	9.80	0.00	2.73	17.08	12.87	23.31
Railroad meander	11.50	57.92	5.30	20.94	9.70	23.07
Sweeney creek	14.25	76.15	11.18	25.85	5.59	22.66
Grandkid's flat	16.00	84.60	15.91	27.87	3.62	22.37
Clubhead creek	16.53	83.99	17.06	28.36	3.13	22.28
Third creek	19.30	92.34	22.87	29.76	1.31	21.78
Yacht club	21.30	93.39	25.42	30.22	0.79	21.39

Distance from Parker Dam shows where along the estuary samples were collected. Clubhead Creek and Sweeney Creek samples were off the main axis of the estuary and their distances were calculated on the basis of the distribution of salinity measured in August 2010

The spatial patterns of salinity during high and low river discharge were estimated using a one dimensional, intertidal, advection–dispersion transport model (Table 3, Fig. 4e). To improve salinity predictions, three parameter sigmoidal Equation $(27.3/(1 + e^{-0.7(x-15.2)})$ for April data; $30.7/(1 + e^{-0.35(x-9.2)})$ for September data were first fitted to the PIE LTER long-term average data. Salinity distributions in the estuary were well explained by a one dimensional, intertidal, advection–dispersion transport model ($R^2 = 0.99$, $p < 0.01$ for April salinity; $R^2 = 1, p < 0.01$ for September salinity). The salinity distribution during the growing season (September salinity) was high enough to support clam growth in all areas of the estuary. During high flow conditions in winter and spring, however, salinity is critically low (<1 psu) for several months in the upper estuary. In April, we found salinity at high tide lower than 2.8 psu from 0 to 10 km.

Relationship between clam growth and environmental factors

The clam growth and environmental conditions at twelve points along the estuary were estimated with the model for each factor (Table 3). The Chl-*a* concentrations for the points from Parker Dam to Yacht Club were estimated with the Chl-*a* function, water temperatures with the $Temp_{summer}$ equation, and salinities with the one dimensional, intertidal, advection–dispersion transport model. The Pearson's correlation analyses showed strong correlations ($r > 0.8$) among environmental factors. Thus, four polynomial and linear candidate models, explaining the relationship between growth and each environmental factor, were employed for the regression analyses (Fig. 5).

All factors significantly explained the spatial variation of clam growth in PIE; the negative correlations with Chl-*a* concentration and water temperature and the positive correlations with salinities (Table 4). Based on the R^2 values of polynomial and linear regression models, all factors showed very good correlations with clam growth: the R^2 values of linear regression models were higher than 0.80 and for polynomial regressions higher than 0.89 (Fig. 5). In particular, April and September salinities best explained the spatial variation of *M. arenaria* growth in PIE, showing the highest R^2 values of polynomial (0.95 for both of them; Fig. 5a, b) and linear regressions (0.86 for April salinity and 0.88 September salinity; Fig. 5a, b). Considering the distributions of environmental factors and clam growth

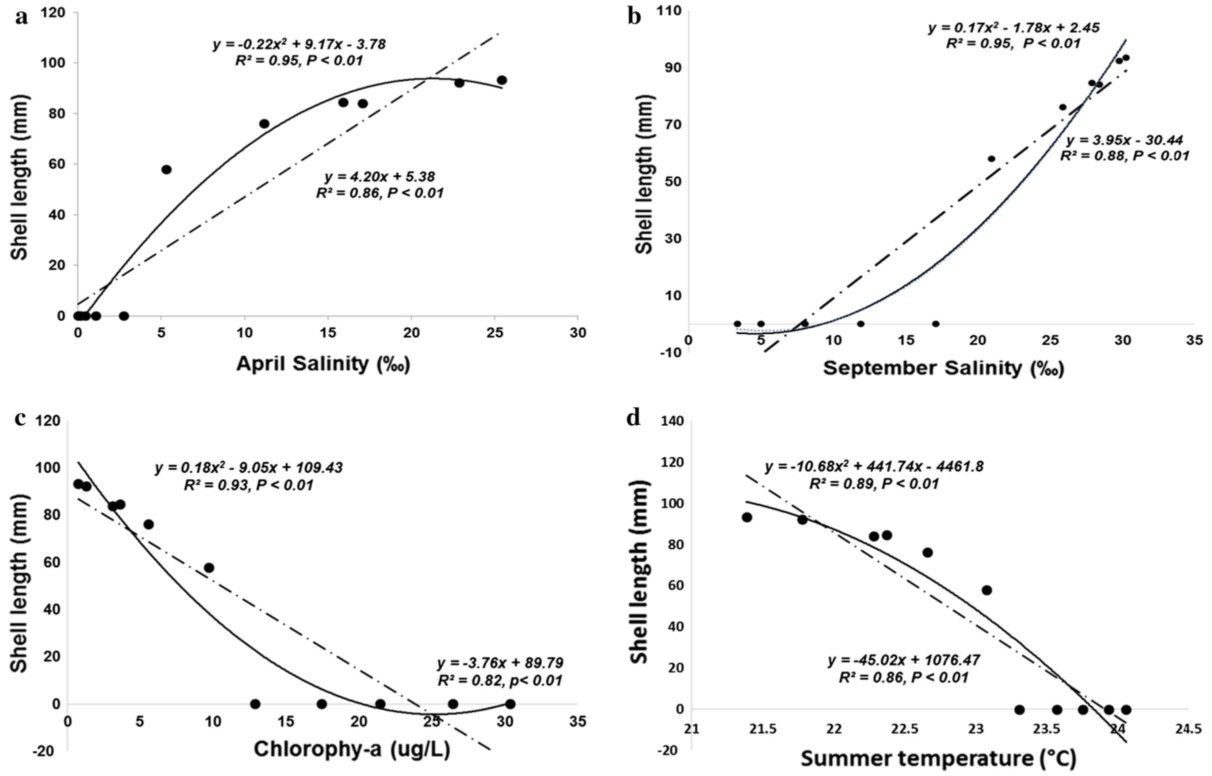


Fig. 5 The correlations between clam growth and environmental factors: April salinity (**a**), September salinity (**b**), Chlorophyll-*a* (**c**), and summer water temperature (**d**)

Table 4 Measures of environmental factors (temperature, salinity and chlorophyll-*a*), maximum shell size of *M. arenaria* in the Plum Island Sound estuary, and the regression results, the results of the linear regression analysis

Environmental factors	Coefficient	Standard error	R^2	*P* value
April salinity	4.20	0.56	0.86	<0.01
September salinity	3.95	0.48	0.88	<0.01
Chlorophyll-*a*	−3.76	0.58	0.82	<0.01
Summer temperature	−45.02	6.02	0.86	<0.01

All environmental factors show very good correlations with shell length (>0.80) and significantly explain the spatial variation of *M. arenaria* growth in the estuary

together along the longitudinal distance, x, in the estuary, the April salinity best explained the up-estuary limit to clam growth (lower than 2.8 psu from 0 to 10 km; Figs. 4e, 6a), and water temperature, April salinity, and September salinity together account for the spatial pattern of clam growth below that up-estuary limit in PIE (Figs. 5, 6). Clam growth was greater at the most oceanic sites, Yacht club (~21.3 km) and Third creek (~19.3 km), with higher salinities and lower water temperature, than the least oceanic sites, Railroad Meander (~14 km)

Discussion

Spatial pattern of *M. arenaria* growth

Our results showed four different spatial patterns on the VBGF growth estimations (growth rate coefficient (*k*), age to reach harvestable size, age to reach L-infinity and L-infinity) and clam wet weight (Table 2). The age to reach harvestable size increased from Yacht Club, the most oceanic site, to Railroad Meander, the most riverine and least oceanic site. In contrast, L-infinity and clam wet weight decreased from Yacht Club to Railroad Meander. There were no apparent spatial patterns for the growth rate coefficient or age to reach L-infinity, other than the extremes being observed at the end-member oceanic and riverine sites. These results suggest that the Yacht Club region could be the best habitat for clam growth and clam mariculture. On the other hand, Railroad Meander was the least favorable site for harvest because of the smallest L-infinity and average clam wet weight. That the oldest clams were found at the Railroad Meander site probably reflects the absence of commercial harvesting and possibly natural predation.

Our estimates of clam growth parameters at each site are potentially biased estimates at the population level because of our small sample size. However, sampling multiple clam patches within a site should minimize those biases. Removing clams with abnormally small or large growth at year 1 could have also biased the estimates of L-infinity and size at each age and resulted in R^2 closed to one. The estimations of our growth parameters, however, are supported by similar estimates of L-infinity reported previously for research conducted at or near the Plum Island estuary (Belding 1930; Brousseau 1979; Carmichael et al. 2004). In addition, VBGF has an inherent limitation in accurately estimating L-infinity, which is an assumption of invariance of environmental variables and biological processes including changes in food web structure and the physiological responses of clams to environmental conditions. Such limitation could result in an overestimation or underestimation of L-infinity under different environmental conditions. Despite this limitation, the growth parameters estimated with VBGF are still helpful in understanding relative differences in clam growth among sites.

Estimation *of M. arenaria* annual growth

During the spawning season, clam growth is very slow, which causes spawning lines to develop on shell cross-sections. Disturbances such as changes in food supply, population density, predation pressure, and stress induced by heat shock and freshwater ‘shutdown’ can also result in lines developing on shell cross-sections (MacDonald and Thomas 1980). Nevertheless, examination of internal and external growth lines of clam shells is still the most common methodology to estimate clam age and growth (Filippenko and Naumenko 2014; Hernández-Otero et al. 2014; Rocchetta et al. 2014).

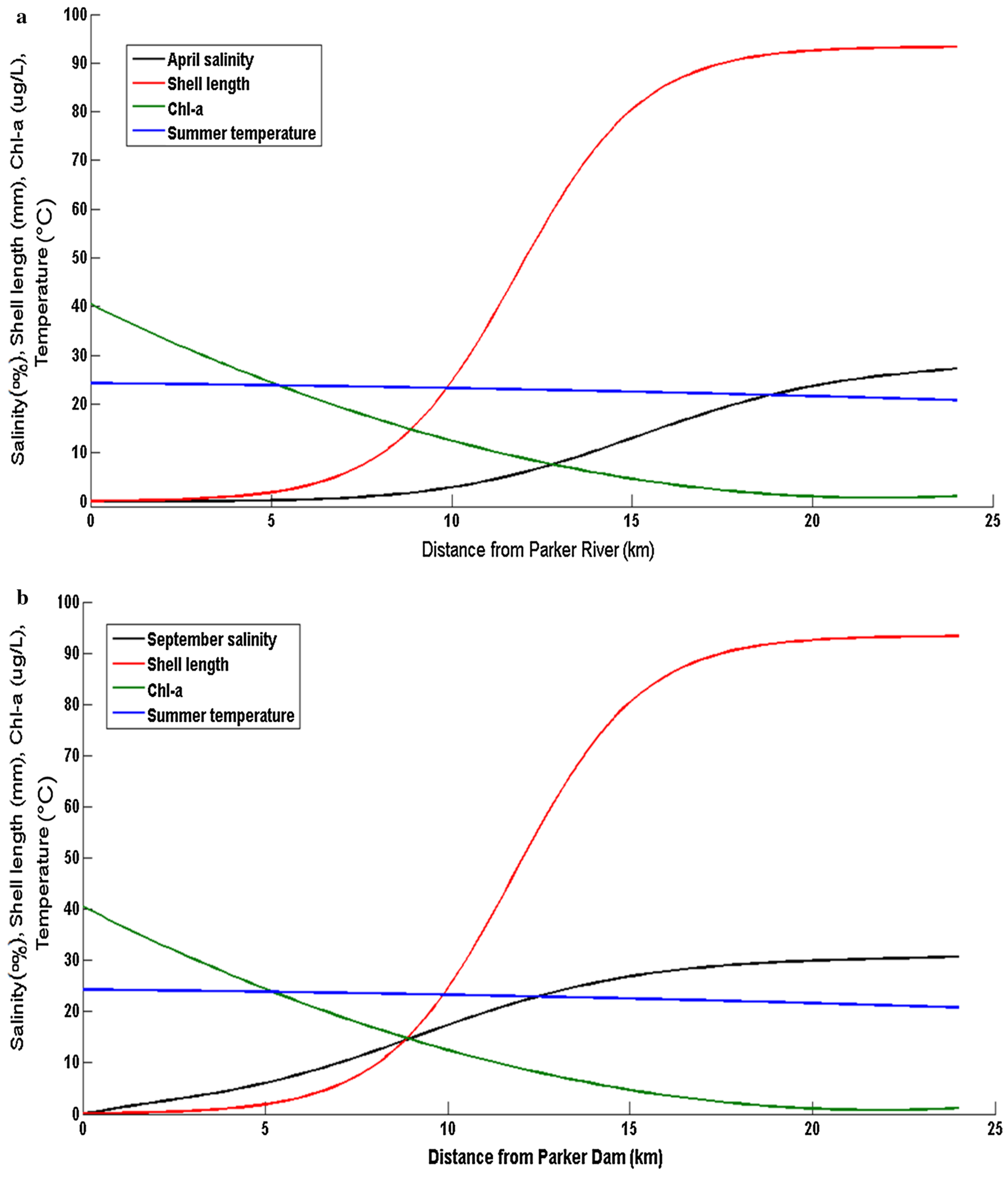


Fig. 6 Spatial patterns of clam growth and environmental factors along the estuary, from Parker dam to the mouth of estuary. **a** Spatial patterns of clam growth and April salinity, Chlorophyll-*a* and summer water temperature. **b** Spatial patterns of clam growth and September salinity, Chlorophyll-*a* and summer water temperature

Color bands on the chondrophore of the shell cross-section have been used for estimating age and growth of *M. arenaria* (Burchell 2014; Cerrato et al. 1991; MacDonald and Thomas 1980). Growth patterns on the chondrophore are accurate in age determination (Cerrato et al. 1991; MacDonald and Thomas 1980), but they are subject to modification during extended periods of shell closure, which results in acidic metabolites partially dissolving the inner shell surface (Crenshaw 1980). This method also has limitations in determining age if shells are missing their first year growth lines (Richardson et al. 1980, 1993, 1999) and consequently in estimating growth, clam size at various ages, and maximum potential size (L-infinity).

The use of oxygen stable isotope composition ($\delta^{18}O$) of shell calcium carbonate has been used as an alternative method for estimating age and growth rates of bivalves (Allard 1988; Gurney et al. 2005; Jones et al. 1989; Jones and Quitmyer 1996). This approach has been used by many to estimate growth of several fully marine bivalve species (Cespuglio et al. 1999; Gurney et al. 2005; Keller et al. 2002; Richardson et al. 1999; Royer et al. 2013). However, the $\delta^{18}O$ approach has been less frequently used in studies of estuarine bivalves because the freshwater inputs modify the carbonate oxygen isotope values and weaken or even swamp the seasonal summer–winter temperature signal reflected in the isotopic composition (Culleton et al. 2009; Strasser et al. 2008). Our own preliminary analysis showed a tremendous seasonal range in $\delta^{18}O$ that was strongly influenced by both seasonal temperature and freshwater variations, especially at the most up-estuary site where salinity fluctuates by up to 32 psu. The difficulty of separating the effects precluded us from further use of this approach for growth estimation.

Other approaches can be used to estimate *M. arenaria* growth, such as tag-recapture experiments and transplant growth experiments, but they suffer from a number of difficulties. For example, tag-recapture experiments have been used to estimate annual growth of surf clams and abalone (Jones et al. 1978; Tarbath 1999). But this method can have low recapture rates, and growth data typically depends on small size classes, especially juveniles (Gurney et al. 2005). Transplant growth experiments can also be negatively impacted by severe storms and heavy predation. Shell cross-section analysis of annual lines is not affected by these limitations. Therefore, despite limitations of internal growth line analysis due to disturbances lines, this method is still the most common methodology to estimate age and growth of clams inhabiting temperate estuaries including PIE (Filippenko and Naumenko 2014).

Selecting shells with minimal signs of shell repair for internal growth line analysis results in the overestimation of growth rate. In particular, compared with other hard shell clams, the shell of *M. arenaria*, a soft-shell clam, could be easily damaged by harsh environments and predators and repaired. Shell repairs may be quite common for *M. arenaria* and will obviously slow down growth. Therefore, shell repairs should be included in the estimations of growth rate at the population level. However, for increasing accuracy of internal growth line analysis, we have to select clams with minimal shell repairs. The scars of repairs produce false growth lines; as a result, they increase uncertainty in identifying annual growth lines and estimating growth rates. We may re-examine the oxygen stable isotope approach and other field based approaches in the future in order to avoid this issue of growth line analysis. However, as was mentioned above, those approaches also have many critical limitations. Thus, despite the limitation of internal growth line analysis on estimating the actual growth rate of *M. arenaria*, we opted for this approach.

Effects of environmental factors on the spatial pattern of *M. arenaria* growth

There was substantial variability from month to month and between stations, but the overall trend of lower Chl-*a* concentrations near the ocean and high concentrations of phytoplankton in the upper estuary (exceeding 27 μg/L at the Mill River and Middle Street sites) held during the ice-free time of year. Accordingly, the regression analysis found the negative correlation between the spatial pattern of *M. arenaria* growth and Chl-*a* concentration in PIE (Table 4; Fig. 4c). However, in general, bivalve growth increases with increasing phytoplankton abundance (Dame 2011). Previous experimental studies showed positive correlations between clam growth and phytoplankton abundance (Beukema et al. 2014; Carmichael et al. 2004; Coutteau et al. 1994; Petter et al. 2014; Weiss et al. 2002). Therefore, considering what we know from previous studies, despite the significance of the correlation, we do not accept the statistical suggestion that growth increases with decreasing food availability. Most likely food is readily available throughout the estuary and other environmental factors play a greater role in controlling the spatial pattern of clam growth in PIE.

Temperature is one of major controlling factors in clam growth and mortality (Dame 2011) and showed very good correlations ($R^2 = 0.89$ for polynomial regression and $R^2 = 0.86$ for linear regression) with clam growth in PIE (Table 4; Fig. 4d). The optimum water temperatures for food assimilation and pumping of *M. arenaria* are approximately 16–20 °C (Baker and Mann 1991; Newell et al. 1986), and the tolerable range is between 1.5 and 34 °C (Harrigan 1956). The observed water temperature from Parker Dam to the mouth of estuary during the growing season, approximately 20–25 °C, is within the tolerable range and close to the optimum range as reported by others. In particular, the water temperatures from Railroad Meander to Yacht Club clam sampling sites are between 20.7 and 23.5 °C, and this range is too narrow to explain the spatial pattern and the distribution boundary of *M. arenaria* growth in PIE. Previous studies also have not found significant effects of water temperature on the spatial variation of *M. arenaria* growth at the estuary scale (Appeldoorn 1983; Filippenko and Naumenko 2014; Kautsky 1982). Therefore, despite the significance of correlations, the water temperature could not be a critical factor in explaining the spatial pattern of clam growth in PIE. However, marginal temperatures decrease clam tolerance to low salinity (Baker and Mann 1991). Therefore, warmer temperatures above Railroad Meander (occasionally exceeding 28 °C—km 11.5) could contribute to the decline of clam growth in the upper estuary amplifying the effects of low salinity.

The Chl-*a* concentrations and water temperature of Sweeney Creek and Clubhead Creek sites were calculated with the Chl-*a* and the $Temp_{summer}$ functions after estimating their equivalent along-estuary location from the relation between salinity and distance for the main channel of the estuary (Table 3). This could add some uncertainty in explaining the spatial correlation between Chl-*a* and water temperature versus *M. arenaria* growth. The estimated Chl-*a* concentrations for Sweeney and Clubhead Creeks appear correct however, as they are higher than observed at the Yacht Club and Third Creek sites, which do not receive the same level of nutrient loading from the Rowley River. The spatial pattern of observed temperatures at Sweeney Creek (~24.69 °C) > Grandkid's Flat (~23.77 °C) > Clubhead Creek (23.59 °C) were also similar to the spatial pattern of modeled estimates of temperature at those sites.

Salinities, April and September, well accounted for the spatial pattern of clam growth in PIE (Figs. 5a–d, 6a, b). However, the April salinity distribution best explained the spatial pattern of *M. arenaria* growth in PIE, especially the upper distributional limit (Fig. 6a). Preferred salinities for *M. arenaria* are 10–33 ppt in Massachusetts (Belding 1930). Adult *M. arenaria* cannot survive below 4 psu for longer than a few days and cannot grow below 8 psu (Matthiessen 1960). In PIE, *M. arenaria* "sees" optimum salinities in the more oceanic middle and lower reaches of the estuary. Low salinity (lower than 2.8 psu from 0 to 10 km) appears to limit *M. arenaria* to the lower estuary. Other studies also noted obvious declines of *M. arenaria* growth in lower salinity regions of estuaries (Filippenko and Naumenko 2014; Kautsky 1982). *M. arenaria* growth declined along the steady but progressive salinity gradient in the southern Baltic Sea (Filippenko and Naumenko 2014).

We are well aware that factors other than we considered here, such as sediment type and grain size, disease and pollution, may also contribute to the spatial distribution of *M. arenaria* growth. The growth rate of *M. arenaria* has been shown previously to vary with sediment type, increasing from gravel to muddy sediment (Belding 1930; Newell and Hidu 1982). *M. arenaria* expends more metabolic energy but is at a lower risk from predation in coarse sediments such as sand and gravel, compared to finer sediments like muds (Thomson and Gannon 2013). In Chesapeake Bay, larger populations of *M. arenaria* are reported for muddy sands than in pure muds (Holland et al. 1987). Based on our observations, the sediments of all our sampling sites were sandy with moderate mud content except for the Railroad Meander site, which was mostly mud with low sand content. It may reflect that *M. arenaria* grows better at sites with sandy sediments than the ones with mud. However, an apparent variability in sediment types was not found among other sites, and high clam densities were observed at non-sampling sites with mud sediments. Further research is needed to understand the relationship between clam growth and sediment type in PIE. Disease and parasitism, such as disseminated neoplasia and germinomas, have been known to occur in *M. arenaria* (Strasser 1998) with neoplasia causing high clam mortality, up to 78 %, in the Long Island Sound (Brousseau and Baglivo 1991). However, such diseases have not been found in PIE yet. In addition, bottom water anoxia brought about by eutrophication can also control clam distribution witness the large declines in growth of *M. arenaria* in hypereutrophic waters of western Sweden (Rosenberg and Loo 1988). Pollution, such as heavy metal contamination, also can reduce clam growth and increase clam mortality (Brousseau-Fournier et al. 2013).

Further research is needed to fully understand patterns of *M. arenaria* growth and distribution in relation to environmental factors in PIE. For example, considering the extensive suburbanization occurring in the PIE watershed and the resultant phytoplankton blooms in the upper oligohaline regions of PIE, a profitable line of research could be to better understand clam growth dynamics and distribution in areas most likely to be affected by variations in the magnitude of freshwater runoff (hence salinity distribution), sediment delivery (hence sediment distribution), and N-enrichment and pollution (hence anoxia from eutrophication and stress). While additional research could increase our understanding of the fine scale distribution of *M. arenaria* growth, unquestionably, salinity is the major factor limiting the spatial distribution of *M. arenaria* in PIE. Similar conclusions have been reached in studies conducted in other estuaries (Filippenko and Naumenko 2014; Kautsky 1982). This fundamental understanding of the controlling role of salinity is important because we know that freshwater discharge into coastal estuaries of the northeastern US is dramatically impacted by climate change and land-use change (Claessens et al. 2006).

Conclusions

Understanding the factors contributing to the spatial distribution of clam growth in relation to environmental conditions is fundamental to effective shellfish management in estuaries undergoing rapid change due to cultural eutrophication, climate change and sea-level rise. We found broad patterns in the spatial variation of clam growth in the Plum Island Sound estuary, which were best explained by salinity, especially spring salinity. Salinity at the beginning of the growing season accounted for the up-estuary boundary of *M. arenaria* distribution and 95 % of spatial variation of *M. arenaria* growth. Chl-*a* and water temperature were not critical factors in explaining the spatial variation of clam growth in PIE. In particular, Chl-*a*, which represents the primary food stock of clams, was negatively correlated with clam growth. In our opinion, it indicates food is not limiting anywhere in the estuary. Our results showing such a strong influence of salinity on clam growth suggest that future management should pay close attention to future changes in spatial pattern of salinity due to sea-level rise and increased freshwater inputs due to projected increases in impervious areas and precipitation in the northeastern USA.

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