Estuarine, Coastal and Shelf Science 313 (2025) 109059

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Clam diet and production in relation to the spatial pattern of food source inputs and quality: A stable isotope approach

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ARTICLE INFO

Keywords:
Mya arenaria
Diet composition
Spatial variability
Plum Island sound estuary
Organic matter loading
Organic matter quality

ABSTRACT

We used four stable isotopes to determine the spatial variability in the diet of *Mya arenaria* in the Plum Island Sound estuary, Massachusetts, USA and compared diet to the production rate of dietary food sources. Clams were collected for a year along the estuary and their diet determined at each site with four stable isotopes, δ^{13}C, δ^{15}N, δ^{34}S and δ^{2}H, using the Bayesian mixing model (MixSIAR). We compared diet composition and its quality to patterns of clam production. The results showed that *M. arenaria* depended on locally produced organic matter, the availability of which varied along the estuary. For the lower estuary, the dominant food source for clams was ocean/estuarine unicellular algal particulate organic matter followed by salt marsh detritus. Brackish and riverine organic matter sources were of secondary importance. For the upper estuary, the relative importance of brackish marsh and riverine organic matter increased. The net inputs of organic matter from the river, tidal marshes and unicellular algae were closely matched with the dietary composition of clams. The down estuary pattern of increasing clam productivity was best predicted by a similar pattern in suspended particulate organic matter quality as indicated by the ratio of C:N. The C:N ratio decreased from about 10.5:1 to 7.4:1 along the region of clam growth. We also found that δ^{2}H was a useful tracer, effectively discriminating between marsh-derived and aquatic algae-derived organic matters and significantly increasing the predictive power and reliability of the mixing model. Our study provides fundamental knowledge on suitable habitats for the *M. arenaria* growth in the Plum Island estuary and insights into selecting stable isotopes for elucidating feeding ecology and trophic dynamics of estuarine organisms.

1. Introduction

Temporal fluctuations of river discharge and tidal seawater mixing create a great range of environmental habitats and gradients across the estuarine landscape, which result in considerable spatial heterogeneity in organic matter sources potentially supporting estuarine consumers and secondary productivity (Deegan and Garritt, 1997; Mwijage et al., 2017). Most estuarine consumers, characterized as opportunistic feeders with broad diets, tend to use locally available organic matter and show spatial variability in their diets (Bergamino and Richoux, 2015; Deegan and Garritt, 1997; Howe and Simenstad, 2011; McMahon et al., 2005; Mwijage et al., 2017; Nelson et al., 2015). Understanding the spatial patterns of the consumers' diet, coupled with species physiological performance (e. g. growth rate, reproduction success, metabolic rates, and temperature tolerance) throughout an estuarine landscape will provide fundamental information on evaluating the potential effects of environmental change on the estuarine consumers and estuarine secondary production.

Suspension-feeding bivalves, often considered opportunistic feeders, are essential and beneficial biological components of estuarine ecosystems (Herman et al., 1999; Lefebvre et al., 2009). They link primary production and detritus to the higher-level consumers, which increases food web stability and efficiency (Herman et al., 1999; Lefebvre et al., 2009). Most bivalve studies have concentrated on finding the dietary sources alone to understand trophic dynamics and feeding behaviors (Bergamino and Richoux, 2015; Hondula and Pace, 2014; Lefebvre et al., 2009) or on species performance in relation to the environmental conditions they tolerate (Carmichael et al., 2004; Gurr et al., 2021; Koo et al., 2017; Santos et al., 2020; Zhang et al., 2019). Even though some studies have correlated the diets of bivalves to habitat heterogeneity or

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https://doi.org/10.1016/j.ecss.2024.109059
Received 16 February 2023; Received in revised form 12 August 2024; Accepted 20 November 2024

environmental drivers (Deegan and Garritt, 1997; Howe et al., 2012; Marchais et al., 2013; Nelson et al., 2015; Schaal et al., 2015; Takar et al., 2021; Van Colen et al., 2020), the linkage with species performance has not been considered. However, knowledge of bivalve diet and performance in conjunction with the complexity of the estuarine landscape will be critical to understanding the response of bivalves to a changing environment and their role in maintaining estuarine ecosystem stability and function.

The suspension-feeding soft-shell clam, *Mya arenaria*, is a dominant benthic species in the Plum Island Sound estuary (PIE) of northeastern Massachusetts, USA (Belding, 1930; Brousseau, 2005). As do other suspension-feeding bivalves, *M. arenaria* plays a critical role in the Plum Island estuarine food web and provides valuable ecosystem services (Deegan and Garritt, 1997; Nelson et al., 2015). It supports an important commercial fishery in the region due to its treasured taste and high abundance (Belding, 1930; Brousseau, 2005; Glaspie et al., 2017). Several food web studies in the Plum Island estuary addressed the spatial variability in consumers' diets (Deegan and Garritt, 1997; Nelson et al., 2015). Deegan and Garritt (1997) reported the general unimportance of terrestrial organic matter sources in the diets of most consumers. Nelson et al. (2015) also found spatial patterns in consumers' diets in Plum Island, but unlike the result of Deegan and Garritt (1997), did find that riverine and terrestrial invertebrate sources were important to some species, such as the fish, *Fundulus heteroclitus*. While organic matter of salt marsh macrophyte and phytoplankton origin has been emphasized as important food sources to intertidal bivalves, the dominant food source for *M. arenaria* in the large open water regions of Plum Island Sound found phytoplankton to be the dominant food source (Deegan and Garritt, 1997; Nelson et al., 2015). These studies, however, did not examine the full range of habitats throughout the Plum Island estuary, especially those in upper estuary brackish waters; as a result, the spatial pattern in the diet of *M. arenaria* across the estuarine landscape is not yet fully understood.

Previous studies have documented great variability in the relative importance of vascular plant (e.g., marsh macrophytes) and algal organic matter sources in support of estuarine food webs, including suspension feeders. Differences in the relative magnitude of these two input sources and their digestibility along with differences in connectivity between habitats have been proposed to explain some of the variability in food source importance (Deegan and Garritt, 1997). While the areal extent and overall level of production of marsh macrophytes might exceed that of algae, algae are produced directly where suspension-feeders live, and the digestibility of algae with a Carbon: Nitrogen (C:N) makeup similar to suspension-feeders themselves is far greater than that of marsh macrophytes with their high C:N tissue composition. The magnitude of marsh plant organic matter input to tidal creeks and sounds likely also varies with the extent of tidal marshes relative to water area and volume and with tidal range. Tidal range dictates marsh flooding frequency, extent, duration, and the flow of water needed to carry marsh plant particulate organic matter from the marsh to creeks, sounds and bays where suspension feeders, such as *M. arenaria*, live.

Stable isotope analysis has been used for quantitative measures of organisms' diet (Fry, 2006; Nelson et al., 2015). The stable isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N) have been commonly used in studies of trophic dynamics and consumer feeding ecology (Fry, 2006; Martínez del Rio et al., 2009; Rigolet et al., 2014). However, use of only two stable isotopes has limited power to discriminate multiple food sources of consumers within complex food webs (Forero et al., 2004; Moreno et al., 2010). Thus, additional isotopes are recommended for improving discrimination accuracy: sulfur (δ^{34}S) is a third dietary tracer especially important in wetland-dominated estuaries, and deuterium (δ^{2}H) has recently been recommended for discriminating terrestrial from estuarine aquatic food sources (Duarte et al., 2018; Hondula and Pace, 2014; Martínez del Rio et al., 2009; Peterson, 1999; Thompson et al., 1999; Vander Zanden et al., 2016). The increased discriminatory ability of δ^{34}S is due to the importance of reduced sulfur in the nutrition of wetland macrophytes (Duffill Telsnig et al., 2019; Fry, 2006; Hebert et al., 2008; Moreno et al., 2010; Peterson, 1999; Peterson and Howarth, 1987). Applications of δ^{2}H have also recently increased due to potential of δ^{2}H in tracing the organisms' dietary sources in relations with the spatial patterns in the precipitation δ^{2}H values (Bowen et al., 2005; Vander Zanden et al., 2016). In addition, in many cases the multiple tracers together can be more powerfully resolve contributions of potential food sources because the biogeochemical controls on each of the elements are different (Vander Zanden et al., 2016). Therefore, feeding and food web studies in estuaries have used δ^{34}S and more recently δ^{2}H as well as δ^{13}C and δ^{15}N (Adame et al., 2018; Moreno et al., 2010; Peterson and Fry, 1987; Ramos et al., 2009; Resano-Mayor et al., 2014).

The aims of our study were 1) to identify the spatial variability in the diet of *M. arenaria* coupled with its performance, based on clam maximum growth projections, in order to better understand the relation between habitat complexity across the Plum Island Sound estuarine landscape and *M. arenaria* growth throughout the Plum Island estuary; and 2) to test the effectiveness of δ^{2}H a stable isotopic tracer of food sources of estuarine filter-feeders. For this, we first characterized the isotopic compositions of food sources and clams across the estuarine landscape. Second, the site-specific diet composition of clams was analyzed by employing Bayesian stable isotope mixing models and four stable isotope tracers, carbon (δ^{13}C), nitrogen (δ^{15}N), sulfur (δ^{34}S), and deuterium (δ^{2}H). Then, we analyzed the relationships between the diet composition and clam maximum growth along the estuary, including potential supply and quality of organic matter sources. We tested whether δ^{2}H is a useful tracer by comparing the predictive powers of four mixing models with various combinations of $\delta\ ^{13}$C, $\delta\ ^{15}$N, $\delta\ ^{34}$S and δ^{2}H.

2. Materials and methods

2.1. Study area

This study was conducted in the Plum Island Sound estuary in northeastern Massachusetts, USA (Fig. 1), which is a productive system for *Mya arenaria* (Koo et al., 2017). This 24 km long estuary has a vertically well-mixed water column with an along-estuary horizontal gradient and temporal range in salinity of 0–32 and water temperature of −1.0 to >28 °C (Vallino et al., 1998). The estuary is approximately 60 km^2 in extent with about 40 km^2 as intertidal wetlands and 20 km^2 as open water creeks and sounds. The ratio of tidal wetland to water ranges along the estuary from >10:1 in the upper 10 km to about 1:1 in Plum Island Sound and the lower 10 km. 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 experience annual average salinities ranging from approximately 20 to 32. (Koo et al., 2017). The mean tidal range of the estuary is about 2.6 m, and the mean depth is about 1.6 m at mean low water (Deegan and Garritt, 1997). *M. arenaria* (Mya) is found in the lower 3/5s of the estuary where there are large intertidal flats at low tide, many of which could be clam habitats if managed properly. Phytoplankton densities and inorganic nutrient concentrations reflect seasonal cycles 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. Tidal wetlands range from oligohaline marshes dominated by *Typha* spp. and *Spartina patens* in the upper 5 km, to brackish and saline marshes dominated by *S. patens* and *Spartina alterniflora* in the lower estuary. Overall productivity of the system is high with net autotrophic tidal wetlands (Forbrich et al., 2018) and net heterotrophic tidal waters

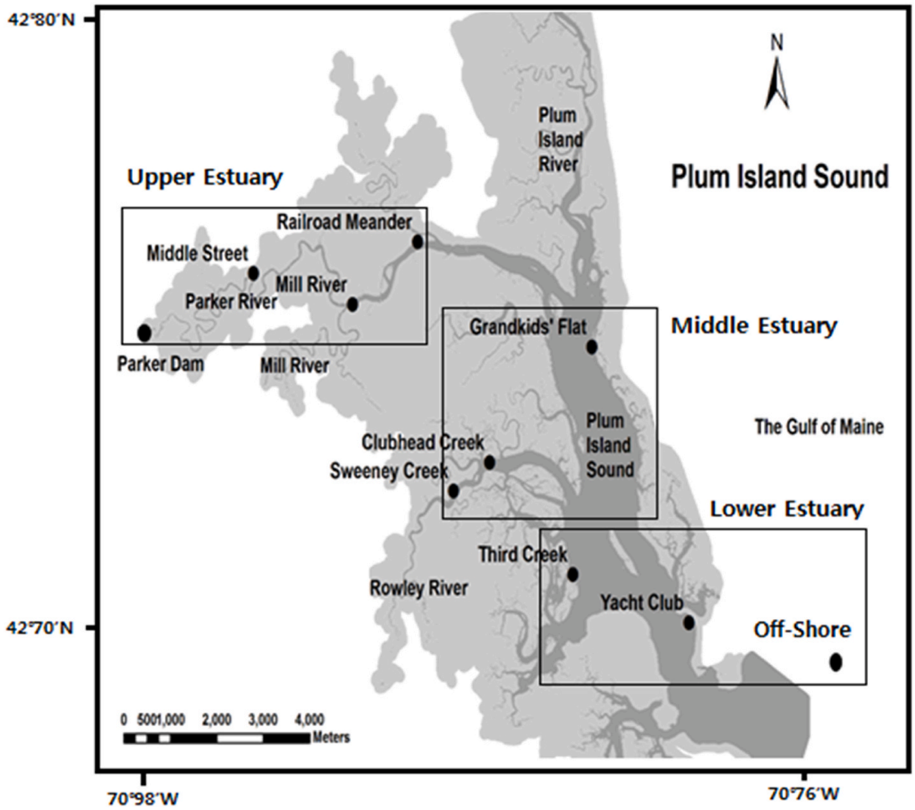

Fig. 1. Map of the Plum Island Sound estuary in northeastern Massachusetts, U.S.A. showing locations (black dots) where *M. arenaria*, water samples and plants were collected. The Parker Dam (dot left-most position on map) shows the landward end of the estuary and where riverine organic matter was sampled. The lightly shaded area denotes intertidal wetlands along the mainstem of the estuary.

(Vallino et al., 2005).

2.2. Data collection and processing

Previous studies reported that suspended particulate organic matter was the dominant food source of *Mya* in the Plum Island estuary (Deegan and Garritt, 1997; Nelson et al., 2015) and that marsh plants in general were important sources to estuarine consumers (Bergamino and Richoux, 2015; Howe and Simenstad, 2011; Peterson et al., 1985; Raoult et al., 2018). We considered all the major food sources in the estuary as potential sources of particulate organic matter supporting *Mya* growth: terrestrial inputs via rivers, detritus of intertidal brackish and saline marshes, and algae/phytoplankton from estuarine and tidal oceanic waters. Suspended particulate organic matter (POM) end-member sources were isolated from water samples collected from the Parker River dam at the head of the estuary (terrestrial/riverine labeled RPOM) and the mouth of the estuary (estuarine and oceanic algae/phytoplankton labeled OEPOM). For marsh organic matter input sources, live aboveground tissue samples were collected from the primary brackish (*Spartina patens* and *Typha* sp.) and saline (*S. patens* and *S. alterniflora*) macrophytes.

Clams (Juvenile <5 cm and Adult >5 cm) were collected at 7 sites from 3 regions along the estuary (Fig. 1). The 7 sites span the full along-estuary range of *Mya* clam beds (from about km 9 to 24). Their upstream distribution mostly stops 9 km from the head of the estuary due to nearly freshwater conditions further upstream in late winter when Parker River runoff is at its greatest (Fig. 1). The upper sampling region, including the Mill River and Railroad Meander sites, is characterized by a deep tidal river channel with terrestrial inputs of POM from upstream, brackish and salt marsh organic matter inputs from the broad flanking intertidal wetlands (C3 marsh plant *Typha* sp. and C4 marsh plant *Spartina* sp.), and algal inputs from the ocean and lower estuary (Deegan and Garritt, 1997). Average annual salinity in this region is from about 20 to 28 (Koo et al., 2017; Nelson et al., 2015). The middle estuary region, including Grandkids' Flat, Clubhead Creek, and Sweeney Creek, is characterized by extensive salt marsh habitats (C4 marsh plant species, low marsh *S. alterniflora* and high marsh *S. patens*) flanking the broad Plum Island Sound with its well-developed muddy sand flats. Salinity is intermediate in this region with average annual salinity approaching 30 (Koo et al., 2017; Nelson et al., 2015). The lower estuary region, Yacht Club and Third Creek, is also part of the broad Plum Island Sound with extensive intertidal flats, but the flanking salt marsh is smaller, and the water column reflects strong exchange with the coastal ocean and salinities up to 32 (Koo et al., 2017; Nelson et al., 2015).

Water temperature, salinity, and food availability and quality are the major factors controlling *M. arenaria* growth, reproduction, and survival (Belding, 1930; Carmichael et al., 2004; Dame, 2011; Filippenko and Naumenko, 2014). However, water temperature and salinity show a strong correlation in the Plum Island estuary. As water temperatures in the estuary are in the optimal range for *M. arenaria* (Koo et al., 2017; Nelson et al., 2015) water salinity is used here to describe their environmental gradient. September water salinity, clam growing season salinity, and clam maximum growth at our seven clam sampling sites, Mill River to Yacht Club (Fig. 1), were obtained from Koo et al. (2017). Salinity at each sampling site was estimated with a one dimensional, intertidal, advection-dispersion transport model developed by Vallino et al. (1998) (Koo et al., 2017). Koo et al. (2017) verified the model projections of salinities with the field data collections. Clam maximum growths were projected by fitting the age-size measurements to a von Bertalanffy growth model, and the age-size measurements were obtained from the internal growth line analyses (Koo et al., 2017).

Descriptors of the along-estuary gradient in organic matter quality of the clam diet, including the concentration of total suspended solids (TSS), the concentration of unicellular algae (mostly phytoplankton but some benthic microalgae) relative to bulk suspended POM and the C to N ratio of suspended organic matter, were obtained from over 20 yrs of data collections by the Plum Island Ecosystems Long-Term Ecological Research (PIE-LTER) project. Water quality parameters can be found online at https://pie-lter.ecosystems.mbl.edu/data. Briefly, these measures are based on water sample filters for which TSS is measured as dry weight, POM as ash free dry weight, C and N from CHN analysis, and algal C biomass from Chl-*a* and phaeopigment extraction with a 70:1 OC:Chl-*a* conversion ratio. When converting from POM to OC or vice versa a 50% OC:POM ratio was used.

We estimate the total amount of each food source entering the estuary to evaluate the relationship among clam growth, clam diet composition, and the quantity of each dietary source. Data on the relative magnitude of organic matter inputs, allochthonous and autochthonous, are from the estuarine carbon budget of Vallino et al. (2005), Forbrich et al. (2018) and Hopkinson and Weston (in review). Lacking sufficient detail to estimate the amount of inputs for the four potential food sources of clams (RPOM, salt marsh detritus, brackish marsh detritus, and OEPOM), we lump inputs into 3 categories: riverine organic matter inputs from the watershed (named hereafter River), marsh organic matter inputs combined for brackish and saline marsh detritus (named hereafter Marsh), and algae (name hereafter Algae), which includes macro and micro benthic algae, phytoplankton, and oceanic dissolved organic carbon (Vallino et al., 2005). We present the amount of inputs based on the gross inputs of organic matter from the 3 categorized sources (River, Marsh, Algae): total organic matter export from all rivers entering the estuary (River), marsh gross primary production (GPP) and marsh edge erosion (Marsh), and gross aquatic primary production for the entire aquatic portion of the estuary (Algae), including macro and micro benthic algae, phytoplankton, and oceanic dissolved organic carbon, plus oceanic organic matter decomposed while residing within the estuary. We also tabulated net organic matter inputs to the aquatic portions of the estuary based on the net export of organic matter from the marsh and edge erosion of marsh peat, the portion of river organic matter export that is consumed within the estuary, as opposed to that flushed through prior to being processed, and, as above, aquatic GPP plus the utilization of oceanic organic matter. Briefly, marsh GPP is based on the eddy covariance approach (Forbrich et al., 2018). Export of marsh organic matter to tidal waters is based on net marsh ecosystem production minus organic matter burial. Edge erosion is from change analysis of LiDAR images from 2005 to 2011 (Hopkinson et al., 2018). Aquatic GPP is based on free water diurnal changes in dissolved oxygen measured over the entire length of the estuary (Staehr et al., 2010; Paulsson and Widerlund, 2023). The use of oceanic organic matter is based on its lability and residence time in the estuary (Vallino et al., 2005). Gross and net input amounts are calculated in terms of C and N, assuming C:N of 7:1 for algae, and 25:1 for terrestrial POM and marsh detritus.

2.3. Stable isotope analysis and mixing models

2.3.1. Sample preparation

We used four stable isotopes, carbon (δ^{13}C), nitrogen (δ^{15}N), sulfur (δ^{34}S), and deuterium (δ^{2}H), for mixing models to describe the relative dietary importance to clams of four organic matter sources: OEPOM, RPOM, saltmarsh detritus, and brackish marsh detritus (see Table 1a–c). Carbon and nitrogen were used for mixing models to describe the relative source contributions of POM from each of the clam sampling sites. The stable isotope values of carbon and nitrogen for saltmarsh detritus, brackish marsh detritus, OEPOM and RPOM were taken from Nelson et al. (2015) originally obtained from the Plum Island Long-Term Ecological Research (PIE LTER) site stable isotope survey (Deegan and Garritt, 1997; Nelson et al., 2015), and the values of sulfur and deuterium from our sampling sites (Fig. 1). For the four stable isotope values for clams, the stable isotope analyses of carbon, nitrogen, sulfur, and deuterium were performed on adductor muscles of clams collected at seven sampling sites, Mill River to Yacht Club (Fig. 1). There was a time lag between PIE LTER sampling and our sampling for the stable isotope data, but we assume the isotopic composition of source materials is constant from year to year (Nelson et al., 2015).

Table 1
Data used in mixing models and statistical analyses for Plum Island Sound estuary. a shows data for food sources, **b** data for juvenile clams, and **c** data for adult clams. Tables show mean δ^{13}C, δ^{15}N, δ^{34}S and δ^{2}H with standard deviation (SD) for diet sources and clams at each site and percent concentration in parentheses. **d** shows clam maximum growth and salinity estimated by Koo et al. (2017).

a

Sources	δ^{13}C Mean (SD)	δ^{15}N Mean (SD)	δ^{34}S Mean (SD)	δ^{2}H Mean (SD)
OEPOM	−22.5 (1.4)	5.5 (0.4)	19.6 (1.1)	−145.5 (12.5)
Salt Marsh Plants	−13.1 (0.4)	4.7 (0.6)	10.1 (2.0)	−115.0 (6.5)
Brackish Marsh Plants	−26.0 (1.6)	5.0 (0.5)	2.8 (1.7)	−108.4 (4.0)
RPOM	−30.2 (0.7)	5.7 (1.0)	−1.7 (0.1)	−161.0 (16.0)

b

Juvenile clams	Sampling Site	δ^{13}C Mean (SD)	δ^{15}N Mean (SD)	δ^{34}S Mean (SD)	δ^{2}H Mean (SD)
Upper Estuary	Mill River	−21.5 (1.5)	8.6 (0.3)	7.5 (2.2)	−125.8 (3.5)
	Railroad Meander	−20.2 (0.6)	9.0 (0.2)	9.4 (2.6)	−123.6 (7.5)
Middle Estuary	Sweeny Creek	−19.3 (0.2)	9.3 (0.2)	11.1 (0.2)	−134.1 (0.7)
	Clubhead Creek	−18.7 (1.6)	8.7 (0.3)	11.0 (2.9)	−136.4 (9.3)
	Grandkids' Flat	−19.9 (0.2)	8.5 (0.3)	12.1 (0.9)	−134.4 (2.4)
Lower Estuary	Third Creek	−19.7 (0.3)	8.2 (0.4)	15.3 (0.8)	−133.6 (4.4)
	Yacht Club	−19.5 (0.2)	8.4 (0.4)	15.9 (0.6)	−132.7 (2.3)

c

Adult clams	Sampling Site	δ^{13}C Mean (SD)	δ^{15}N Mean (SD)	δ^{34}S Mean (SD)	δ^{2}H Mean (SD)
Upper Estuary	Mill River	−23.8 (0.0)	9.3 (0.0)	9.0 (0.0)	−131.5 (0.0)
	Railroad Meander	−19.9 (0.4)	9.3 (0.4)	11.0 (1.2)	−125.2 (2.8)
Middle Estuary	Sweeny Creek	−19.3 (0.0)	9.4 (0.1)	10.3 (0.8)	−130.9 (1.7)
	Clubhead Creek	−19.2 (0.2)	9.4 (0.1)	12.2 (0.9)	−132.6 (2.9)
	Grandkids' Flat	−19.5 (0.2)	8.9 (0.3)	12.6 (1.0)	−133.7 (2.3)
Lower Estuary	Third Creek	−19.3 (0.1)	8.8 (0.3)	15.1 (0.7)	−133.7 (2.0)
	Yacht Club	−19.3 (0.2)	8.8 (0.4)	15.7 (0.8)	−130.3 (2.4)

d

Site	Salinity	Maximum Growth
Mill River	17.1	n.a.
Railroad Meander	20.9	57.9
Sweeny Creek	25.9	76.2
Clubhead Creek	27.9	84.6
Grandkid's Flat	28.4	84.0
Third Creek	29.8	92.3
Yacht Club	30.2	93.4

Clam samples of two growth-stages, juvenile (<5 cm) and adult (>5 cm), were collected monthly from May to November in 2010 and April 2011 at seven sites, Mill River to Yacht Club, along the estuary between kilometers 9 and 21 (Table 1b and c). Approximately 40 clams (20 for juvenile and 20 for adult clams) were collected monthly at each site, except at Mill River where 5 clams were collected only in November (could not be located at other times). Sampled clams were immediately frozen after collection and transported to the laboratory for dissection. In the laboratory, they were thawed, the adductor muscles removed, and washed with distilled water. The samples were freeze dried and then homogenized into fine powder using a ball mill.

Detailed information on the collection methods and data for food sources, salt marsh plants, brackish marsh plants, and OEPOM and RPOM obtained from water samples, as part of the PIE LTER site stable isotope survey, can be found at (http://ecosystems.mbl.edu/PIE/data/HTL/HTL-PIE-YearlyIsotopeSurvey.html). These primary producer samples were collected annually in the fall (August–September) from 1999 to 2013 at the upper (42.75° N 70.92° W), the middle (42.76° N 70.83° W) and the lower (42.70° N 70.78° W) regions of the estuary (Nelson et al., 2015). Water column POM (a mix of live phytoplankton and detritus) was collected via 50 μm plankton net on three replicate tows, and the samples were stored frozen (−20 °C). The sample was rinsed of carbonates using 10% HCl, then filtered under suction in a 25 mm Gelman filter tower and flask onto a 25 mm 0.7 μm nominal pore size ashed, glass microfiber filter, and dried at 50 °C (Tobias et al., 2003). The POM samples remained on the filters for isotope analysis. The ashed glass filters do not contain carbon or nitrogen and do not affect the stable isotope values (Jones et al., 1999). Fifteen live leaves of *S. alterniflora* and *S. patens* were collected from various locations within the salt marsh. Live leaves were cleaned, rinsed with DI, and dried after collection. Live *Spartina* and *Spartina* detritus in the water column have the same isotopic value, so this study does not distinguish between the two (Haines and Montague, 1979).

For the stable isotope values of sulfur and deuterium, water samples were collected three times at Parker Dam and off-shore as well as at the seven clam sampling sites during low flow in November 2010 and high flow in April and low flow again in August 2011 (Fig. 1). Plant samples were collected once at Parker Dam, Mill River, and Grandkids' Flat in April 2011 (Fig. 1). The water samples were processed in the same way as the water samples of the PIE LTER site (https://pie-lter.mbl.edu/). Plant samples were washed with distilled water, frozen, and dried in a freeze-dryer. The freeze-dried plant tissues were then ground with a ball mill.

2.3.2. *Stable isotope sample analyses*

For the stable isotope values of PIE LTER and the values of sulfur and deuterium for POM, stable isotope analysis was performed using a Europa ANCA-SL elemental analyzer attached to a continuous flow Europa 20-20 gas source stable isotope ratio mass spectrometer at the Marine Biological Laboratory in Woods Hole, MA. For each sample, approximately 500 μg of tissue was wrapped in a tin capsule and analyzed for δ^{13}C, δ^{15}N, δ^{34}S, δ^{2}H, %C, %N, %S, and %H. For the four stable isotope values for clams and the values of sulfur and deuterium for plants, the isotope samples were analyzed by the Colorado Plateau Stable Isotope Laboratory at Northern Arizona University. Isotope analyses were done by the combination of an elementary analyzer (NA 1110, CE Instruments, Milan, Italy) with an isotope ratio mass spectrometer (DELTA + XL, Finnigan MAT, Bremen, Germany) (Werner and Brand, 2001). The coupling was interfaced by a modified ConFlo II™ open split interface. All isotope values are expressed in δ notation according to the following equation:

$$\delta X = [(R_{sample}/R_{standard})\text{-}1] \times 1000$$

where X represents ^{13}C, ^{15}N, ^{34}S, and ^{2}H and R represents the ratio of heavy to light isotopes. Standards used for δ^{13}C, δ^{15}N, δ^{34}S, and δ^{2}H values were PeeDee Belemnite (PDB), ambient air (AIR), and Canyon Diablo Troilite (CDT), respectively. Duplicate values were obtained for ~20% of the samples for quality assurance purposes.

2.3.3. *Mixing model and statistical analyses*

Dual stable isotope plots and a mixing model were used 1) to identify the diet sources of *M. arenaria* and 2) to estimate the proportional contribution of each source to the clam diets. Dual stable isotope plots have been used to estimate the dietary sources of consumers in feeding ecological studies and food web studies (Peterson and Howarth, 1987; Peterson et al., 1985), and stable isotope mixing models increasingly used to quantify consumer diets (Phillips et al., 2014). The proportional contributions of the sources to the clam diet were estimated at each site with the Bayesian Mixing Models in R (MixSIAR v.3.1.10), the R-package of Bayesian isotope mixing model (https://cran.r-project.org/web/packages/MixSIAR/MixSIAR.pdf). To test the usefulness of δ^{2}H, we ran four different mixing models and then compared their predictive powers with the Deviance information criterion (DIC) value (Spiegelhalter et al., 2002) and Gelman-Rubin convergence diagnostics (Gelman and Rubin, 1992). Four mixing models were called Mya_CN, Mya_CND, Mya_CNS, Mya_CNDS: Mya_CN consisted of δ ^{13}C and δ ^{15}N; Mya_CND δ ^{3}C, δ ^{15}N and δ^{2}H; Mya_CNS δ ^{13}C, δ ^{15}N and δ ^{34}S; and Mya_CNDS δ ^{3}C, δ ^{15}N, δ^{2}H and δ ^{34}S.

We checked the normality of stable isotope values with the Shapiro-Wilk test and performed a one-way analysis of variance (ANOVA) to examine locational differences of the stable isotope values. Levene's test was implemented to check heteroscedasticity, and Welch's correction was used subsequently. Pearson's correlation analysis was used to account for the relationships among clam diets, growth, and salinity (September water salinity), which was a proxy of the distance from the ocean in the estuary (Table 1d). All statistical analyses were done in R v.4.2.2. (www.R-project.org).

3. Results

3.1. *Spatial characteristics of stable isotopic values for food sources*

The four stable isotope tracer values differed significantly among the food sources (see Nelson et al., 2015 for δ^{13}C and δ^{15}N; $F_{3,15} = 8.65$, $P < 0.01$ for δ^{34}S; $F_{3,4} = 15.05$, $P < 0.05$ for δ^{2}H). The stable isotope values of primary organic matter sources (POMs) varied along a spatial gradient relative to oceanic vs terrestrial freshwater inputs, and the lower to the upper estuary (Table 1a, Fig. 1). The mean δ^{13}C, δ^{15}N, δ^{34}S and δ^{2}H values of POM were −22.5 ‰, 5.5 ‰, 19.6 ‰, −145.5 ‰ and in the lower estuary, respectively, and −30.2 ‰, 5.7 ‰, −1.7 ‰, −161.0 ‰ and in the upper estuary (Table 1a). While the δ^{13}C and δ^{34}S values showed a considerable decline from the lower to the upper (decreases of ~7.7 ‰ for δ^{13}C and ~21.3‰ for δ^{34}S), the δ^{15}N values presented a little increase (~0.2 ‰ for δ^{15}N). The three isotope values, δ^{13}C, δ^{15}N and δ^{34}S, of brackish marsh were positioned between the values of OEPOM and RPOM. Salt marsh presented the lowest δ^{15}N value and the highest δ^{13}C value. In particular, the δ^{34}S values of four food sources clearly varied along the spatial gradient of sampling sites across the estuary. The values decreased from the lower to the upper estuary: OEPOM (19.6 ‰) > salt marsh (4.9 ‰) > brackish marsh (1.8 ‰) > RPOM (−1.7 ‰). On the other hand, the δ^{2}H values showed a different spatial pattern; highest in the middle estuary and lowest in the upper. The highest value was found in brackish marsh and the lowest in RPOM. The δ^{2}H values significantly distinguished between organic matter sourced from intertidal marsh macrophytes and organic matter originating from aquatic plants and algae (RPOM and OEPOM).

3.2. *Spatial characteristics of stable isotopic values for M. arenaria*

The four isotopic values of *M. arenaria* juvenile and adult clams, presented significant differences among the sampling sites ($F_{welch\ 6,11} = 5.58$, $F_{welch\ 5,10} = 5.37$ for δ^{13}C; $F_{6,34} = 6.03$, $F_{5,28} = 4.92$ for δ^{15}N and $F_{6,34} = 21.73$, $F_{5,28} = 31.91$ for δ^{34}S, $F_{6,34} = 6.18$, $F_{5,28} = 12.16$ for δ^{2}H juvenile and adult clams, respectively; all $P < 0.05$; Table 1b and c, Fig. 1) and varied along an upper to lower estuary spatial gradient, Mill

River to Yacht Club. The lowest value of δ^{13}C was found at Mill River for juvenile clams and Railroad Meander for adult clams and the highest at Clubhead Creek for juvenile and adult clams. The δ^{15}N value was lowest at Third Creek and highest at Sweeny Creek for juvenile and adult clams. The δ^{34}S was highest at Yacht Club for juvenile and adult clams and lowest at Mill River for juvenile clams and Sweeny Creek at adult clams. The spatial pattern of δ^{34}S showed strong negative correlations with distance from Yacht Club to Mill River ($r = -0.91$ for adult clams; $r = -0.95$ for juvenile clams, for all $P < 0.05$). The δ^{2}H value was highest in the upper estuary and lowest in the middle or lower estuary for adult and juvenile clams, but the differences of δ^{2}H among sites were very small.

3.3. *Comparing performances of four mixing models*

Four different mixing models, Mya_CN ($\delta\ ^{13}$C and $\delta\ ^{15}$N), Mya_CND ($\delta\ ^{3}$C, $\delta\ ^{15}$N and δ^{2}H), Mya_CNS ($\delta\ ^{13}$C, $\delta\ ^{15}$N and $\delta\ ^{34}$S), Mya_CNDS ($\delta\ ^{3}$C, $\delta\ ^{15}$N, δ^{2}H and $\delta\ ^{34}$S), were run and compared by their predictive powers, Deviance information criterion (DIC) and Gelman-Rubin diagnostics (GRD), to find a best fitting model to explain the clam dietary sources and its spatial variability (Table 2). All models showed good GRD values, <1.05, especially the GRD values of Mya_CND, Mya_CNS and Mya_CNDS which were less than 1.01. The lowest value of DIC was found in Mya_CND, the second lowest in Mya_CN, and the third in Mya_CNDS. The highest value of DIC was found in Mya_CNS.

Based on the DIC and GRD values, Mya_CND was the best model to explain the clam dietary source and its spatial variability in PIE. However, as considering that DIC is only valid when the posterior probability distribution is approximately multivariate normal, the DIC estimates of Mya_CN and Mya_CND are not valid because their posterior distributions are not multivariate normal (Fig. SD1 of online supplementary). The Mya_CNS' posterior distributions were partially multivariate normal because OEPOM and salt marsh only showed normal posterior distributions. The posterior distributions of Mya_CNDS were approximately multivariate normal, showing the normal posterior probability distributions for all four food sources. Therefore, the DIC estimates reliably validated the model predictive power only for the Mya_CNDS.

We also compared the predictive uncertainty of four models with the dispersion of predictions and the standard deviations (Table 2, Fig. 3). Compared with other three models, the Mya_CNDS prediction showed the lowest uncertainty, the lowest standard deviation and the smallest dispersion. The second lowest predictive uncertainty was found on the Mya_CNS prediction and the third on the Mya_CND prediction. The Mya_CN prediction showed the highest uncertainty. The Mya CNDS model was the only model that reliably explained the contributions of the four food sources to the clam diet, based on considering the estimates of DIC with the posterior distribution pattern, Gelman-Rubin diagnostics, standard deviation, and the dispersion of predictions all together.

The predictive uncertainty and model reliability generally decreased with increasing the number of isotope parameters, showing the lowest uncertainty and most valid prediction in the Mya_CNDS. Adding the sulfur isotope to mixing model decreased the predictive uncertainty, Mya_CN vs. Mya_CNS and Mya_CND vs. Mya_CNDS. Adding the deuterium to the model improved the predictive powers, Mya_CN vs. Mya_CND and Mya_CNS vs. Mya_CNDS. When comparing two mixing models with the same number of parameters, Mya_CNS and Mya_CND, Mya_CNS was better than Mya_CND in model reliability but Mya_CND was better than Mya_CNS in predictive power. The δ^{34}S increased the reliability of the estimate, and the δ^{2}H the predictive power.

3.4. *Spatial variability in food sources for M. arenaria*

The δ^{15}N values provided more information about trophic levels than about spatial variations in diet (Fig. 2a). The average δ^{15}N value was 8.7 ‰ for adult clams and 9.1 ‰ for juveniles, both of which were enriched compared to the average δ^{15}N value of 5.2 ‰ from dietary sources (Table 1). Upward isotopic shifts of approximately +3.5 ‰ for adult clams and +3.9 ‰ for juvenile clams from primary producers to clams were observed (Table 1), suggesting primarily herbivorous feeding. The isotopic combinations of δ^{34}S and δ^{13}C (Fig. 2b) and δ^{2}H and δ^{13}C (Fig. 2c) indicated clams tended to depend on different organic matter sources, which varied by location within the estuary. Clams relied more on brackish marsh detritus in the upper estuary than in the lower, salt marsh detritus more so in the middle estuary than in upper and lower regions, and OEPOM more so in the lower estuary than further up estuary. The importance of terrestrial organic matter as estimated from RPOM showed a minimal contribution throughout the estuary (Fig. 2a–f).

The results of Mya_CNDS, providing a valid and reliable prediction, and Mya_CND, presenting the lowest DIC, suggested that the primary food source of juvenile and adult clams in the Plum Island estuary is oceanic/estuarine organic matter (OEPOM - unicellular algae), and salt marsh detritus (Tables 2 and 3, Figs. 3 and 4, Fig. SD2-5). However, the two mixing models suggested different relative contributions of OEPOM and salt marsh detritus. Mya_CNDS predicted OEPOM was more important than salt marsh detrital organic matter while Mya_CND suggested just the opposite – that salt marsh detritus was more important than OEPOM at all sampling sites. In addition, the two mixing models also suggested different relative contributions of riverine and brackish marsh sources. Mya_CNDS predicted brackish marsh detritus was more important than riverine organic matter but Mya_CND suggested the opposite at all sampling sites.

Mya_CNDS best reflects the spatial variability of clam diet along the landscape continuum from upper to middle and to lower estuary. It shows a diet that reflects the spatial distribution of marsh habitats along the estuary, a declining importance of OEPOM up-estuary, and minimal importance of RPOM that declines down-estuary. *M. arenaria* relies on locally available food sources. The predictions of Mya_CNDS showed that the contributions of OEPOM to the clam diet decreased going upstream in accordance with a decrease in open water habitats relative to the area of fringing brackish marshes and a decrease in salinity, which reflects increased freshwater and terrestrial organic matter inputs.

Table 2

Performance of two mixing models and their estimates of food source contributions to *Mya* diet. Model performance assessed with the Deviance Information Criterion (DIC) and Gelman-Rubin diagnostics.

MixSIAR model	Stable Isotopes		Ocean/Estuarine POM		Salt Marsh		Brackish Marsh		Riverine POM	
		DIC (GRD)	Mean (SD)	Lower/Upper 95%	Mean (SD)	Lower/Upper 95%	Mean (SD)	Lower/Upper 95%	Mean (SD)	Lower/Upper 95%
Mya_CN	δ^{13}C, δ^{15}N	62.7 (<1.05)	0.43 (0.25)	0.05/0.83	0.3 (0.12)	0.10/0.48	0.09 (0.08)	0/0.25	0.19 (0.13)	0.01/0.42
Mya_CND	δ^{13}C, δ^{15}N, δ^{2}H	39.7 (<1.01)	0.31 (0.18)	0.04/0.62	0.34 (0.09)	0.19/0.48	0.15 (0.06)	0.04/0.25	0.2 (0.11)	0.03/0.38
Mya_CNS	δ^{13}C, δ^{15}N, δ^{34}S	173.7 (<1.01)	0.45 (0.06)	0.35/0.55	0.29 (0.05)	0.20/0.37	0.09 (0.08)	0/0.26	0.18 (0.06)	0.05/0.26
Mya_CNDS	δ^{13}C, δ^{15}N, δ^{2}H, δ^{34}S	169.4 (<1.01)	0.44 (0.05)	0.35/0.53	0.27 (0.05)	0.18/0.35	0.19 (0.06)	0.09/0.29	0.1 (0.05)	0.03/0.18

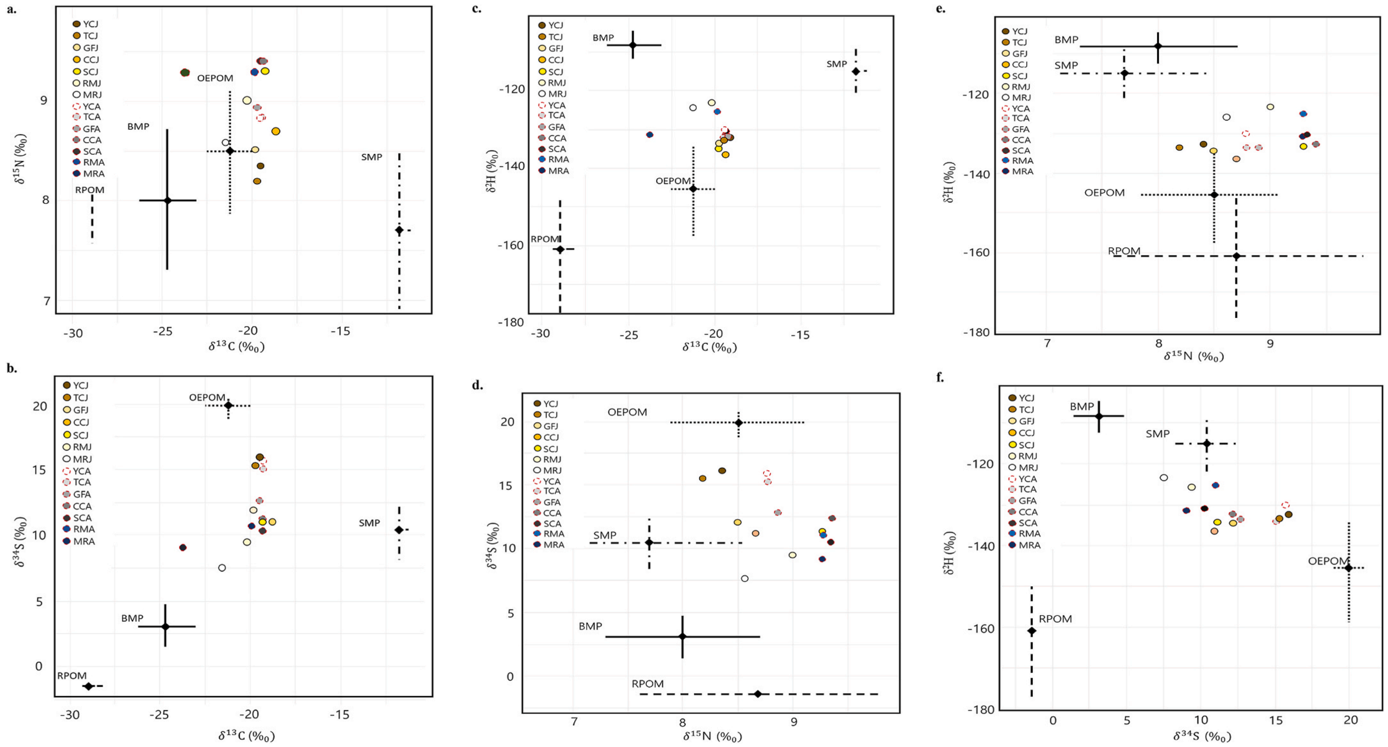

Fig. 2. Dual stable isotope plots. OEPOM (······) indicates ocean/estuarine particulate organic matters, RPOM (– – –) riverine particulate organic matters, SMP (·· – ·) salt marsh plants, and BMP (——) brackish marsh plants. Abbreviations on the legend on the upper left show the sampling site and clam growth stage: YC = Yacht Club, TC = Third Creek, GF = Grandkids Flat, CC = Clubhead Creek, SC = Sweeny Creek, RM = Railroad Meander, MR = Mill River, J = Juvenile clams (solid lined circle), A = Adult clams (dashed lined circle). So, YCJ indicates Yacht Club Juvenile clams.

Compared with other food sources, salt marsh showed similar contributions to the clam diet at six sample sites. The importance of brackish marsh increased at the upper sites, Railroad Meander and Mill River (>20 %). According to the Mya_CNDS estimations, RPOM is the least important food source.

3.5. *Organic matter inputs to the estuary*

The overall production of organic matter within the Plum Island estuary and the loading of organic matter from the rivers draining into the estuary estimated for the broad categories of total algal production (same as OEPOM), total marsh production and OC loading from the Ipswich and Parker Rivers is about 48,000 MT C yr^{-1} or 2600 MT N yr^{-1}. The marsh dominates these inputs whether measured in C or N units – 80% and 60%, respectively. Algal production is secondary in magnitude, representing 13 and 35% of total inputs for C and N, respectively. The difference in C:N ratio of these broad categories of input accounts for the increase in algal importance based on N compared to C (7:1 vs 25:1 for algae vs marsh or riverine organic matter). Loading of organic matter via the rivers is much lower than it is for marshes or algae – 7% or 5% depending on whether C or N is compared.

Most of the primary production that occurs on the marsh never reaches the tidal waters where Mya feeds. It is mostly decomposed in place or stored in marsh sediments. Only 24% of total production reaches tidal creeks (Forbrich et al., 2018), either with ebb tide drainage or via edge erosion (Hopkinson et al., 2018). Relatively low lability of riverine dissolved organic matter (Uhlenhopp et al., 1995) and short estuarine transit times means that 80% passes directly to the ocean. We assume that all POC and a portion of DOC that flocculates in the estuary are potential food sources for clams however. Based on net inputs of organic matter from rivers and marshes and all algal production, organic matter inputs accessible to clams is 16,200 MT C/yr. Based on net C inputs, the marshes provide 58% of the total followed by algae (38%) and the river (4%). Using N as the currency of importance to clams, marshes provide only 29% of total inputs, while algae are responsible for 69%. Again this dramatic difference in the relative importance of algae stems from its low C:N compared to marsh and riverine organic matter.

3.6. *Relationships between clam diet and growth along the estuary*

The clam maximum growths at sampling sites were projected with adult clams; thus, the growth was correlated with adult clam diet compositions predicted by the Mya_CNDS and the Mya_CND (Tables 3b and 4b). The Mya_CND predictions did not show significant correlations with the clam growth due to similar contributions of four food sources at all sampling sites. Contrarily, the proportions of OEPOM and brackish marsh of the Mya_CNDS predictions presented significant correlations with the clam growth but salt marsh and RPOM did not.

Based on the Mya_CNDS prediction, the maximum growth was positively correlated with the proportion of OEPOM in the clam diet ($r = 0.95$, $P < 0.01$) and the negatively with brackish marsh ($r = -0.85$, $P < 0.05$). The positive correlations were also found between the maximum growth and the proportion of salt marsh, with a marginal significance ($r = -0.71$, $P = 0.12$). Therefore, the suitable habitat conditions for clam growth were well explained by the proportion of OEPOM and salt marsh assimilated into body mass and the spatial variability of OEPOM and salt marsh in PIE. Better growth was found at the habitats with more OEPOM and salt marsh supplies, reflecting the open water habitats in the lower and the extensive salt marsh habitats in the middle estuaries in PIE.

4. Discussion

4.1. *Clam diet and the power of four isotopes*

The δ^{13}C, δ^{15}N, δ^{34}S and δ^{2}H values clearly discriminate the primary

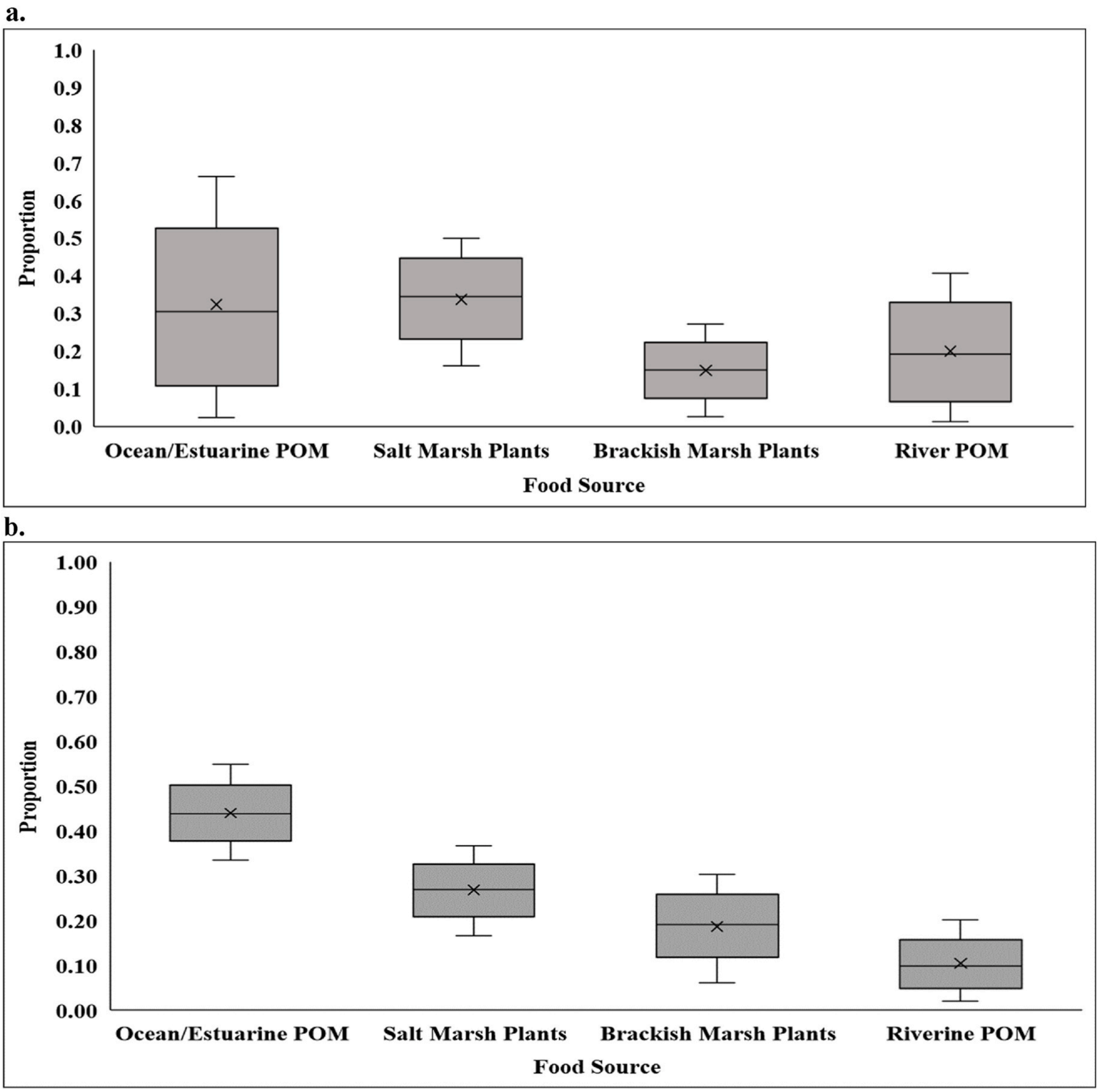

Fig. 3. The overall mean contribution of each food source in the clam diet. a shows the mean contributions of dietary sources to the clam diets predicted by Mya_CND, and **b** presents the mean contributions predicted by Mya_CNDS.

sources of organic matter inputs to the Plum Island estuary and the spatial variability of clam diet. The δ^{13}C values excel at discriminating between salt marsh and RPOM food sources. The δ^{34}S values discriminate well between OEPOM and RPOM sources. The δ^{2}H values are extremely useful for discriminating between wetland macrophytes (brackish and saline marshes) and the riverine and oceanic/estuarine algae (OEPOM and RPOM). The δ^{15}N values have the least discriminating power of the four isotopes with only about a 1‰ difference between the four food sources but δ^{15}N is a useful tracer of anthropogenic nitrogen inputs to the Plum Island estuary.

The power of adding δ^{34}S isotopes to the standard easily and inexpensively measured C and N isotopes has long been recognized in estuarine food web studies (Peterson and Fry, 1987; Peterson and Howarth, 1987; Peterson et al., 1985). Sulfur (δ^{34}S) is especially important in wetland-dominated estuaries because isotopically light sulfides are produced in anoxic sediments and then assimilated by rooted wetland plants. That light S signal can then be traced into consumers of wetland detritus (Duffill Telsnig et al., 2019; Fry, 2006; Peterson, 1999; Peterson and Howarth, 1987). Sulfur has been also recommended for discriminating terrestrial from oceanic food sources because of much lower isotopic values of terrestrial organic matter compared with oceanic sources (Hebert et al., 2008; Moreno et al., 2010; Peterson, 1999). Our study agrees with these previous findings. Our results identified the lower value of sulfur of salt and brackish marsh macrophytes, 4.9 ‰ and 1.8 ‰ respectively, compared with OEPOM, 19.6 ‰. Sulfur also helped discriminate terrestrial from oceanic food sources, with our lightest values originating in RPOM. Overall there was a decrease in δ^{34}S values for POM along the length of estuary: OEPOM (19.6 ‰) > salt marsh (4.9 ‰) > brackish marsh (1.8 ‰) > RPOM (−1.7 ‰). The results of mixing modeling further strengthen the argument for the inclusion δ^{34}S because adding δ^{34}S to the mixing model certainly decreases the predictive uncertainty, Mya_CN vs. Mya_CNS and Mya_CND vs. Mya_CNDS, and increases the predictive power, Mya_CN vs. Mya_CNS.

Deuterium, δ^{2}H, is rarely used in trophic ecology because tissue H isotopic composition is influenced by diet as well as environmental water. It has been widely used in the study of the hydrological cycle however, by tracing water origin and reconstructing past climate (Clark and Fritz, 1997; Duarte et al., 2018; Vander Zanden et al., 2016). Recently, the application of deuterium in trophic ecology has increased

Table 3

The results of the Mya_CND and Mya_CNDS models. Based on the Mya_CND, the mean contribution of each food source to the juvenile clam diet (Mean) and its standard deviation (SD) are shown in table **a**, and to the adult clam in table **b**. Based on the Mya_CNDS, the mean contribution of each food source to the juvenile clam diet (Mean) and its standard deviation (SD) are shown in table **c**, and to the adult clam in table **d**.

a.

	Ocean/Estuarine POM		Salt Marsh		Brackish Marsh		Riverine POM	
Site	Mean (SD)	Lower/Upper 95%	Mean (SD)	Lower/Upper 95%	Mean (SD)	Lower/Upper 95%	Mean (SD)	Lower/Upper 95%
Mill River	0.30 (0.17)	0.04/0.64	0.34 (0.10)	0.18/0.49	0.17 (0.09)	0.04/0.32	0.20 (0.11)	0.02/0.39
Railroad Meander	0.30 (0.17)	0.04/0.60	0.35 (0.09)	0.19/0.49	0.16 (0.08)	0.04/0.29	0.19 (0.11)	0.02/0.38
Sweeny Creek	0.32 (0.18)	0.04/0.64	0.34 (0.10)	0.17/0.49	0.14 (0.06)	0.04/0.25	0.20 (0.11)	0.02/0.38
Clubhead Creek	0.32 (0.19)	0.04/0.64	0.34 (0.10)	0.17/0.49	0.14 (0.06)	0.04/0.24	0.20 (0.11)	0.02/0.38
Grandkids' Flat	0.32 (0.18)	0.04/0.64	0.34 (0.10)	0.17/0.49	0.15 (0.06)	0.04/0.25	0.20 (0.11)	0.02/0.39
Third Creek	0.32 (0.18)	0.04/0.63	0.34 (010)	0.18/0.49	0.15 (0.06)	0.04/0.26	0.20 (0.11)	0.02/0.38
Yacht Club	0.31 (0.18)	0.04/0.62	0.34 (0.10)	0.18/0.49	0.15 (0.06)	0.04/0.26	0.20 (0.11)	0.03/0.38

b.

	Ocean/Estuarine POM		Salt Marsh		Brackish Marsh		Riverine POM	
Site	Mean (SD)	Lower/Upper 95%	Mean (SD)	Lower/Upper 95%	Mean (SD)	Lower/Upper 95%	Mean (SD)	Lower/Upper 95%
Mill River	0.32 (0.19)	0.05/0.65	0.31 (0.10)	0.14/0.46	0.16 (0.08)	0.04/0.29	0.21 (0.13)	0.02/0.42
Railroad Meander	0.30 (0.17)	0.04/0.60	0.35 (0.10)	0.19/0.50	0.16 (0.08)	0.04/0.29	0.19 (0.11)	0.02/0.38
Sweeny Creek	0.31 (0.18)	0.04/0.62	0.35 (0.10)	0.18/0.50	0.15 (0.07)	0.04/0.26	0.19 (0.11)	0.02/0.38
Clubhead Creek	0.32 (0.18)	0.04/0.63	0.34 (0.10)	0.18/0.49	0.15 (0.06)	0.04/0.25	0.20 (0.11)	0.02/0.38
Grandkids' Flat	0.32 (0.18)	0.04/0.63	0.34 (0.10)	0.18/0.49	0.15 (0.06)	0.04/0.25	0.20 (0.11)	0.02/0.38
Third Creek	0.32 (0.18)	0.04/0.63	0.34 (0.10)	0.18/0.49	0.15 (0.06)	0.04/0.25	0.20 (0.11)	0.02/0.38
Yacht Club	0.31 (0.17)	0.04/0.61	0.35 (0.10)	0.19/0.50	0.15 (0.07)	0.04/0.26	0.19 (0.11)	0.02/0.38

c.

	Ocean/Estuarine POM		Salt Marsh		Brackish Marsh		Riverine POM	
Site	Mean (SD)	Lower/Upper 95%	Mean (SD)	Lower/Upper 95%	Mean (SD)	Lower/Upper 95%	Mean (SD)	Lower/Upper 95%
Mill River	0.36 (0.09)	0.22/0.50	0.27 (0.07)	0.15/0.37	0.27 (0.12)	0.09/0.47	0.11 (0.06)	0.03/0.21
Railroad Meander	0.38 (0.08)	0.26/0.51	0.29 (0.07)	0.17/0.39	0.23 (0.09)	0.08/0.39	0.10 (0.05)	0.03/0.20
Sweeny Creek	0.45 (0.08)	0.33/0.58	0.27 (0.07)	0.16/0.38	0.18 (0.06)	0.07/0.28	0.11 (0.05)	0.03/0.20
Clubhead Creek	0.46 (0.08)	0.33/0.60	0.27 (0.07)	0.15/0.39	0.17 (0.06)	0.07/0.27	0.11 (0.05)	0.03/0.20
Grandkids' Flat	0.46 (0.08)	0.34/0.59	0.26 (0.07)	0.15/0.36	0.18 (0.06)	0.07/0.28	0.11 (0.05)	0.03/0.20
Third Creek	0.48 (0.09)	0.35/0.63	0.26 (0.07)	0.15/0.37	0.17 (0.06)	0.07/0.28	0.10 (0.05)	0.03/0.18
Yacht Club	0.47 (0.08)	0.35/0.63	0.27 (0.07)	0.15/0.37	0.17 (0.06)	0.07/0.27	0.09 (0.05)	0.03/0.18

d.

	Ocean/Estuarine POM		Salt Marsh		Brackish Marsh		Riverine POM	
Site	Mean (SD)	Lower/Upper 95%	Mean (SD)	Lower/Upper 95%	Mean (SD)	Lower/Upper 95%	Mean (SD)	Lower/Upper 95%
Mill River	0.42 (0.07)	0.30/0.55	0.22 (0.07)	0.10/0.33	0.23 (0.09)	0.08/0.31	0.13 (0.07)	0.03/0.26
Railroad Meander	0.39 (0.08)	0.26/0.52	0.29 (0.07)	0.18/0.40	0.22 (0.09)	0.08/0.38	0.10 (0.05)	0.03/0.19
Sweeny Creek	0.42 (0.07)	0.30/0.54	0.28 (0.07)	0.17/0.39	0.19 (0.07)	0.08/0.31	0.11 (0.05)	0.03/0.20
Clubhead Creek	0.45 (0.07)	0.33/0.57	0.28 (0.07)	0.16/0.33	0.18 (0.07)	0.07/0.29	0.10 (0.05)	0.03/0.19
Grandkids' Flat	0.46 (0.08)	0.34/0.59	0.27 (0.07)	0.16/0.37	0.18 (0.06)	0.07/0.28	0.10 (0.05)	0.03/0.19
Third Creek	0.48 (0.08)	0.35/0.62	0.26 (0.07)	0.15/0.37	0.17 (0.06)	0.07/0.27	0.10 (0.05)	0.03/0.18
Yacht Club	0.46 (0.08)	0.33/0.60	0.28 (0.07)	0.16/0.39	0.18 (0.07)	0.07/0.29	0.09 (0.05)	0.03/0.18

due to its high potential in tracing dietary sources of organisms taking food both from terrestrial and aquatic environments (Duarte et al., 2018; Vander Zanden et al., 2016). The deuterium ratio has the advantage of large differences between aboveground or terrestrial plants and aquatic or submerged plants (averaging 40‰–80‰) because terrestrial plants become enriched with deuterium when they transpire lighter water. Aquatic plants on the other hand use lighter water and therefore become heavy (Brett et al., 2018; Doucett et al., 2007; Solomon et al., 2011). In our Plum Island study, we included δ^2H in order to better discriminate between intertidal marsh macrophyte organic matter and aquatic sources from within the river or estuary/ocean. We found clear separation between these two source types with intertidal marsh organic matter averaging −111.7 ± 3.3‰ and riverine and oceanic/estuarine POM averaging −153.3 ± 7.8‰. That RPOM was relatively light, suggests minimal input from soil erosion or woody vegetation within the watershed, which would likely be heavy, as with the marsh macrophytes. It could be because our sampling sites were below the dam, and, accordingly, the plant detritus is mostly trapped by the dam. Much of the organic carbon exported from the river is ^{14}C young (Raymond and Hopkinson, 2003), and in combination with our δ^2H results suggests that a major fraction of the RPOM assimilated by clams may have been aquatic in origin, including freshwater submerged aquatic vegetation and associated epiflora. The 42 ‰ difference contrasts the smaller differences seen with carbon, sulfur and nitrogen isotopic values for these sources. Inclusion of δ^2H into the Mya CN and Mya CNS mixing models increased both the predictive power and DIC values.

Coastal waters are increasingly enriched with nitrogen as a result of river runoff from watersheds experiencing anthropogenic activities including urbanization and intense agriculture (Fry et al., 2003; Mazumder et al., 2015; McClelland et al., 1997; Vander Zanden et al., 2005; Warry et al., 2016). Nitrogen isotopes are often a useful tracer of anthropogenic nitrogen inputs to estuarine and coastal ecosystems (Bannon and Roman, 2008; Fry et al., 2003; Mazumder et al., 2015; McClelland et al., 1997). Higher δ^{15}N values of estuarine organisms are related to increased urban and agricultural land use in watersheds (Mazumder et al., 2015; McClelland et al., 1997; Vander Zanden et al., 2005; Warry et al., 2016) and are typical in estuaries experiencing N-enrichment (Aberson et al., 2016; Orlandi et al., 2014; Vander Zanden et al., 2005). The δ^{15}N values of clams in our study are significantly higher in the middle and upper regions of the Plum Island Sound estuary

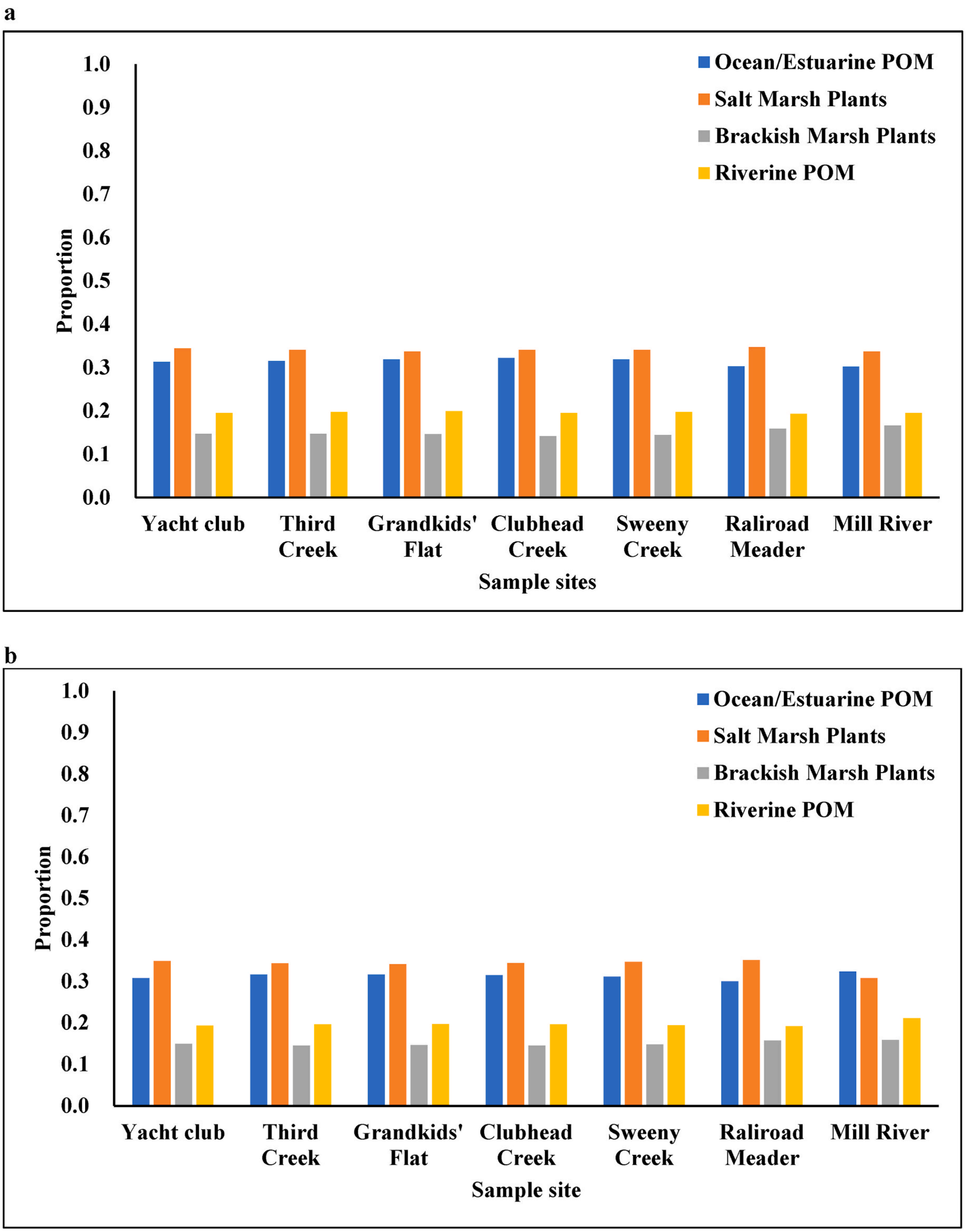

Fig. 4. The predictions of MixSIAR models at each site. The Mya_CND results for juvenile clams are shown in (a) and for adult clams in (b). The Mya_CNDS results for juvenile clams are presented in (c) and for adult clams in (d).

than in the lower, closer-to-the-ocean clam region. Elevated $\delta^{15}N$ clam values from Sweeny Creek, Clubhead Creek and Railroad Meander may reflect anthropogenic nitrogen inputs from upstream of these sites. We note that the Town of Ipswich has a sewage sludge composting operation in the headwaters of Sweeney Creek. Clubhead Creek might see N inputs from Sweeney creek and the Rowley river. The Railroad Meander site is likely influenced by N inputs from the Parker River, the Mill River and Little River (Fig. 1). In addition, we note higher $\delta^{15}N$ values in clams than previously reported. Deegan and Garritt (1997) found in 1995 $\delta^{15}N$ values of 8.3 ‰ in the middle estuary (near Sweeny Creek and Clubhead Creek) and 8.0 ‰ in the lower estuary (near Yacht Club and Third Creek). These contrast our observations of $\delta^{15}N$ values, ~9.2 ‰ in the middle and ~8.5 ‰ in the lower. This increase likely reflects ongoing suburbanization in the Parker and Ipswich River watersheds (Runfola

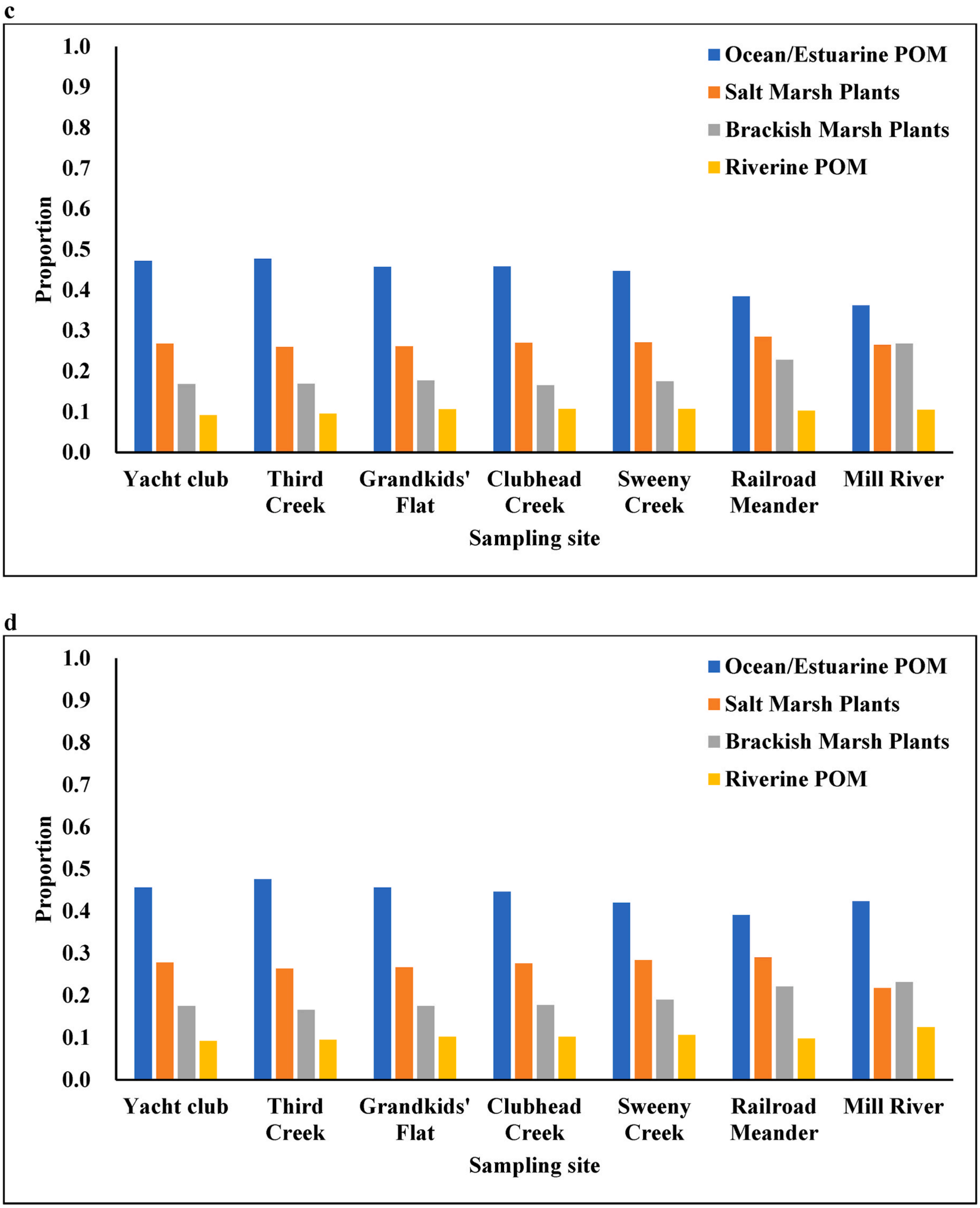

Fig. 4. (*continued*).

et al., 2013a) and expansion of sewage sludge composting. On the other hand, in addition to anthropogenic inputs, the presence of heavy nitrogen in benthic mollusks is also influenced by biogeochemical processes such as denitrification and nitrification. For instance, elevated levels of heavy nitrogen have been observed in heterotrophic mollusks inhabiting zones of strong denitrification, such as the highly organic-rich sediments found at the bottom of oxygen minimum zones (Amorim et al., 2022).

4.2. *Clam diet and the mixing models*

The Mya_CNDS model provides the most reliable and valid estimation of clam dietary sources among the four mixing models. It has a lower predictive uncertainty than the Mya_CND and Mya_CN models and better predictive power than the Mya_CNS model (Table 2, Fig. 3). The CNDS model estimates that OEPOM and salt marsh detritus are the primary food sources of clams in the Plum Island estuary with minor contributions from RPOM and the brackish marsh. OEPOM and salt marsh detritus make up 44% and 27% of the diet of adult and juvenile clams, but brackish marsh detritus and RPOM contribute to the clam diet

19% and 10%, respectively (Table 2, Fig. 3b). The dominance of salt marsh and OEPOM for clam nutrition was previously reported in the Plum Island estuary (Deegan and Garritt, 1997; Nelson et al., 2015).

The Mya_CNDS model shows that clam diet composition varies non-linearly with position along the estuary (Table 3c & d, Fig. 3b). The relative importance of clam dietary sources varies little from the lower to the middle regions of the estuary, varying less than 2% for any dietary source. However, there is a significant decrease in the contribution of OEPOM and salt marsh sources to the clam diet in the upper region. In contrast to the decreases of OEPOM and salt marsh contributions, there is the increased importance of brackish marsh, from about 18% in the lower and middle estuary to 23–27% in the upper estuary, and RPOM, from about 10% to 11–13%. The increased importance of RPOM and brackish marshes is as expected since these inputs originate in the upper estuary – either the watershed for RPOM via the Parker, Mill, Little rivers and Cart Creek or the upper 4–5 km of the Plum Island estuary for brackish marshes.

Previous studies did not examine clam diet in the upper regions of the estuary where they grow in the Plum Island estuary (Deegan and Garritt, 1997; Nelson et al., 2015) and consequently did not address spatial patterns in diet. As we did examine diet throughout their geographic extent in the estuary, we find shifts in diet between lower, middle and upper regions, suggesting that clams eat the locally available sources. Variations in diet that match variations in source inputs has been observed for most consumers in the Plum Island estuary (Deegan and Garritt, 1997; Nelson et al., 2015).

We find that the addition of a fourth tracer significantly improves our ability to differentiate clam diet in an estuarine system with a multitude of potential, spatially variable food sources. The addition of δ^2H to the more commonly used δ^{13}C, δ^{15}N and δ^{34}S stable isotopes improves predictive power by decreasing the DIC value. Thus, we agree with the previous suggestion that multiple tracers together better trace the use of multiple potential food sources of consumers due to the different biogeochemical controls acting on each of the elements (Vander Zanden et al., 2016). We note however, that due to very high predictive uncertainty of the Mya_CND model and the violation of the fundamental mixing model assumptions, caution should be taken in replacing sulfur with deuterium as a third tracer. We need much further research in diverse ecosystems to address the effectiveness of δ^2H in dietary modeling studies and to explore the trade-off between δ^{34}S and δ^2H. Such information will provide the ecosystem-specific guidelines for selecting which isotopes for feeding ecological and food web studies.

4.3. Clam diet and the magnitude of source inputs

A stable isotope rule is that “you are what you eat” (Fry and Smith, 2002). While we know the relative composition of food sources supporting clam growth in the Plum Island estuary, we know less about the quantitative input of food sources and their diet. It was hypothesized more than half a century ago that aquatic consumers in estuaries dominated with intertidal wetlands, (e.g., mangroves and salt marshes) were detritivores and growth dependent mostly on detritus of macrophyte origin (Darnell, 1967; Newell, 1984; Odum, 1967; Odum and Helad, 1975). Considering that 2/3 to 3/4 of the primary production of many tidal wetland dominated U.S.A. east coast estuaries is derived from the emergent macrophytes (Pomeroy et al., 1981), it was not surprising that detritus was the primary constituent often found in aquatic consumer guts (Odum, 1970) and thus classified as detritivores. Haines and Montague (1979) questioned the macrophyte detritus paradigm on the basis of C stable isotope composition of many aquatic invertebrates. Based on a simple 2 endmember mixing model, they found a greatly diminished role for marsh macrophytes and an enhanced importance of terrestrial organic matter sources and unicellular algae (e.g., benthic microalgae and phytoplankton). It was not until the use of 3 stable isotopes, especially S, that a dominant importance of intertidal macrophytes was reestablished (Currin et al., 1995; Moncreiff and Sullivan, 2001; Peterson and Howarth, 1987). It remains unclear however what controls the relative diet of consumers. Is it simply a matter of the relative availability of food sources or is it also a matter of palatability or food source quality? Odum, (1984) argued from the supply side that spatial gradients and landscape-based controls influence diet such that macrophyte detritus is more important where inputs are likely strongest in an estuary. Others argued from the qualitative perspective that quality is important and that readily assimilative food, such as algae, trump the relatively refractory macrophyte material (Currin et al., 1995; Newell et al., 1995). Macrophyte detritus is composed primarily of structural plant polymers including cellulose and lignin, which are typically considered slow and difficult to degrade (Benner et al., 1988; Spivak et al., 2019).

We find that availability does play a role in controlling the diet of Mya clams in the Plum Island estuary. We quantified the overall availability of 3 major classes of food source in the estuary: riverine organic matter, marsh macrophyte organic matter, and algae of oceanic and estuarine origin. We used both C and N as currencies for these budgets as C is the dominant element in organic matter but N perhaps better reflects quality (Spivak et al., 2019). The C:N ratio of algae is close to that described by Redfield (1963), while it is much higher for marsh plants and for organic matter originating from watersheds (e.g., 25:1).

According to the Mya_CNDS isotope model, the biomass of Mya clams in the Plum Island estuary is comprised of 46% intertidal marsh organic matter, 44% of algal material and 10% of riverine organic matter (Fig. 5a and b). We note again that here we combine the inputs of salt marsh and brackish marsh sources for the purpose of creating an input budget. The overall levels of autochthonous and allochthonous productivity in the Plum Island system, based on gross primary production of macrophytes and algae as well as gross dissolved and particulate organic matter inputs from the estuarine watershed, are 38,781, 6,206, and 3290 MT C/yr for marsh, algae and river, respectively. Using a 7:1 CN for algae and 25:1 for marsh macrophytes and riverine organic matter, gross organic matter inputs to the estuary are 1,551, 887, and 132 MT N/yr. When compared to the diet of clams (Fig. 5a), gross C productivity of the estuary greatly overpredicts the relative importance of marsh inputs (80% input vs 46% composition) and tremendously underweights the importance of algae (13% input vs 44% composition). With N as the currency (Fig. 5b), gross inputs better match that of clams (60 vs 46% for marsh; 35 vs 44% algae and 5% vs 10% river).

It may be unreasonable to predict diet on the basis of primary production of the marsh and total organic matter inputs from the river however, because the vast majority of marsh production is metabolized in place or buried, leaving only 18% to be exported to tidal waters where it would be available to clams (Hopkinson and Weston in review). The same is true for organic matter inputs from the river, as due to its slow rate of decomposition (Uhlenhopp et al., 1995) and short residence time in the estuary (Vallino et al., 1998), the vast majority is swept into the ocean without being available to clams. We estimate that only 19% of total riverine organic matter inputs are sedimented out and degraded in the estuary (Hopkinson and Weston in review). The availability of food sources to Mya based only on net inputs is much closer to the composition of clams with C as the currency (58% input vs 46% marsh composition, 38% vs 44% for algae and 2% vs 10% for river). The availability based on N inputs however are skewed heavily toward algae (Fig. 5b, 69% algae input vs 44% algal composition). There is a concomitant decrease in the predicted importance of marsh organic matter sources: 29% marsh input vs 44% marsh composition. Inputs from the watershed are also lower relative to the clam composition (2% river inputs vs 10% river composition).

The isotopic composition of clams in the Plum Island estuary is reasonably well predicted by the relative composition of allochthonous and autochthonous food source inputs to estuarine tidal waters – that predicted from a net input budget with a C currency (Fig. 5a). Both composition and food input results show intertidal marsh as the primary food source, closely followed by ocean/estuarine algae, and with

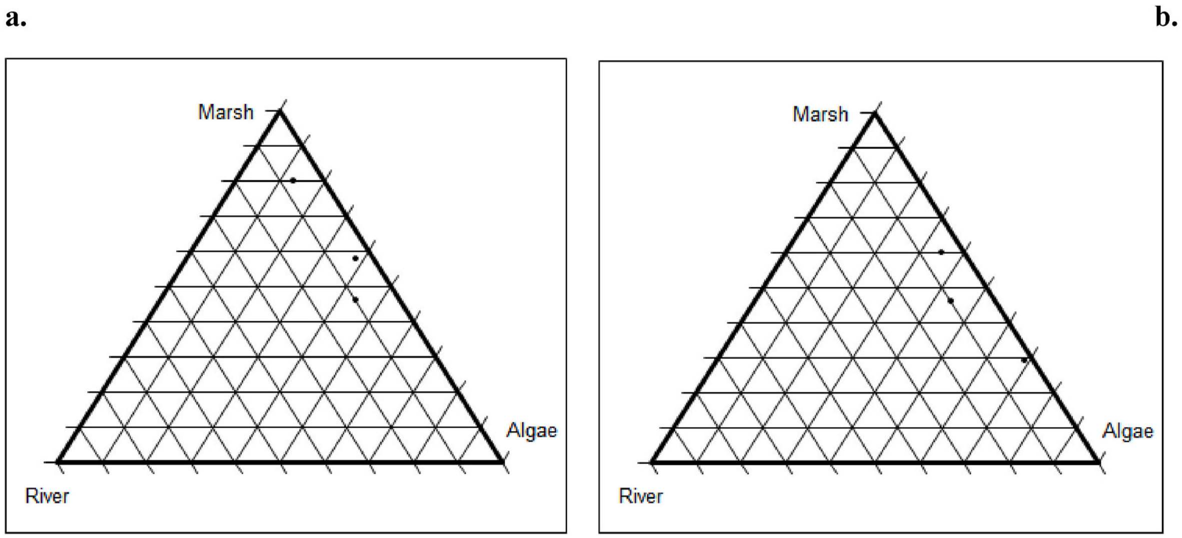

Fig. 5. Ternary plots of the relation between the magnitude of food source inputs and the composition of *Mya arenaria* as determined from the Mya_CNDS stable isotope mixing model. Food sources are simplified to contrast inputs from all marshes (brackish and saline), from the river, and from unicellular algae of estuarine and oceanic origin (mostly phytoplankton and resuspended benthic microalgae). a) compares gross and net inputs compared to clams based on organic carbon accounting and b) compares gross and net inputs based on organic nitrogen accounting.

riverine organic matter of minor importance. The input budget overpredicts the importance of marsh and underpredicts the importance of riverine derived organic matter. We conclude that Mya, is a relatively indiscriminate estuarine filter feeder heavily dependent on marsh derived detritus. It would appear that clams are what they are served – as well as being what they eat.

4.4. Clam growth and patterns of food availability and quality

Mya clam growth demonstrates a strong positive, down-estuary spatial gradient in the Plum Island estuary (Koo et al., 2017, Fig. 6a). This pattern is seen with growth measured as either the maximum potential size a clam can reach (L-infinity from the von Bertalanffy Growth Function) or the rate of growth as measured by the age to reach the local harvestable size of 50.8 mm (i.e., 50.8 mm/years to 50.8 mm) (Fig. 6a). Maximum size ranged from 93.4 mm at the Yacht Club station, which is closest to the ocean, to 57.9 mm at the Railroad Meander station, furthest upstream from the ocean and the relationship is described by the linear equation – L-infinity = 3.43 * distance from dam +24.54 (R^2 = 0.92).

We question whether a pattern of increasing growth down the estuary also reflects the magnitude of dietary inputs to the estuary or whether it reflects food source quality. While we lack data on the spatial pattern of allochthonous organic matter inputs from the tidal marshes, we do note that the relative area of marsh to tidal water decreases down estuary, from about 10:1 in the upper region of clam growth to about 2:1 in the lower Plum Island Sound (Hopkinson et al., 2018). This pattern is the opposite of the growth pattern, suggesting that quality may be more important. Clams do not "see" the inputs however, they "see" what is suspended in the water column.

The concentration of suspended solids, the substrates clams filter from the water, decreases down estuary throughout the entire range of where Mya grows in the Plum Island estuary (Plum Island Long-term Ecological Research database dates since 1994, https://pie-lter.mbl.edu/). Total suspended solids (TSS) decrease from about 20 to 6 mg/l, and particulate organic matter decreases from about 2.8 to 0.9 mg/l along the region of clam growth (Fig. 6b and c). Chlorophyll-a OM (C-aOM calculated from 70:1 C to Chl-a for phytoplankton/unicellular algae and 2:1 C to POM) also decreases in this zone from about 0.6 to 0.3 mg/l (Fig. 6c), but the pattern reverses during the time of high river flow in later winter – from about 8% to 33% of POM (Fig. 6e). In late summer and early fall, when river flow is low, C-aOM decreases from about 41% to 25% of total POM (Fig. 6e). Considering growth is temperature dependent, most growth occurs during the period when Chl-a decreases down estuary. Annual average Chl-a concentrations decrease downstream.

The spatial patterns of organic matter suspended in the water column are reverse the pattern of growth (Fig. 6a vs c). Indeed, there is also a strong negative relation between the concentration of C-aPOM and growth rate (Koo et al., 2017). Thus, concentration alone does not explain the pattern of clam growth observed in the Plum Island estuary. This is not surprising as the standing stocks of suspended particulate organic matter in the water column do not reflect their productivity or rate of supply (Colón-Gaud et al., 2008). Rather, turnover times and water residence time interact to control instantaneous concentrations. This enables clam growth to increase even as food concentrations decline.

The quality of suspended organic matter does increase in the direction of clam growth. We see evidence of quality increasing in the C:N ratio of the POM. The C:N decreases downstream from about 10.5:1 to 7.4:1 (Fig. 6d). N is an essential macronutrient for organisms, being a critical component of proteins, nucleic acids and compounds such as ATP (adenosine triphosphate). Unicellular plants and animals (e.g., phytoplankton and micro-organisms) have relatively low C:N – about 6–7:1 (Elser et al., 1996; Evans-White and Halvorson, 2017). Marsh plants have a relatively high C:N of about 25:1 (Abu-Zied et al., 2024; Cloern et al., 2002). Clams cannot grow efficiently on high C:N material because they can only incorporate 7 of the 25 C atoms to build biomass with about a 7:1 ratio. An increase in relative N content of the POM can then promote clam growth.

Another line of evidence that quality improves is seen in the proportion of POM in the water column that is composed of unicellular algae. This is often estimated by measuring the chlorophyll-a content of suspended solids. On an annual basis, the C-aOM proportion of POM increases down estuary in parallel with growth from about 21% to 29% from the upper to lower regions where clams grow (Fig. 6f). Phytoplankton/unicellular algae has a C:N of about 6.6:1 (Redfield, 1963), which suggests that the detrital "other" material in POM, has a C:N that ranges from about 7.5:1 to 8.9:1. Such low C:Ns for the non-algal component of POM shows that the riverine and marsh macrophyte-derived organic matter has undergone extensive modification during decomposition, as has been observed in freshwater and

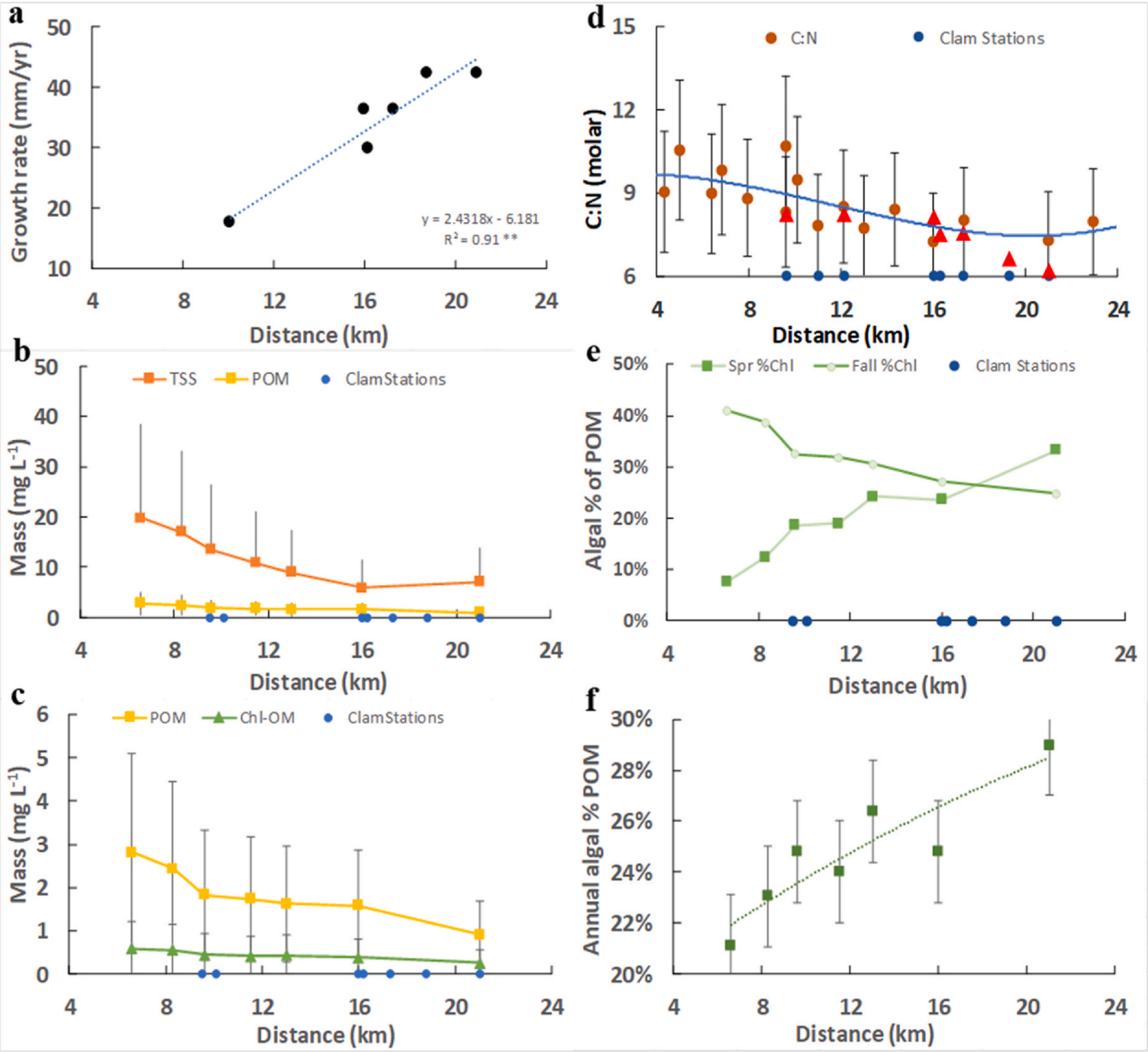

Fig. 6. Spatial patterns and relations between *Mya arenaria* growth and measures of water column particulates. a) the pattern of clam growth rate along the estuary. **b**) long-term average concentrations of TSS and POM along the estuary, with clam sampling stations identified as circles along x axis. **c**) long-term average concentrations of POM and unicellular algae (as determined from scaling measures of chlorophyll-a) along the estuary, with clam sampling stations identified as circles along the x axis. **d**) Long-term average C:N composition of POM along the estuary and with clam sampling locations identified as circles along the x axis. **e**) Long-term average contribution of unicellular algae relative to total POM along the estuary during high riverine inputs of spring vs low riverine inputs of late summer/early fall, with clam sampling locations shown as circles along x axis. **f**) The long-term average annual contribution of unicellular algae relative to total POM along the estuary.

terrestrial ecosystems for decades (Darnell, 1967; Melillo et al., 1982). Marsh derived organic matter undergoes N enrichment during decomposition and the process of becoming detritus. N-rich bacteria and fungi coat detrital surfaces, respire detrital organic carbon for energy production, and sometimes assimilate inorganic N from the water column to grow (Vallino et al., 1996). Over time the detrital particle loses C relative to N (Evans-White and Halvorson, 2017; Newell, 1984). The C:N ratio of detritus decreases for detritivores during the aging process. The spatial variation in the C:N ratio of POM explains 92% of the variation in growth (Fig. 7). C:N decreases downstream as C:N of marsh grass derived detritus decreases during aging and as the proportional content of algae in POM increases.

We are unaware of similar analyses of filter feeder diet relative to the relative input of organic matter sources to the estuarine water column. Further studies using the four isotopes, C, N, D and S, are needed for a better understanding of the relationship and the relative assimilation efficiency of detritus in the Plum Island estuary. Knowledge of this relationship and the relative assimilation efficiency of detritus of varying source composition is information critical to determining the

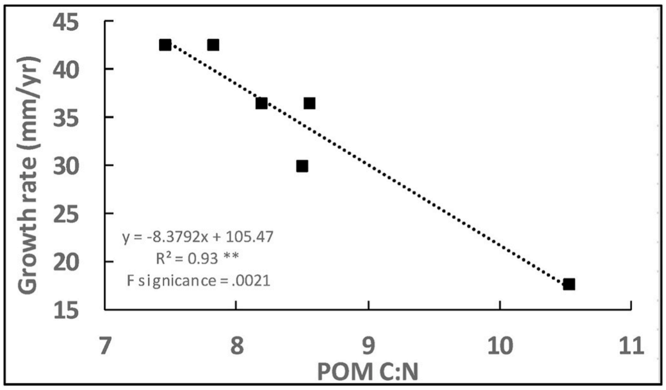

Fig. 7. The relation between *Mya arenaria* growth rate and the quality of suspended detritus along the estuary as estimated from the long-term average POM C:N ratio. The relation is highly significant.

sustainability and future productivity of filter feeders as anthropogenic activities will likely change the relative distribution and productivity of the primary food sources currently supporting these organisms.

4.5. *Clam diet, growth, and climate and land-use changes*

Our research into the distribution, growth and diet dynamics of *M. arenaria* gives us insight into the potential effects of land-use change, climate change and sea-level rise in the Plum Island estuary and watershed. The effects will likely impact both the distribution and spatial extent of Mya habitat and the nature and quality of diet, thereby influencing clam growth potential. Two of the primary controls on the distribution of clams in the Plum Island estuary are salinity and the availability of intertidal habitat (Koo et al., 2017). Climate change and land-use change will affect salinity patterns in multiple ways. Warming will affect the hydrologic budget, increasing evapotranspiration and decreasing watershed runoff (Claessens et al., 2006; Seybold et al., 2019). Countering this will be an increase in precipitation, especially an increase in the frequency of extreme precipitation events and winter rain in northeastern U.S.A. (Horton et al., 2014; Wuebbles et al., 2017). Land-use change will also add to variations in freshwater inputs, as the increase in impervious area associated with urbanization will increase the rate and volume of runoff (Castillo et al., 2014; Chang, 2004; Seybold et al., 2019). Increased reliance on sewers and treatment outside the watershed (Boston metropolitan region) will decrease freshwater export to the estuary (Runfola et al., 2013a, 2013b). These effects are inter-related so it will be challenging to predict whether clam habitat will expand in conjunction with an increase in the spatial extent of brackish water (less oligohaline habitat) or contract in conjunction with increased frequency and magnitude of killing freshets associated with storm runoff during winter.

The availability of clam suitable habitat is also related to the extent of intertidal areas, which currently is thought to be lessening due to increased erosion and deepening brought about by increased storminess, sea-level rise, and sediment starvation (Hopkinson et al., 2018; Mariotti and Fagherazzi, 2010).

Land-use change, sediment starvation, and sea-level rise will also affect food availability and quality in the estuary, which will then affect the growth of *Mya arenaria* in the Plum Island Sound estuary. Marshes are decreasing in areal extent throughout the estuary because of sea-level rise and sediment starvation (Hopkinson et al., 2018). These factors will also lead to a decrease in marsh elevation within the tidal range, which will result in increased flooding frequency and duration and the conversion from *S. patens* to *S. alterniflora* marshes (FitzGerald et al., 2021). To evaluate the effect on Mya clams, we need to balance the positive effects with the negative effects. Increased frequency and depth of tidal flooding will likely increase the export of organic carbon to adjacent creeks (Colombano et al., 2021; FitzGerald et al., 2021). Decreased marsh area due to edge erosion however will likely decrease the total production of marsh organic matter potentially available for export to tidal waters however (Colombano et al., 2021; Elsey-Quirk et al., 2019; FitzGerald et al., 2021). Urbanization leads to increased nutrient enrichment in the estuary (Seybold et al., 2019; Williams et al., 2004; Wollheim et al., 2005). This, combined with the expansion of aquatic areas relative to marshlands, may enhance the production of nutritionally high-quality phytoplankton (Bricker et al., 2008), which could support greater clam growth. However, it can also cause eutrophication and harmful algal blooms, leading to low oxygen levels in the estuary, which in turn decreases clam growth. So, the predictions are challenging and complicated.

Climate and land-use changes will affect the growth and diet of *M. arenaria* in PIE, but the effects of those changes depend on the complex interactions among multiple factors, such as a variety of environmental drivers (e.g., ocean currents, watershed hydrology) and environmental gradients (e.g., salinity, temperature, dissolved oxygen), and trophic dynamics (Lauchlan and Nagelkerken, 2020). Such complexity will increase uncertainty in predicting their effects on the clam diet and growth. Therefore, we need future studies to understand the effects of the changes on the dynamics of clam diet and growth in the complex interactions with a variety of environmental drivers, environmental gradients and the trophic dynamics for the sustainable management and conservation practice for *M. arenaria* in the Plum Island estuary. Recent studies support the urgent need to understand both short- and long-term effects of climate and land-use change on tidal ecosystem, food webs, and fisheries support (Colombano et al., 2021).

CRediT authorship contribution statement

Kyung Ah Koo: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **James A. Nelson:** Methodology, Formal analysis. **Emily S. Davenport:** Writing – original draft, Validation, Methodology, Formal analysis, Data curation. **Charles S. Hopkinson:** Writing – review & editing, Writing – original draft, Resources, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We would like to thank Jack Grundstrom, the Town of Rowley shellfish commissioner, and his commercial clammer son, John Grundstrom, for their help throughout the planning and field trip portions of this project. We also thank the Plum Island Sound LTER (PIE-LTER) for help with field logistics. The program was funded by the NSF CNH and LTER programs (BCS-0709685 and OCE 1238212) and supported by Korea Institute of Marine Science & Technology Promotion (Project number: 2022-068(R)) and Korea Environment Institute (Project number: GP2023-15).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2024.109059.

Data availability

Data will be made available on request.

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