Journal of the Marine
Biological Association of the
United Kingdom

cambridge.org/mbi

Oyster allometry: growth relationships vary across space

Alexandria R. Marquardt, Melissa Southworth and Roger Mann

Virginia Institute of Marine Science, William & Mary, Gloucester Point, VA, USA

Abstract

Oysters have unique life history strategies among molluscs and a long history in the fossil record. The Ostreid form, particularly species from the genus *Crassostrea*, facilitated the invasion into intertidal, estuarine habitats and reef formation. While there is general acknowledgement that oysters have highly variable growth, few studies have quantified variability in oyster allometry. This project aimed to (1) describe the proportional carbonate contributions from each valve and (2) examine length–weight relationships for shell and tissue across an estuarine gradient. We collected 1122 *C. virginica* from 48 reefs in eight tributaries and the main stem of the Virginia portion of the Chesapeake Bay. On average, the left valve was responsible for 56% of the total weight of the shell, which was relatively consistent across a size range (24.9–172 mm). Nonlinear mixed-effects models for oyster length–weight relationships suggest oysters exhibit allometric growth ($b < 3$) and substantial inter-reef variation, where upriver reefs in some tributaries appear to produce less shell and tissue biomass on average for a given size. We posit this variability may be due to differences in local conditions, particularly salinity, turbidity, and reef density. Allometric growth maximizes shell production and surface area for oyster settlement, both of which contribute to maintaining the underlying reef structure. Rapid growth and intraspecific plasticity in shell morphology enabled oysters to invade and establish reefs as estuaries moved in concert with changes in sea level over evolutionary time.

Research Article

Cite this article: Marquardt AR, Southworth M, Mann R (2024). Oyster allometry: growth relationships vary across space. *Journal of the Marine Biological Association of the United Kingdom* **104**, e119, 1–14. https://doi.org/10.1017/S0025315424001140

Received: 27 March 2024
Revised: 22 October 2024
Accepted: 18 November 2024

Keywords:
allometry; *Crassostrea virginica*; length–weight relationships; life history strategies

Corresponding author:
Alexandria R. Marquardt;
Email: armarquardt@vims.edu

Introduction

Among Bivalvia, oysters have unique growth patterns and life history strategies. Bivalves are characterized by laterally compressed soft bodies enclosed in paired valves, which are attached to one another by a dorsal hinge. Typically, the bivalve morphology includes two adductor muscles, one anterior and one posterior to the hinge, and an extendable foot that facilitates burial. Valve morphology is generally conservative across the class and the vast majority of bivalve species are infaunal. Few groups in Bivalvia stray from this general plan; however, oysters have lost both the anterior adductor muscle and the foot. Modern oysters in the Family Ostreidae, particularly the cupped oysters of the genus *Crassostrea*, show remarkable variation in individual shape and allometry, and are gregarious, forming complex, three-dimensional reefs. Reef formation is facilitated by the oyster life history, where pelagic larvae preferentially settle, metamorphose, and cement themselves onto the shells of extant adults (Bonar *et al.*, 1990; Turner *et al.*, 1994; Tamburri *et al.*, 1996, 2008). Reefs are maintained by rapid growth and variable shell morphology, which maximizes shell production relative to biomass and provides abundant substrate for larval settlement (Powell and Stanton Jr, 1985; Mann *et al.*, 2009*a*, 2022; Powell *et al.*, 2016). Though unusual, the oysters' life history strategy led to their success over geological time scales.

Oysters provide critical hard benthic structure in temperate estuaries worldwide. The oyster form emerged in the Triassic (252–251 mya) as the fossil *Liostrea sp*, which were epifauna on ammonites in marine habitats (Hautmann *et al.*, 2017). The subsequent *Gryphaea sp.* shifted to shallow subtidal habitats and exhibited thick, deeply cupped asymmetrical valves (McRoberts, 1992; El-Sabbagh and El Hedeny, 2016; Hautmann *et al.*, 2017). The modern Ostreidae oysters occupy shallow coastal and estuarine habitats (Gunter, 1954; Li *et al.*, 2021). The Ostreid form, particularly those in the genus *Crassostrea*, facilitated the invasion into intertidal, estuarine habitats. The success of this form is predicated on individual plasticity in growth and shell shape across the post settlement life stages, such as rapid juvenile growth along irregular substrates, development of asymmetrical valves, and longevity to a large terminal size which ensures accumulation and maintenance of the underlying reef structure.

Understanding allometric relationships is a fundamental part of fisheries science. Length–weight relationships are used to relate easily measured dimensions, such as length, to biomass for a variety of taxa (Hilborn and Walters, 1992; Froese, 2006; Sousa *et al.*, 2020). Traditionally, length–weight relationships are described using the model formulation $W_i = aL_i^b$, where W_i is the weight and L_i is the length for the i^{th} individual. The parameter b is a coefficient that controls the strength of the exponential relationship, which facilitates inference on growth patterns (e.g. isometric *vs* allometric growth). For bivalves and a variety of other molluscs, the parameter b is approximately 3, indicating isometric growth (Powell and Stanton Jr, 1985; Tokeshi *et al.*, 2000; Gaspar *et al.*, 2001; Hemachandra, 2008). In contrast, many oyster species, due to indeterminate growth and highly variable conditions across estuaries (e.g. salinity, temperature, reef density), *b* may be below 3, indicating allometric growth (Powell *et al*., 2016). While there is a general acknowledgement that oysters have highly variable growth, few studies have quantified variability in oyster allometry (Galtsoff, 1964; Kennedy *et al*., 1996; Mann *et al*., 2009*b*; Nagi *et al*., 2011; Powell *et al*., 2016).

Herein, we explore variation in allometry for eastern oysters (*C. virginica* Gmelin, 1791) collected from reefs in the western tributaries and main stem in the Virginia portion of the Chesapeake Bay. The specific project objectives are to: (1) describe the proportional carbonate contributions from each valve; and (2) examine oyster allometry, for both shell and tissue weight, in the Chesapeake Bay using a nonlinear mixed-effects model framework.

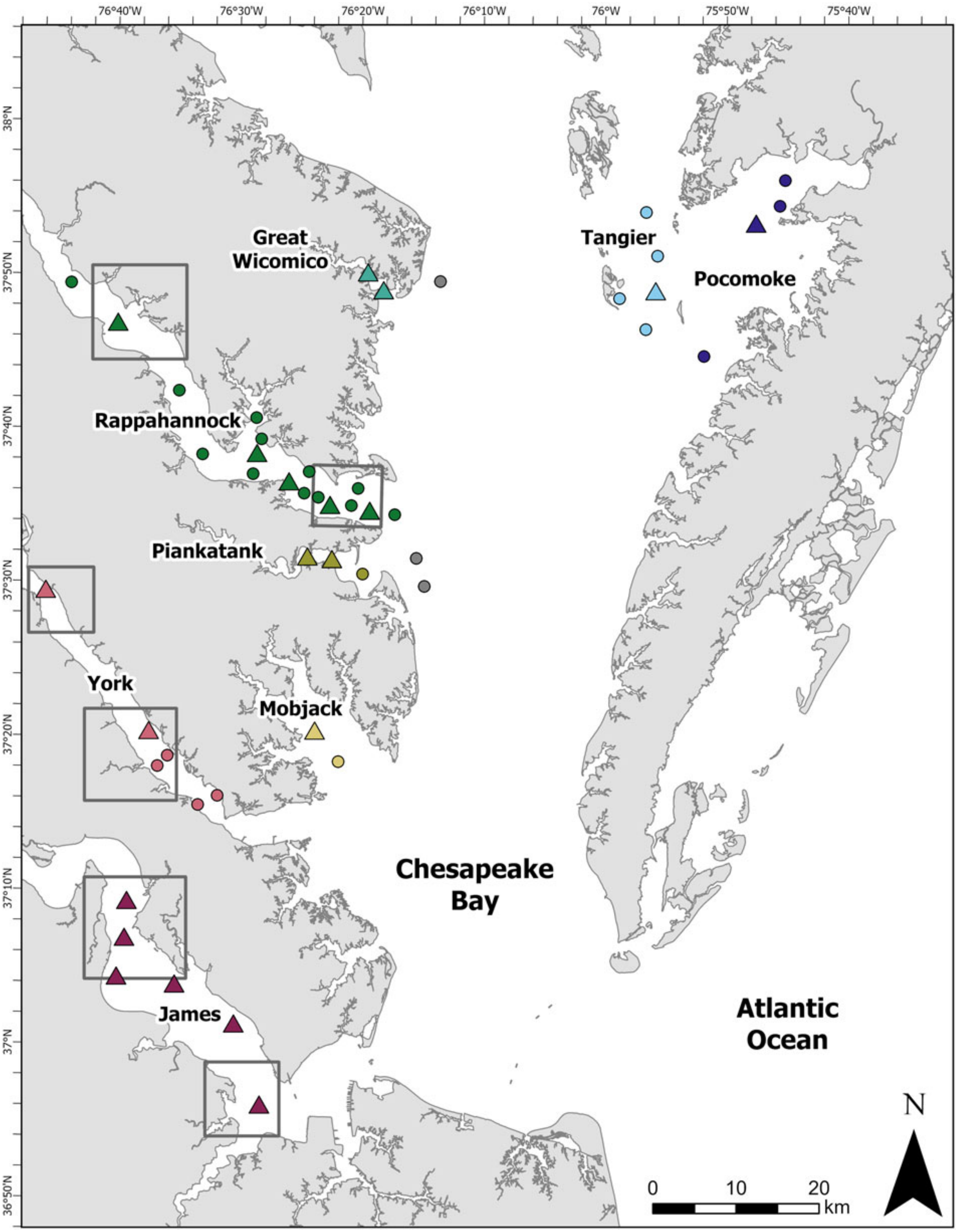

Figure 1. Map of the Virginia Portion of the Chesapeake Bay showing the locations of 48 reefs where samples were collected. Sites with ≥20 individuals collected (triangles) were used in the length–weight model. Grey boxes indicate spatial domain for Virginia Estuarine Coastal Observing System (VECOS; http://vecos.vims.edu/) data flow programme, which was used to compare environmental conditions.

Table 1. Summary of oyster collections in the Virginia portion of the Chesapeake Bay

Tributary	Reef	Latitude	Longitude	*n*	Mean length (SD)	Length range	Mean dry shell (SD)	Dry shell range	Mean dry tissue (SD)	Dry tissue range
Pocomoke	PG 10	37.936453	−75.749611	1	140		243.21		5.42	
	PG 11	37.923577	−75.746143	3	147.1 (16.3)	128.4–158	215.99 (74.18)	151.61–297.11	4.14 (0.7)	3.70–4.95
	PG 13	37.900994	−75.789253	52	73.6 (24.4)	32.2–172	66.41 (61.14)	5.44–374.31	1.32 (0.95)	0.07–4.82
	Onancock	37.748559	−75.860277	2	127.4	124.7–130	166.79	156.71–176.86	3.58	3.23–3.93
Tangier	Fox Island	37.904649	−75.939199	2	147.5	130–165	294	185.07–402.92	3.3	2.93–3.68
	Thoroughfare	37.865019	−75.924865	7	138.2 (7.1)	127–148.8	173.81	107.11–234.26	2.96 (0.68)	2.11–3.89
	California	37.821698	−75.926698	58	79.5 (28.4)	28.1–145.5	68.07 (53.36)	2.47–272.93	1.67 (1.17)	0.1–5.06
	Cod Harbour	37.810046	−75.981845	6	130.2 (10.0)	120.7–144.7	164.31	87.09–193.52	3.49 (0.65)	2.82–4.58
	Johnson’s	37.783133	−75.94854	2	133.3	125.4–141.2	176.35	161.12–191.58	2.83	2.76–2.90
Chesapeake Bay	Blackberry Hang	37.857216	−76.23835	2	127.4	118.6–136.1	212.55	170.08–255.01	3.9	3.34–4.45
	Beverly’s	37.5322	−76.253	2	140.4	127.7–153	190.7	165.08–216.32	3.44	2.83–4.05
	Deep Rock	37.5078	−76.2428	9	137.0 (9.7)	121–155	254.48 (45.87)	158.22–309.67	2.62 (0.79)	0.97–3.56
Great Wicomico	Shell Bar	37.822896	−76.314369	50	71.5 (19.0)	26.4–103.4	47.25 (24.84)	4.43–96.5	0.66 (0.33)	0.11–1.47
	Cranes Creek	37.809679	−76.300474	50	69.3 (16.2)	33–101.1	54.33 (32.76)	6.28–135.48	0.79 (0.4)	0.19–1.97
Rappahannock	Long Rock	37.8135	−76.7084	2	144.1	139.6–148.5	308.33	289.52–327.14	3.07	2.73–3.40
	Morattico	37.7853	−76.659	50	72.3 (18.5)	40.1–112.3	73.31 (43.89)	15.54–175.27	1.14 (0.59)	0.33–2.80
	Little Wicks	37.690456	−76.572079	2	132.6	131.1–134	270.67	161.7–379.65	4.08	3.53–4.63
	Hog House	37.63911	−76.543085	2	129	123–135	203.91	30.41–225.41	2.48	2.04–2.92
	Middle Ground	37.683324	−76.471457	1	139		165.29		2.76	
	Drumming Sanc.	37.653349	−76.461933	1	136.8		215.41		2.82	
	Drumming	37.644602	−76.464977	50	68.8 (18.9)	28.6–110.8	54.3 (35.1)	2.18–143.93	0.8 (0.44)	0.06–1.80
	Temple Bay 5	37.617093	−76.481124	1	122.9		190.89		3.38	
	Parrot	37.605837	−76.421667	55	76.6 (25.8)	33.1–144	78.51 (72.44)	5.08–330.47	1.32 (0.92)	0.18–4.91
	Larson’s	37.627778	−76.389769	2	124.7	118.8–130.6	251.65	211.78–291.52	3.63	2.56–4.71
	Bush Park Stone	37.5862	−76.386583	3	125.8 (7.3)	120.4–134.1	177.73 (37.23)	136.71–209.38	2.48 (0.67)	1.78–3.12
	Sturgeon Bar W.	37.582121	−76.370099	2	131.2	118–144.3	153.08	145.92–160.24	2.95	2.52–3.39
	Sturgeon Sanc.	37.583509	−76.324589	28	131.6 (12.1)	113–163	205.34 (79.12)	89.25–405.96	2.64 (0.88)	1.42–5.60
	Butler’s	37.608173	−76.303956	11	132.2 (10.6)	117.8–152	185.37 (82.89)	106.71–402	2.83 (1.88)	1.55–8.20
	Lower Edge	37.576721	−76.301911	7	127.6 (10.9)	117.1–143.7	182.86 (32.27)	154.36–249.5	2.56 (0.45)	2.17–3.37
	Broad Creek	37.576876	−76.316258	57	76.6 (22.9)	41.5–140	76.71 (69.22)	12.66–299.01	1.06 (0.76)	0.19–3.44
	Spike	37.575024	−76.285712	13	127.8 (16.0)	106.9–160	204.82 (34.76)	147.44–266.01	3.19 (0.65)	2.30–4.06

(*Continued*)

Table 1. (*Continued.*)

Tributary	Reef	Latitude	Longitude	*n*	Mean length (SD)	Length range	Mean dry shell (SD)	Dry shell range	Mean dry tissue (SD)	Dry tissue range
Piankatank	Ginney Point	37.532729	−76.402456	49	72.4 (18.6)	34.3–117.9	60.33 (36.05)	8.5–178.96	0.92 (0.46)	0.15–2.07
	Palace Bar	37.528182	−76.367176	50	67.1 (18.0)	33.6–127.8	47.34 (28.94)	6.71–126.68	0.77 (0.47)	0.15–2.66
	Hill’s Bay	37.507955	−76.319508	1	135.6		196.38		3.14	
Mobjack	Tow Stake	37.337445	−76.389583	50	74.3 (15.4)	45.4–106.3	63.98 (32.73)	10.81–142.78	0.92 (0.39)	0.26–1.97
	Brown’s Bay	37.309992	−76.353241	9	137.5 (9.5)	126.7–158	201.02 (63.36)	110.62–284.55	2.83 (0.62)	2.07–3.91
York	Bell Rock	37.484167	−76.7497	49	68.9 (14.5)	41.5–98.6	49.26	6.41–127.69	0.85 (0.46)	0.22–2.34
	Aberdeen	37.333991	−76.598701	57	83.0 (28.8)	30.4–157	85.98	3.66–307.95	1.46 (1.04)	0.15–4.66
	Page’s Rock	37.312652	−76.584207	10	131.9 (6.7)	122–145	218.85	179.01–284.95	3.5 (0.61)	2.27–4.20
	Cheatham	37.307143	−76.602643	5	133.2 (11.6)	120.6–143.5	235.3	213.05–262.91	3.67 (0.39)	3.07–4.07
	Indian Field	37.274301	−76.559388	3	137.4 (9.7)	129.9–148.4	329.96	266.79–401	3.7 (0.25)	3.49–3.98
	Timberneck	37.2724	−76.529543	7	141.1 (11.2)	127.6–162	264.86	207.08–342.7	3.81 (0.88)	2.71–5.31
James	Upper Deep	37.149569	−76.629733	49	61.8 (19.2)	24.9–113	12.15 (7)	1.02–31.84	0.45 (0.25)	0.03–1.00
	Middle Horse	37.106735	−76.636425	50	67.2 (21.6)	32.1–123.6	14.28 (7.78)	2.87–30.41	0.46 (0.29)	0.09–1.48
	Point of Shoal	37.074163	−76.645795	50	71.6 (21.7)	34.4–124.6	13.26 (7.48)	2.38–32.4	0.39 (0.26)	0.07–1.24
	Wreck	37.061667	−76.571667	50	67.0 (17.6)	32.4–101.4	34.95 (22.61)	3.47–94.22	0.67 (0.41)	0.10–1.70
	Thomas	37.028861	−76.494706	50	69.9 (19.3)	34.1–108.4	51.61 (34.35)	6.65–117.45	0.88 (0.45)	0.18–1.99
	Nansemond	36.933168	−76.450811	50	74.0 (25.1)	33.2–141.4	58.08 (41.48)	3.95–164.98	1.18 (0.92)	0.13–4.16

Shell lengths are reported in mm, dry shell and dry tissue weights are reported in g, and *n* denotes the sample size from each reef. Standard deviations are only reported in cases where there are ≥3 individuals collected. Shaded rows indicate reefs with ≥20 individuals which were included in the length–weight model.

Materials and methods

Sample collection

To describe oyster morphometric relationships, oysters were collected during annual fall (September through December) stock assessment surveys (dredge and patent tong) in the western tributaries and the main stem of the Chesapeake Bay as well as Tangier and Pocomoke Sounds. Dredge survey methods are described in detail in Southworth and Mann (2020) and Mann *et al.* (2009*b*). Patent tong survey methods are described in Southworth *et al.* (2010) and Harding *et al.* (2010). The stock assessment programme collects oysters across a size range from 19 reef locations annually to monitor body condition and shell morphometrics. Collections from 2021 and 2022 were included in the analyses. Additionally, large oysters, >100 mm in shell length (umbo to ventral margin), were opportunistically collected across all survey locations in 2019, 2020, and 2021. We collected a total of 1122 oysters from 48 reefs in eight tributaries and the main stem of the Virginia portion of the Chesapeake Bay (Figure 1; Table 1). Oyster collections reflect the size availability in extant populations, except for Lower Sturgeon Sanctuary, where collections focused on larger individuals.

All oysters were brought back to the lab for processing. We removed biofouling from the exterior of the shell and measured shell length (umbo to ventral margin) to the nearest 0.1 mm. Soft tissue was removed from the valves and both tissue and shells were dried to a constant weight at 80°C (72 h) to obtain dry shell and dry tissue weights. All measurements were to the nearest 0.01 g.

Proportional shell weight

To estimate the proportional weight of the left valve, we dried and weighed the left and right valves of specimens with fully intact valves. The proportional weight was defined as the dry weight of the left valve divided by the combined dry weight of both valves. We calculated the mean proportional weight of the left valve across specimens. We investigated the relationship between the proportional weight of the left valve and oyster length using a simple linear regression.

Length–weight relationships

Traditionally, length–weight relationships are described using the following nonlinear model formulation:

$$\begin{aligned} W_i &= aL_i^b + \varepsilon_i \\ \varepsilon_i &\sim N(0,\, \sigma_\varepsilon^2) \end{aligned} \qquad (1)$$

where W_i = weight of the i^{th} individual, L_i = length of the i^{th} individual, a and b are constants, and ϵ_i is the error associated with the i^{th} individual. The parameter b is a coefficient controlling the strength of the exponential relationship. Often this formulation, specifically the normally distributed error structure, is inappropriate, due to increasing variability in weight as individuals increase in size (heteroscedasticity). The nonlinear model formulation can be modified to incorporate a multiplicative error structure (2) and transformed to a log-log linear model (3) to make the errors additive and stabilize variance.

$$W_i = aL_i^b e^{\varepsilon_i} \qquad (2)$$

$$\begin{aligned} ln(W_i) &= ln(a) + bln(L_i) + \varepsilon_i \\ \varepsilon_i &\sim N(0,\, \sigma_\varepsilon^2) \end{aligned} \qquad (3)$$

Given that oyster reefs are aggregations of individuals living under similar conditions, there is inherent clustering within the data which violates independence (Pinheiro and Bates, 2000; Zuur *et al.*, 2009). Thus, we extended the previous model formulation to a nonlinear mixed-effects model (NLMM) and incorporated reef as a random-slope effect to account for spatial variability (4).

$$\begin{aligned} ln(W_{ij}) &\sim N(ln(a) + b_i ln(L_{ij}),\, \sigma_\varepsilon^2) \\ b_i &\sim N(\mu,\, \sigma_b^2) \end{aligned} \qquad (4)$$

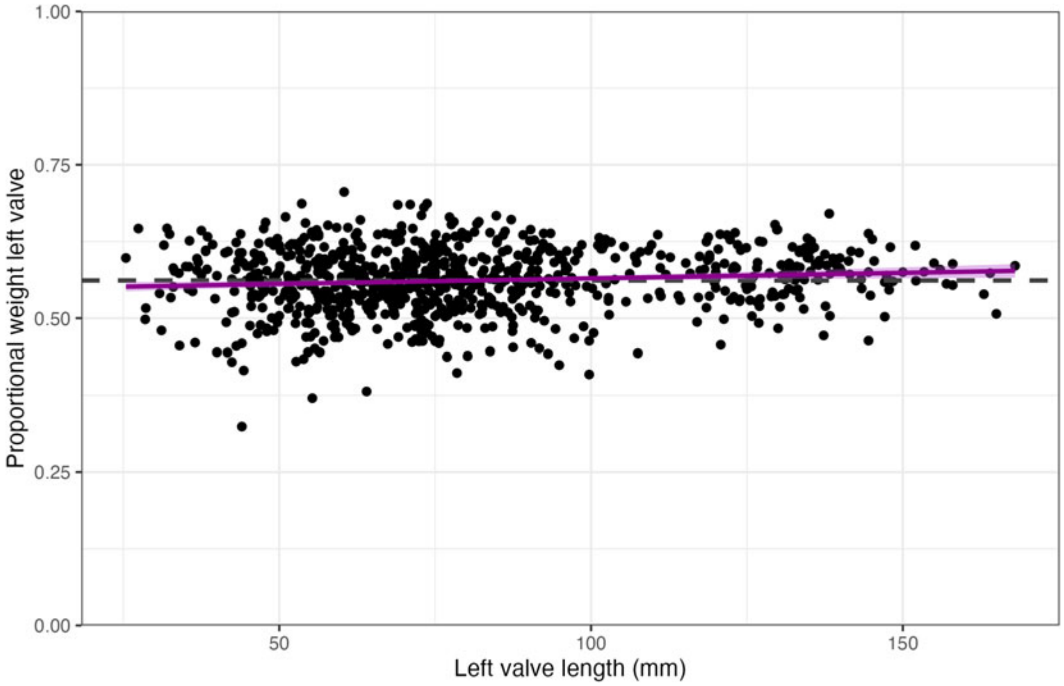

Figure 2. Proportional weight of the left valve for oysters in the Virginia portion of the Chesapeake Bay. The mean proportional weight of the left shell is 0.5614 (±0.002 SE, dashed grey line). The linear relationship is described as LPro = 0.55 + 0.00015×L, where Lpro is the proportional weight of the left valve and L is the valve length in mm (pink line). Pink shading indicates the 95% confidence interval.

In this final model formulation, W_{ij} = weight of the j^{th} individual from the i^{th} reef and L_{ij} = length of the j^{th} individual from the i^{th} reef. We used this model formulation to explore the relationship between oyster biomass, as both dry tissue weight (g) and dry shell weight (g), and length. All statistical analyses were completed in R Version 4.3.1 (R Core Team, 2023) using the nlme package (Pinheiro *et al.*, 2023). Figures were created using the ggplot package (Wickham, 2016).

Local conditions

Long-term water quality monitoring was not available for each reef location. We accessed water quality data from the Virginia Estuarine Coastal Observing System (VECOS, http://vecos.vims.edu/) data flow programme for upriver and downriver regions of tributaries which had concurrent monitoring across rivers. We identified three tributaries (James, York, and Rappahannock) which had biweekly or monthly data flow cruises in 2007 and 2008 (Figure 1). While the VECOS data does not coincide with our oyster collections, it characterizes the general seasonal patterns and the upriver to downriver gradient in environmental conditions. The data flow system pumps water through a YSI 6600 multiparameter sonde and measures salinity, turbidity, water temperature, pH, and dissolved oxygen every 3–4 s. In wider tributaries, such as the James, York, and Rappahannock, the vessel follows fixed depth contours (shallow <2 m; mid-depth ∼5 m; channel >10 m) running parallel to the shoreline to characterize water conditions throughout a tributary segment.

Oyster population density data was available from annual fisheries independent patent tong surveys run by the Virginia Institute of Marine Science and Virginia Marine Resources Commission. During fall surveys, a patent tong is used to sample 1 m^{-2} of bottom reef habitat on oyster reefs in the main stem and western tributaries of the Chesapeake Bay, as well as Tangier and Pocomoke sounds (Mann and Wesson, 1994, 1997; Mann *et al.*, 2009*b*; Harding *et al.*, 2010; Southworth *et al.*, 2010). Oysters were measured from umbo to ventral margin (length) to the nearest millimetre and qualitatively assessed as either young of the year or adult oysters (Southworth *et al.*, 2010). We accessed oyster population data from 2019 to 2021 during the time period when oysters were collected and quantified mean adult oyster density for each reef.

Results

Collection summary

A total of 1122 individual oysters were collected from 48 reefs in eight tributaries and the main stem of the Chesapeake Bay (Figure 1, Table 1). An average of 23.4 individuals (±23.3 SD, range 1–58) were collected from each reef. Shell lengths, measured from umbo to ventral margin, ranged from 24.9 to 172 mm. Dry shell weights and dry tissue weights ranged from 1.02 to 405.95 and 0.03 to 8.20 g, respectively.

Proportional shell weight

A subset of individuals with intact valves (n = 807) were used to estimate the proportional weight of the left valve. These individuals comprised the entire range of shell lengths from the collections (24.9–172 mm). On average, the proportional weight of the left valve was 0.5614 or approximately 56% (±0.2% SE) of the total weight of the shell. The best-fit equation describing the

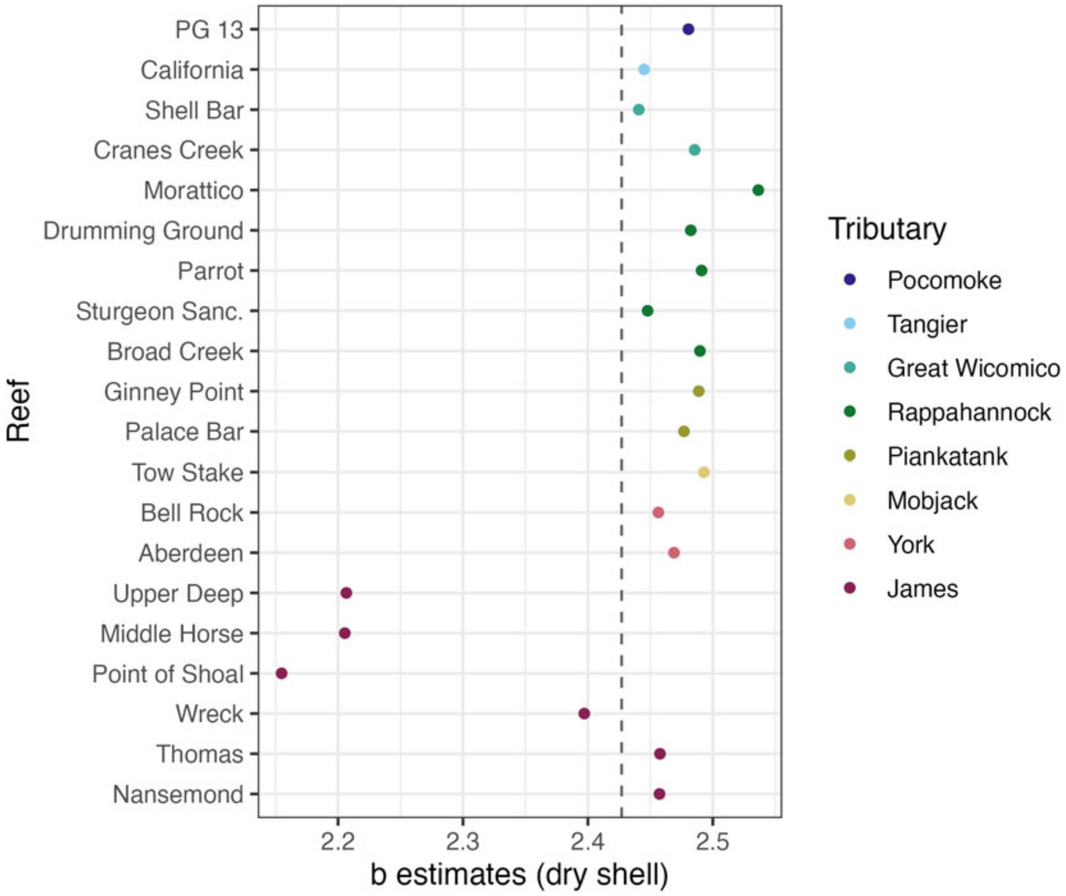

Figure 3. Estimated random-effect coefficients from the dry shell length–weight relationship for reefs (n = 20) in the eight tributaries of the Chesapeake Bay. Dashed line indicates the mean response. For tributaries with multiple reefs, the reefs are organized from upriver (top) to downriver (bottom).

relationship between proportional weight of the left valve (Lpro) and valve length (L) was Lpro = 0.55 + 0.00015×L (Figure 2). Despite a significant relationship, the model only explained 0.6% of the variation in proportional weight of the left valve ($F = 6.24$, df = 1, 805, $P < 0.05$, adjusted $R^2 = 0.006$) and provides evidence for a minute increase in the proportion of the total weight contributed by the left valve as individuals grow.

Length–weight relationships

To examine length–weight relationships for oysters, we focused our analysis on reefs where ≥20 individuals were collected (Table 1). We included 20 reefs across eight tributaries and 1004 individual oysters in an NLMM. In the NLMM with dry shell weight as the response, on average b was estimated as 2.43 (95% CI = 2.35, 2.51). The random effect provides insight on the change in weight associated with an oyster growing on a particular reef. The random effect b coefficients were variable among reef locations (Figure 3). Notably, three reefs in the James (Upper Deep, Middle Horse, Point of Shoal) had lower reef specific b coefficients than other sites and, therefore, oysters collected from these reefs had less shell biomass on average for a given length (Figure 4). Reef as a random effect explained 11.42% of the total random variance in dry shell weight.

In the NLMM with dry tissue weight as the response, on average b was estimated as 2.03 (95% CI = 1.97, 2.10). Similar to dry shell weight, the random effect b coefficients were variable among reef levels (Figure 5). The same three reefs in the James (Upper Deep, Middle Horse, Point of Shoal) had lower reef specific b coefficients than other sites which indicates oysters collected from these reefs had lower tissue biomass on average for a given length (Figure 6). Reef as a random effect explained 5.3% of the total random variance in dry tissue weight.

Local conditions

We accessed VECOS data flow monitoring data for upriver and downriver segments of the James, York, and Rappahannock tributaries. The VECOS programme measured water quality at 227,845 points across the six tributary segments. We excluded 1432 observations (<1%) due to being outliers. On average, the upper James had lower salinity in both 2007 and 2008 compared to the other tributary segments (Figure 7). In spring months (March, April, May), the upper James had substantially higher turbidity in both 2007 and 2008 compared to the other tributary segments (Figure 7). All segments had comparable variability in temperature, dissolved oxygen saturation, and pH during the 2007 and 2008 survey period (Supplementary Figure S1).

The annual patent tong surveys included 19 of the 20 reefs included in the length–weight model. Only Bell Rock in the York tributary did not have oyster population data available. Across

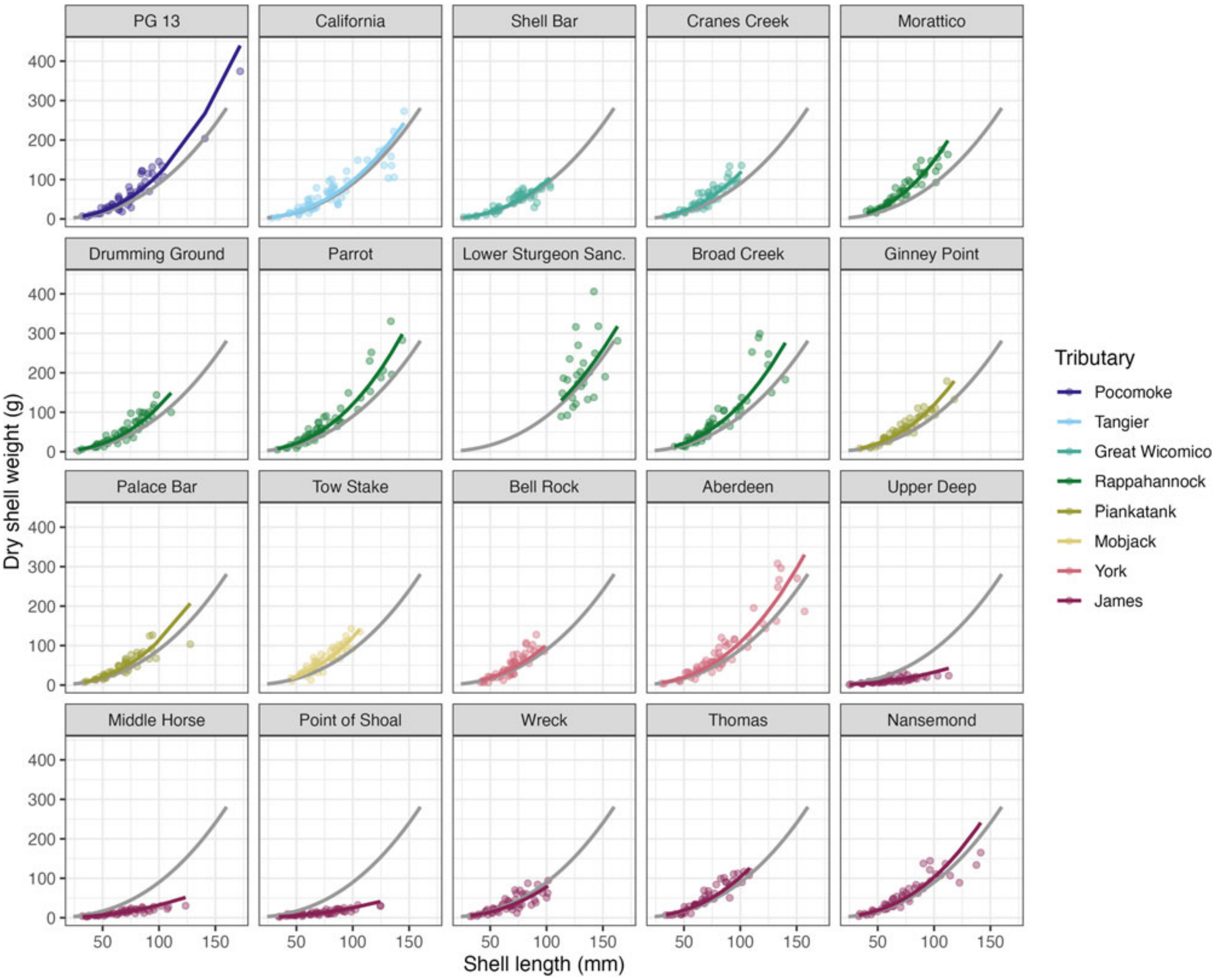

Figure 4. Predicted dry shell length–weight relationships for reefs ($n = 20$) in the eight tributaries of the Chesapeake Bay. Grey lines indicate the mean response across all reefs. Coloured lines indicate the predicted length–weight relationship for each reef. Points show data observations. Colours correspond to the tributary of origin.

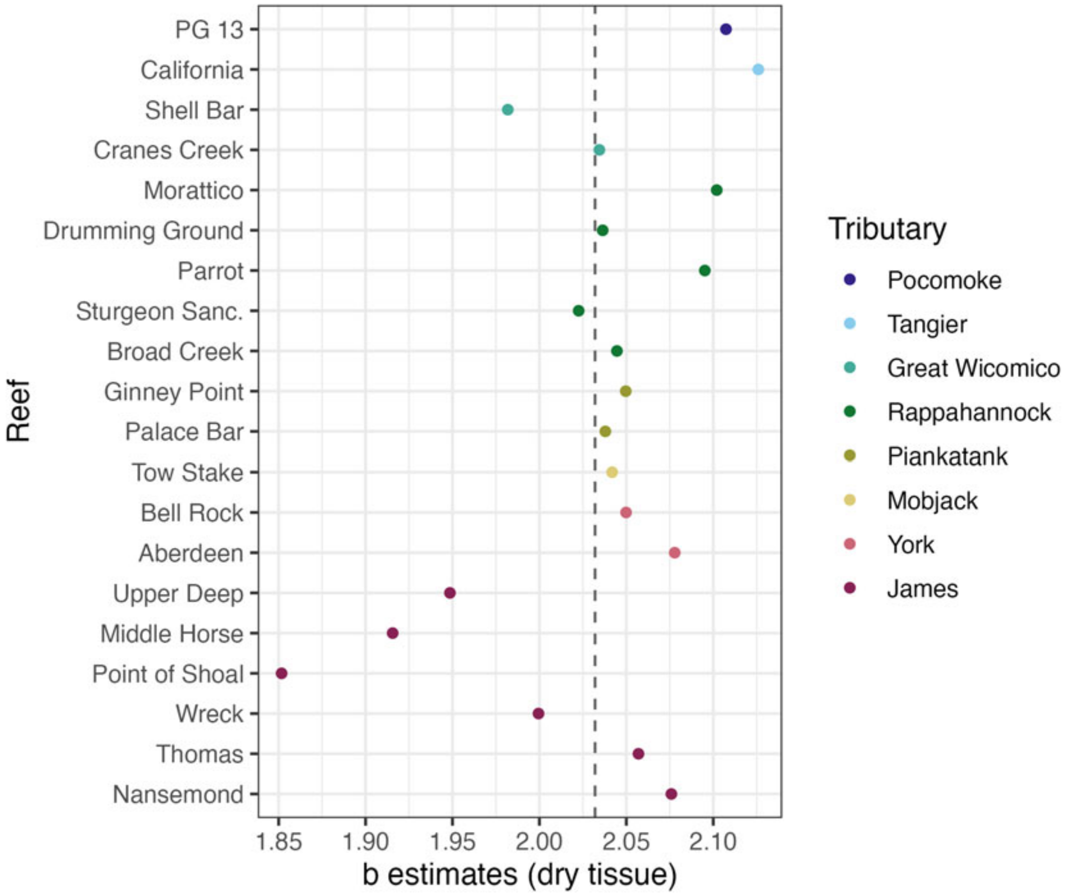

Figure 5. Estimated random-effect coefficients from the dry tissue length–weight relationship for reefs ($n = 20$) in the eight tributaries of the Chesapeake Bay. Dashed line indicates the mean response. For tributaries with multiple reefs, the reefs are organized from upriver (top) to downriver (bottom).

the 19 reefs, adult oyster density ranged from 7.0 to 492.9 oysters m^{-2} on average (Figure 8A). Reefs in the upper James (Upper Deep, Middle Horse, and Point of Shoal) had markedly higher mean oyster densities compared to lower James reefs and reefs in other tributaries. Higher mean oyster densities were associated with lower reef specific *b* coefficients (Figure 8B).

Discussion

This work explores variation in eastern oyster (*C. virginica)* allometry across reefs in the main stem and tributaries of the Virginia portion of the Chesapeake Bay. We documented the proportional relationship between oyster valves across a size range. On average, the left valve was responsible for ~56% of the weight of the shell. Further, oyster length–weight relationships showed substantial inter-reef variation, where upriver reefs in some tributaries appear to produce less shell and tissue biomass on average for a given size. We posit this variability may be due to differences in local conditions. In particular, the upriver James reefs are characterized by high turbidity in spring months and lower salinity throughout the year compared to other sites in 2007 and 2008; though temperature, dissolved oxygen, and pH were similar across all sites. Oyster density is considerably higher at the upriver James reefs relative to other sites. Though concurrent environmental monitoring is not available across all tributaries and reef locations, these observations suggest local conditions may play an important role in determining oyster growth patterns.

Local conditions

Estuaries are highly dynamic environments, where environmental conditions may vary dramatically across temporal scales (e.g. tidal, seasonal, annual). Eastern oysters tolerate a wide range of conditions and occupy estuaries along eastern North America from the Gulf of Mexico to the Gulf of St. Lawrence; however, due to oysters' sessile life history, they are unable to escape physiologically stressful conditions when they occur. Oysters can endure stressful periods by closing their valves and relying on anaerobic metabolism, whereupon they are unable to filter feed or flush accumulated toxic metabolites (Michaelidis *et al.*, 2005; Meng *et al.*, 2018). Therefore, local conditions are intimately linked with oyster growth and carbonate production.

Salinity influences oyster distribution, reproduction, and survival (Loosanoff, 1953; Shumway, 1996; Bayne, 2017; Scharping *et al.*, 2019). Eastern oysters occupy habitats where average salinities exceed 5 (Galtsoff, 1964; Castagna and Chanley, 1973). In low salinity environments, juvenile and adult oysters experience slower growth, but reduced predation and disease pressure (Kraeuter *et al.*, 2007; Munroe *et al.*, 2017; Manuel *et al.*, 2023). In contrast, oysters in high salinity experience faster growth, but increased predation and disease pressure. Oysters living on the upper James reefs experience lower salinity throughout the year, which are either below or on the lower end of the physiological optimum (~12–24 ppt) for oysters (Shumway, 1996). Our oyster collections occurred during the post-spawning rebuilding phase in fall months. During this time, oysters in the upper James are physiologically compromised due to a combination of higher temperatures and lower salinity, which may be causing the observed lower tissue weights for a given size.

Turbidity influences individual oyster survival and growth patterns, as well as reef persistence. Oysters prefer filtering in relatively clear water and, in the presence of suspended sediments, will close their valves (Loosanoff, 1962; Poirier *et al.*, 2021). Valve closure reduces opportunities for oysters to respire and filter feed; however,

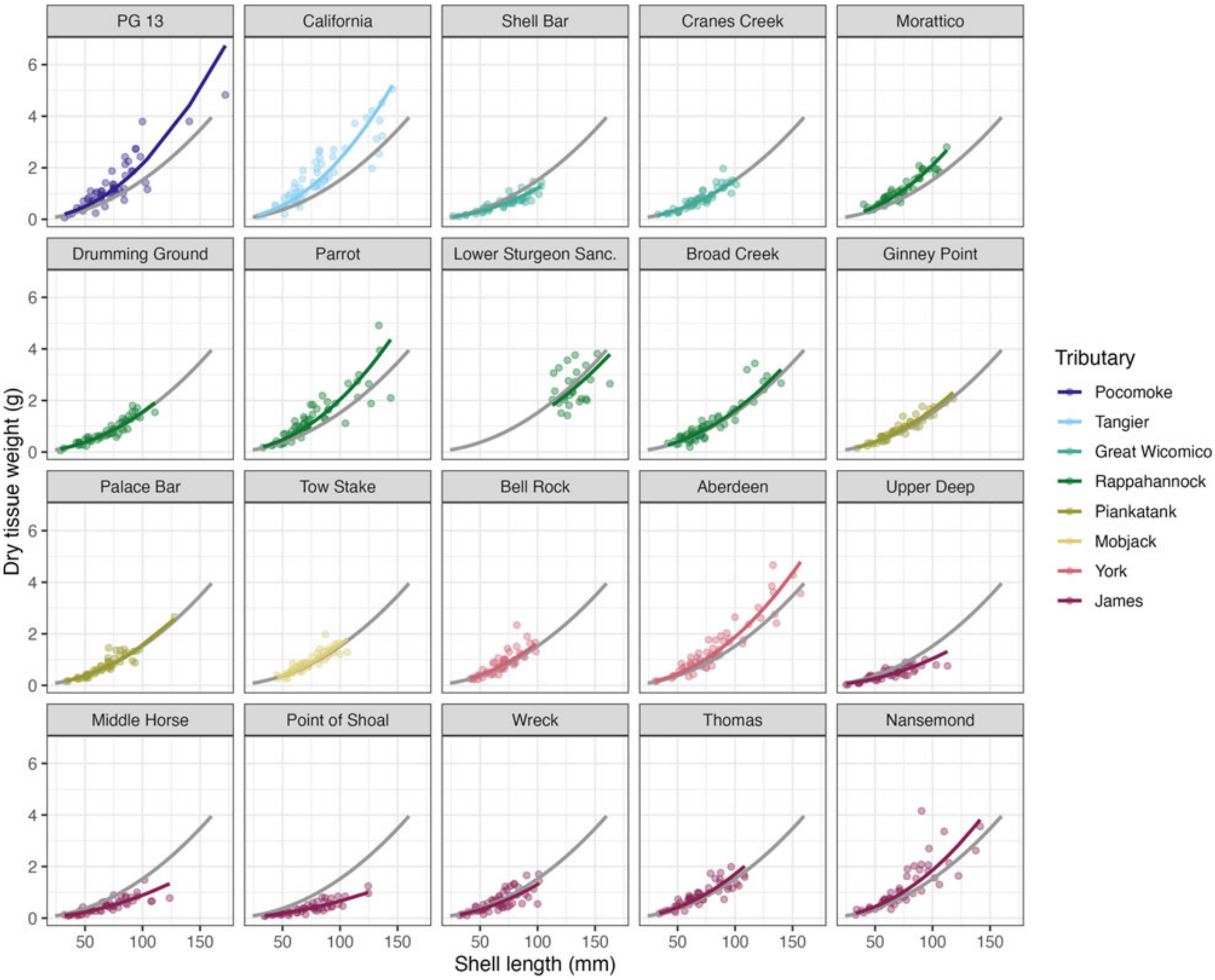

Figure 6. Predicted dry tissue length–weight relationships for reefs ($n = 20$) in the eight tributaries of the Chesapeake Bay. Grey lines indicate the mean response across all reefs. Coloured lines indicate the predicted length–weight relationship for each reef. Points show data observations. Colours correspond to the tributary of origin.

sedimentation or persistent high suspended sediment loads for extended periods of time may directly cause oyster mortality (Rothschild *et al.*, 1994; Comeau, 2014; Poirier *et al.*, 2021). When oyster reefs are crowded and in muddy bottom habitats, oysters tend towards an elongate, narrow shell shape (Galtsoff, 1964; Quayle, 1988). The upper James reefs are high density, patchy reefs with higher reef relief (generally >15 L shell m^{-2} above the sediment-water interface). Higher reef relief helps mitigate the impacts of sedimentation and contributes to overall reef persistence (Colden *et al.*, 2017). Oysters living in the upper James experience both crowding and higher turbidity, which was associated with an elongated growth form relative to other sites. The elongate growth pattern contributes to the observed lower average shell biomass for a given size. Anecdotally, juvenile oyster moved from the upper James to other tributaries as part of 'seed' movements lose the elongate form and adopt the morphological characteristics of the recipient location, which suggests that pressures in the local environment are driving the observed growth patterns.

Oysters have highly variable growth patterns; however, few studies have quantified variability in oyster allometric relationships across an estuarine gradient. Prior work focuses on the relationship between length and tissue biomass. For eastern oysters (*C. virginica*), the average *b* coefficient for length–dry tissue weight relationships is generally close to 2 (Dame, 1972; Powell *et al.*, 1995, 2016; Grizzle *et al.*, 2008; Mann *et al.*, 2009*b*). We estimated the average *b* coefficient as 2.03 in the Virginia portion of the Chesapeake Bay. Previous work estimated *b* as 2.3 in the Piankatank (Harding *et al.*, 2010), 2.7 in the Great Wicomico (Southworth *et al.*, 2010), and, on average, 2.04 (range 1.6–2.8) in the Virginia portion of the Chesapeake Bay (Powell *et al.*, 2016); however, these estimates encompass a narrower size range or are tributary wide averages, which do not explicitly account for differences in oyster growth among reefs. In the James River, *b* was estimated as 2.15 at Swash reef (Mann *et al.*, 2009*b*). Swash is near the upriver sites in the James where we observed the lowest *b* coefficients; however, Swash differs by having substantially lower oyster density and, thus, oysters exhibit more ovoid shape (Mann *et al.*, 2009*b*; Southworth and Mann, 2020). Since the 2010s, oyster densities throughout western tributaries of the Chesapeake Bay have increased (VOSARA: https://cmap22.vims.edu/VOSARA/). Estimates for *b* reported in the literature include values from South Carolina of 2.17 (Grizzle *et al.*, 2008) and 2.21 (Dame, 1972), and values from Delaware Bay ranging from 1.7 to 2.4 (Powell *et al.*, 2016). Prior work estimated shell production in the Chesapeake Bay using, in part, descriptors for the relationship between length and dry shell biomass (Mann *et al.*, 2022). We estimated the average *b* coefficient as 2.43 for length–dry shell weight relationships. Oysters living in the upper James produced less shell on average for a given size (lower *b* coefficient) relative to

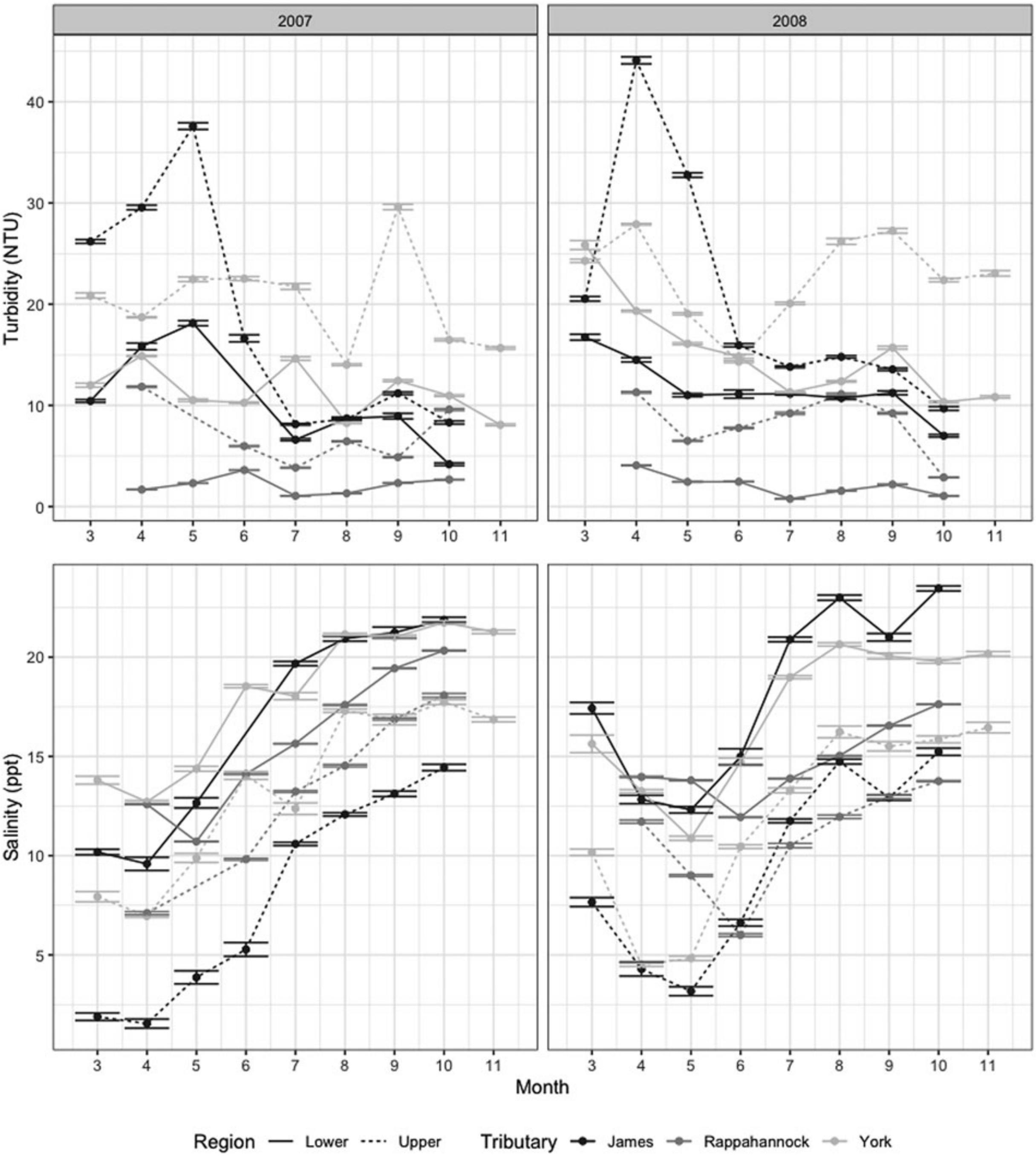

Figure 7. Turbidity (top) and salinity (bottom) measurements from upper and lower regions of the James, Rappahannock, and York tributaries. Data show the monthly means (±SE) from the Virginia Estuarine Coastal Observing System (VECOS; http://vecos.vims.edu/) data flow programme.

other reefs in the Virginia portion of the Chesapeake Bay, which is in agreement with differences in oyster growth patterns (tending towards globose *vs* elongate) among areas and observations from Mann *et al.* (2022). Despite highly variable growth patterns in oysters, the relationship between biomass and size is relatively constant across a wide spatial range and appears to be influenced by environmental conditions local to individual reefs.

Comparing condition indices for oysters across space is challenging. Many bivalves exhibit seasonal variation in body condition across the gametogenic cycle (Barber and Blake, 1981; Ojea *et al.*, 2004; Moura *et al.*, 2008; Peharda, 2012; Gosling, 2015; Marquardt *et al.*, 2022). Sample collection may occur across wide temporal windows, which can be particularly problematic if it spans multiple seasons and therefore different stages of the gametogenic cycle (Powell *et al.*, 2016). Many methods for condition indices are discussed in the literature (Mann, 1978; Crosby and Gale, 1990; Rainier and Mann, 1992), where a ratio between tissue and shell is used as a proxy for environmental signals, to assess gametogenic cycles over time or compare 'meat' quality or nutritive state among populations. We observed disparities in length–biomass relationships among sites for both shell and tissue biomass, which comprises both components in a condition index calculation. Our results suggest that shell and tissue biomass can scale at different rates with size over small spatial scales within tributaries, which may bias condition index comparisons among sites. Sites may be physically close to one another, but still experience dramatically different local conditions that can drive changes in shell morphology. Future studies using condition indices should carefully consider seasonality among collections and variation in local conditions among sites.

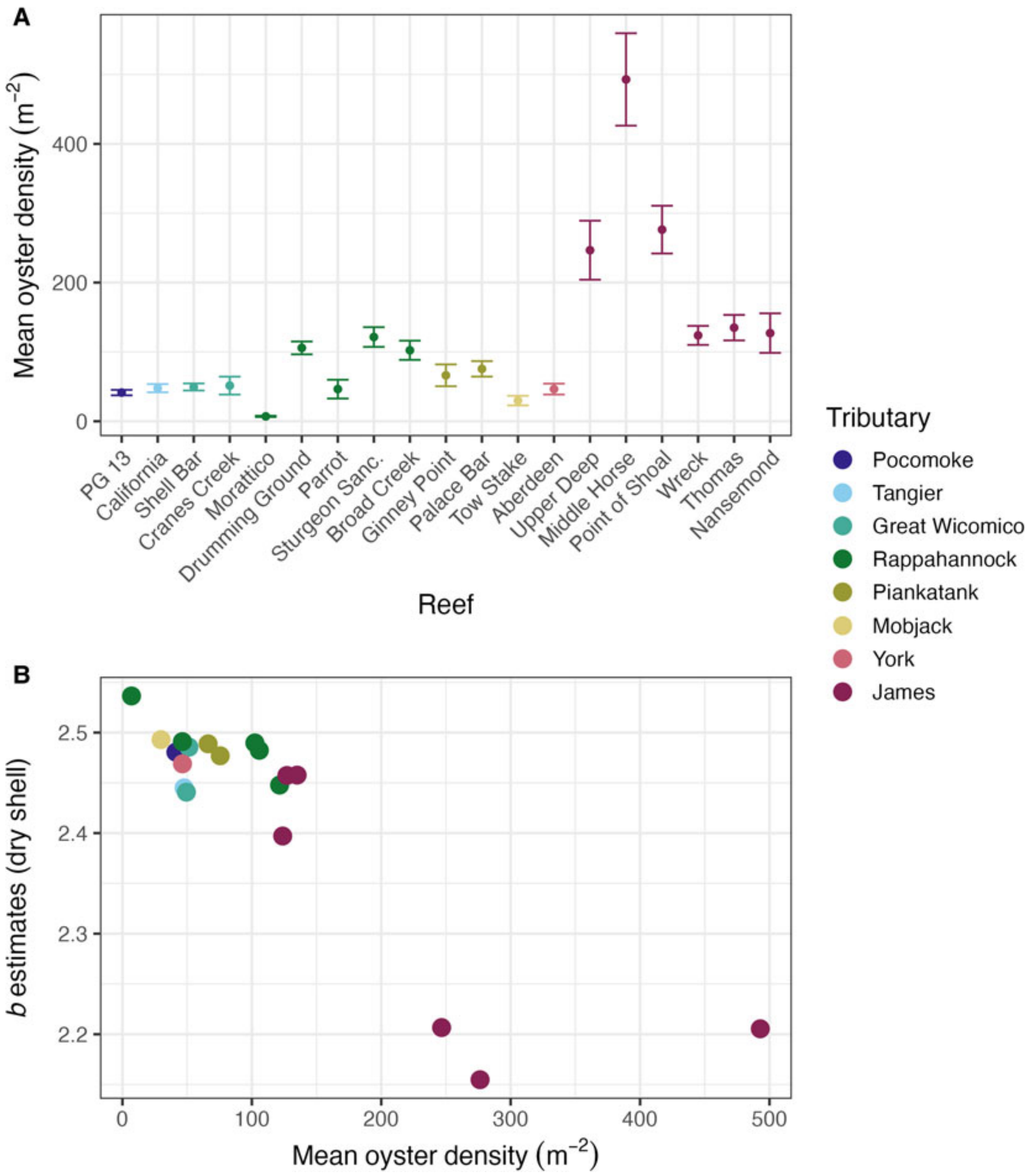

Figure 8. (A) Mean (±SE) oyster density m-2 for 19 reefs within eight Chesapeake Bay tributaries. For tributaries with multiple reefs, the reefs are organized from upriver (left) to downriver (right). (B) Relationship between mean oyster density (m-2) and estimated b coefficients for dry shell weight.

Evolutionary trends

A modest proportion of Bivalvia occupy epifaunal habitats. Notable epifaunal groups found in temperate zones include the scallops (Pectinidae), mussels (Mytilidae), and oysters (Ostreidae). Scallops have a wide variety of lifestyles, from sessile, attached (e.g. *Crassadoma gigantea*) to active free swimming (e.g. *Amusium spp.*) species (Minchin, 2003; Alejandrino *et al*., 2011). Scallops have acute visual systems and all non-attached species have the ability to swim (Speiser and Johnsen, 2008; Serb *et al*., 2011; Palmer *et al*., 2017). Swimming was facilitated by divergence from the typical bivalve morphology, including losing one adductor muscle, reducing the foot, and developing asymmetrical valve inflation. Scallop shell morphology changes over ontogeny (Márquez *et al*., 2010); however, shell morphology is consistent within a species and is influenced by species behaviour (Serb *et al*., 2011). Mussel shells exhibit valve asymmetry, where the anterior adductor muscle is reduced, and the hinge and ligament are shifted anterior to create a wedge shape. Byssal threads, in combination with the wedged shell morphology, allow mussels to form dense, three-dimensional ‘mats’ or beds. Mussels are an important foundation species in temperate and polar littoral zones (Gosling, 2021). Mussel beds provide structural habitat for settlement and refugia for newly recruited juvenile mussels (Seed, 1976; McGrath *et al*., 1988; Gosling, 2021). Atlantic blue mussels, *Mytilus edulis* and *M. trossulus*, were documented to produce more elongate, narrower shells in low salinity or other unfavourable conditions (Telesca *et al*., 2018); however, the intraspecific plasticity in shell morphology for scallop and mussel species is minimal when compared to oysters.

Oysters’ intraspecific plasticity in shell morphology contributes to their success as reef builders in temperate systems. Oyster larvae preferentially cement themselves onto adult oysters (Bonar *et al*., 1990; Turner *et al*., 1994; Tamburri *et al*., 1996, 2008). Juvenile oysters conform their shape to fit into available spaces on the reef, which provides protection during early post-settlement stages and ensures individuals are in close proximity to maximize fertilization success during mass spawning events. Our results suggest that oysters in the

Virginia portion of the Chesapeake Bay exhibit allometric growth, where tissue and shell biomass scales closer to the square ($b < 3$). This more elongate growth form arguably relieves oysters from the terminal size constraints experienced by ovoid bivalve forms, as evidenced by old, large oysters in historic, prehistoric, and fossil records for *C. virginica* (De Broca, 1865; Rick *et al.*, 2016; Kusnerik *et al.*, 2018) and even larger Ostreid forms in the fossil record (Kirby, 2001, Harzhauser *et al.*, 2016). During the Pleistocene, *C. virginica* is described as up to 259 mm shell length (umbo to ventral margin) and were substantially larger than the maximum length we observed in extant populations (172 mm; Table 1). Mortality in the old, large oyster size classes disproportionately contributes to the underlying reef structure (Powell and Stanton Jr, 1985; Mann and Powell, 2007; Waldbusser *et al.*, 2013; Powell *et al.*, 2016). Oysters' gregarious settlement, rapid shell production, and individual longevity support the formation and maintenance of biogeomorphic reef structures in estuaries over decadal or longer time frames (Mann and Powell, 2007; La Peyre *et al.*, 2014; Mann *et al.*, 2022; Smith *et al.*, 2022).

Estuaries are geologically ephemeral features. Oysters occupied Atlantic estuaries, including the Chesapeake Bay, for at least 3 million years, and invaded newly formed estuarine habitat as sea level rose and fell (Smith *et al.*, 2003; Hobbs, 2004; Mann *et al.*, 2009*a*; Rick *et al.*, 2016; Lockwood and Mann, 2019). During the Holocene, sea level rise was rapid and is thought to exceed 10 mm yr^{-1} in the Chesapeake Bay (Kennett, 1982; Bratton *et al.*, 2002; Hobbs, 2004). Estuaries drain large coastal regions and may have high sedimentation rates. Sedimentation rates in the extant Chesapeake Bay are around 0.1–1.0 cm yr^{-1} (Cronin *et al.*, 2003). Further, oyster reefs break down as a result of taphonomic processes, such as shell dissolution, breakage, and bioerosion (Powell *et al.*, 2006; Waldbusser *et al.*, 2011; Carroll *et al.*, 2015; Pace *et al.*, 2020). Oyster shell has high turnover rates and taphonomic losses can be up to or greater than 30% yr^{-1} (Pace *et al.*, 2020; Mann *et al.*, 2022). Reef persistence requires accretion rates exceeding sea level rise, sedimentation, and taphonomic losses. Over geologic timescales, oyster reefs have persisted through these challenging conditions; however, over the last century, oysters in the Chesapeake Bay were subjected to intensive overfishing and disease epizootics (*Perkinsus marinus* and *Haplosporidium nelsonii*), which decreased oyster abundance and individual longevity (Haskins and Andrews, 1988; Rothschild *et al.*, 1994; Andrews, 1996). Despite this diversity of challenges, oysters' spatially variable allometry enabled them to maintain aggregative reef structures, which are central to their evolved life history strategy.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0025315424001140.

Acknowledgements. We thank the Virginia Marine Resource Commission's Shellfish Management Division staff for their collaboration on the annual oyster stock assessment and help with sample collection. Thank you to Nathan Otto for assistance with sample processing. Thank you to Dr Hyman for constructive feedback on methods.

Data availability. Data will be made available on request.

Author contributions. **Alexandria R Marquardt:** conceptualization, methodology, investigation, formal analysis, writing – original draft. **Melissa Southworth:** conceptualization, methodology, investigation, writing – review and editing, project administration. **Roger Mann:** conceptualization, writing – review and editing, supervision.

Financial support. A. R. M. was supported by a Virginia Sea Grant Graduate Research Fellowship.

Competing interest. None.

References

Alejandrino A, Puslednik L and Serb JM (2011) Convergent and parallel evolution in life habit of the scallops (Bivalvia: Pectinidae). *BMC Evolutionary Biology* **11**, 164.

Andrews JD (1996) History of *Perkinsus marinus*, a pathogen of oysters in Chesapeake Bay 1950-1984. *Journal of Shellfish Research* **15**, 13–16.

Barber BJ and Blake NJ (1981) Energy storage and utilization in relation to gametogenesis in *Argopecten irradians concentricus* (Say). *Journal of Experimental Marine Biology and Ecology* **52**, 121–134.

Bayne B (2017) *Biology of Oysters, Volume 41 – 1st Edition*, Vol. **41**. London, UK: Elsevier.

Bonar DB, Coon SL, Walch M, Weiner RM and Fitt W (1990) Control of oyster settlement and metamorphosis by endogenous and exogenous chemical cues. *Bulletin of Marine Science* **46**, 15.

Bratton JF, Colman SM, Thieler ER and Seal RR (2002) Birth of the modern Chesapeake Bay estuary between 7.4 and 8.2 ka and implications for global sea-level rise. *Geo-Marine Letters* **22**, 188–197.

Carroll JM, O'Shaughnessy KA, Diedrich GA and Finelli CM (2015) Are oysters being bored to death? Influence of *Cliona celata* on *Crassostrea virginica* condition, growth and survival. *Diseases of Aquatic Organisms* **117**, 31–44.

Castagna M and Chanley P (1973) Salinity tolerance of some marine bivalves from inshore and estuarine environments in Virginia waters on the western Mid-Atlantic coast. *Malacologia* **12**, 47–96.

Colden A, Latour R and Lipcius R (2017) Reef height drives threshold dynamics of restored oyster reefs. *Marine Ecology Progress Series* **582**, 1–13.

Comeau LA (2014) Spring awakening temperature and survival of sediment-covered eastern oysters *Crassostrea virginica*. *Aquaculture* **430**, 188–194.

Cronin T, Sanford L, Langland M, Willard D and Saenger C (2003) Chapter 6: estuarine transport, deposition, and sedimentation. In Langland M and Cronin T (eds), *A Summary Report of Sediment Processes in Chesapeake Bay and Watershed*. Water-Resources Investigations Report 2003-4123. Reston, VA: U.S. Geological Survey, pp. 61–79. https://pubs.er.usgs.gov/publication/wri034123

Crosby MP and Gale L D (1990) A review and evaluation of bivalve condition index methodologies with a suggested standard method. *Journal of Shellfish Research* **9**, 233–237.

Dame RF (1972) Comparison of various allometric relationships in intertidal and subtidal American oysters. *Fishery Bulletin* **70**, 1121–1126.

De Broca P (1865) *Etude sur l'industrie huitriere des Etats-Unis, faite par ordre de S.E.M. le Comte de Chasse-loup Laubat, ministre de la marine et des colonies*. Paris: Challamel aiine, p. 266.

El-Sabbagh AM and El Hedeny MM (2016) A shell concentration of the Middle Miocene *Crassostrea gryphoides* (Schlotheim, 1813) from Siwa Oasis, Western Desert, Egypt. *Journal of African Earth Sciences* **120**, 1–11.

Froese R (2006) Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations. *Journal of Applied Ichthyology* **22**, 241–253.

Galtsoff PS (1964) The American oyster *Crassostrea virginica*. *Fishery Bulletin* **64**, 1–480.

Gaspar MB, Santos MN and Vasconcelos P (2001) Weight–length relationships of 25 bivalve species (Mollusca: Bivalvia) from the Algarve coast (southern Portugal). *Journal of the Marine Biological Association of the United Kingdom* **81**, 805–807.

Gosling E (2015) *Marine Bivalve Molluscs*, 2nd Edn. Hoboken: John Wiley & Sons, Ltd.

Gosling E (2021) *Marine Mussels: Ecology, Physiology, Genetics, and Culture*. Hoboken, USA: John Wiley & Sons, Inc.

Grizzle RE, Greene JK and Coen LD (2008) Seston removal by natural and constructed intertidal eastern oyster (*Crassostrea virginica*) reefs: a comparison with previous laboratory studies, and the value of in situ methods. *Estuaries and Coasts* **31**, 1208–1220.

Gunter G (1954) The problem in oyster taxonomy. *Systematic Zoology* **3**, 134–137.

Harding JM, Mann R, Southworth MJ and Wesson JA (2010) Management of the Piankatank River, Virginia, in Support of Oyster (*Crassostrea virginica*, Gmelin 1791) Fishery Repletion. *Journal of Shellfish Research* **29**, 867–888.

Harzhauser M, Djuricic A, Mandic O, Neubauer TA, Zuschin M and Pfeifer N (2016) Age structure, carbonate production and shell loss rate in an Early

Miocene reef of the giant oyster *Crassostrea gryphoides*. *Biogeosciences (Online)* **13**, 1223–1235.

Haskins HH and Andrews JD (1988) Uncertainties and speculations about the life cycle of the eastern oyster pathogen *Haplosporidium nelsoni* (MSX). In Fisher WS (ed.), *Disease Processes in Marine Bivalve Molluscs*, Bethesda, MD: American Fisheries Society, p. 21.

Hautmann M, Ware D and Bucher H (2017) Geologically oldest oysters were epizoans on Early Triassic ammonoids. *Journal of Molluscan Studies* **83**, 253–260.

Hemachandra ST (2008) Allometry and condition index in green mussel *Perna viridis* (L.) from St Mary's Island off Malpe, near Udupi, India. *Aquaculture Research* **39**, 1747–1758.

Hilborn R and Walters CJ (1992) *Quantitative Fisheries Stock Assessment: Choice, Dynamics, and Uncertainty*. London, UK: Chapman and Hall.

Hobbs CH (2004) Geological history of Chesapeake Bay, USA. *Quaternary Science Reviews* **23**, 641–661.

Kennedy VS, Newell RIE and Eble AF (1996) *The Eastern Oyster: Crassostrea Virginica*, 2nd Edn. College Park, MD: University of Maryland Sea Grant Publications.

Kennett J (1982) *Marine Geology*. Englewood Cliffs, NJ: Prentice Hall.

Kirby MX (2001) Differences in growth rate and environment between tertiary and quaternary *Crassostrea* oysters. *Paleobiology* **27**, 84–103.

Kraeuter JN, Ford S and Cummings M (2007) Oyster growth analysis: a comparison of methods. *Journal of Shellfish Research* **26**, 479–491.

Kusnerik KM, Lockwood R and Grant AN (2018) Using the fossil record to establish a baseline and recommendations for oyster mitigation in the Mid-Atlantic U.S. In Tyler CL and Schneider CL (eds), *Marine Conservation Paleobiology*, Vol. **47**, Cham: Springer International Publishing, pp. 75–103.

La Peyre MK, Humphries AT, Casas SM and La Peyre JF (2014) Temporal variation in development of ecosystem services from oyster reef restoration. *Ecological Engineering* **63**, 34–44.

Li C, Kou Q, Zhang Z, Hu L, Huang W, Cui Z, Liu Y, Ma P and Wang H (2021) Reconstruction of the evolutionary biogeography reveal the origins and diversification of oysters (Bivalvia: Ostreidae). *Molecular Phylogenetics and Evolution* **164**, 107268.

Lockwood R and Mann R (2019) A conservation palaeobiological perspective on Chesapeake Bay oysters. *Philosophical Transactions of the Royal Society B* **374**, 20190209.

Loosanoff VL (1953) Behavior of oysters in water of low salinities. *Proceedings of the National Shellfisheries Association* **43**, 135–151.

Loosanoff VL (1962) Effects of turbidity on some larval and adult bivalves. *Proceedings of the Gulf and Caribbean Fisheries Institute* **14**, 80–95.

Mann R (1978) A comparison of morphometric, biochemical, and physiological indexes of condition in marine bivalve molluscs. In Thorp JH and Gibbons IW (eds), *Energy and Environmental Stress in Aquatic Systems*. US Department of Energy, Symposium Series (771114). Woods Hole, MA: Woods Hole Oceanographic Institute, pp. 484–497.

Mann R and Powell EN (2007) Why oyster restoration goals in the Chesapeake Bay are not and probably cannot be achieved. *Journal of Shellfish Research* **26**, 905–917.

Mann RL and Wesson JA (1994) *Fishery Independent Standing Stock Surveys of Oyster Populations in the Virginia sub Estuaries of the Chesapeake Bay and a Comparison with Continuing Estimates Obtained from Fishery Dependent Data*. Virginia Institute of Marine Science, William & Mary. https://doi.org/10.25773/x7h1-6132

Mann RL and Wesson J (1997) *Fishery Independent Standing Stock Surveys of Oyster Populations in Virginia 1997*. Virginia Institute of Marine Science, College of William and Mary, p. 54.

Mann R, Harding JM and Southworth M (2009*a*) Reconstructing pre-colonial oyster demographics in the Chesapeake Bay, USA. *Estuarine, Coastal and Shelf Science* **85**, 217–222.

Mann R, Southworth M, Harding JM and Wesson JA (2009*b*) Population studies of the native eastern oyster, *Crassostrea virginica*, (Gmelin, 1791) in the James River, Virginia, USA. *Journal of Shellfish Research* **28**, 193–220.

Mann R, Southworth M, Wesson J, Thomas J, Tarnowski M and Homer M (2022) Oyster shell production and loss in the Chesapeake Bay. *Journal of Shellfish Research* **40**, 451–469.

Manuel EC, Hare MP and Munroe D (2023) Consequences of salinity change, salinity history, and shell morphology on early growth of juvenile oysters. *Journal of Shellfish Research* **42**, 21–28.

Marquardt AR, Clark NM, Maietta EG, Park SK and Ruttenberg BI (2022) Reproduction, body condition, age, and growth of a large sandy intertidal bivalve. Tivela stultorum. *Aquatic Biology* **31**, 19–30.

Márquez F, Amoroso R, Gowland Sainz M and Van Der Molen S (2010) Shell morphology changes in the scallop *Aequipecten tehuelchus* during its life span: a geometric morphometric approach. *Aquatic Biology* **11**, 149–155.

McGrath D, King PA and Gosling EM (1988) Evidence for the direct settlement of *Mytilus edulis* larvae on adult mussel beds. *Marine Ecology Progress Series* **47**, 103–106.

McRoberts CA (1992) Systematics and paleobiogeography of Late Triassic *Gryphaea* (Bivalvia) from the North American Cordillera. *Journal of Paleontology* **66**, 28–39.

Meng J, Wang T, Li L and Zhang G (2018) Inducible variation in anaerobic energy metabolism reflects hypoxia tolerance across the intertidal and subtidal distribution of the Pacific oyster (*Crassostrea gigas*). *Marine Environmental Research* **138**, 135–143.

Michaelidis B, Haas D and Grieshaber MK (2005) Extracellular and intracellular acid-base status with regard to the energy metabolism in the oyster *Crassostrea gigas* during exposure to air. *Physiological and Biochemical Zoology* **78**, 373–383.

Minchin D (2003) Introductions: some biological and ecological characteristics of scallops. *Aquatic Living Resources* **16**, 521–532.

Moura P, Gaspar MB and Monteiro CC (2008) Gametogenic cycle of the smooth clam *Callista chione* on the south-western coast of Portugal. *Journal of the Marine Biological Association of the United Kingdom* **88**, 161–167.

Munroe D, Borsetti S, Ashton-Alcox K and Bushek D (2017) Early post-settlement growth in wild eastern oyster (*Crassostrea virginica* Gemlin 1791) populations. *Estuaries and Coasts* **40**, 880–888.

Nagi HM, Shenai-Tirodkar PS and Jagtap TG (2011) Dimensional relationships in *Crassostrea madrasensis* (Preston) and *C. gryphoides* (Schlotheim) in Mangrove ecosystem. *Indian Journal of Geo-Marine Sciences* **40**, 559–566.

Ojea J, Pazos AJ, Martínez D, Novoa S, Sánchez JL and Abad M (2004) Seasonal variation in weight and biochemical composition of the tissues of *Ruditapes decussatus* in relation to the gametogenic cycle. *Aquaculture* **238**, 451–468.

Pace SM, Poussard LM, Powell EN, Ashton-Alcox KA, Kuykendall KM, Solinger LK, Hemeon KM and Soniat TM (2020) Dying, decaying, and dissolving into irrelevance: first direct in-the-field estimate of *Crassostrea virginica* shell loss – a case history from Mississippi sound. *Journal of Shellfish Research* **39**, 245–256.

Palmer BA, Taylor GJ, Brumfeld V, Gur D, Shemesh M, Elad N, Osherov A, Oron D, Weiner S and Addadi L (2017) The image-forming mirror in the eye of the scallop. *Science* **358**, 1172–1175.

Peharda M (2012) Growth and longevity of *Glycmeris nummaria* (Linnaeus, 1758) from the eastern Adriatic, Croatia. *Journal of Shellfish Research* **31**, 947–950.

Pinheiro JC and Bates DM (2000) *Mixed-Effects Models in S and S-PLUS*. New York: Springer-Verlag.

Pinheiro JC and Bates DM and R Core Team (2023) nlme: Linear and nonlinear mixed effects models.

Poirier LA, Clements JC, Coffin MRS, Craig T, Davidson J, Miron G, Davidson JDP, Hill J and Comeau LA (2021) Siltation negatively affects settlement and gaping behaviour in eastern oysters. *Marine Environmental Research* **170**, 105432.

Powell EN and Stanton Jr RJ (1985) Estimating biomass and energy flow of molluscs in Paleo-communities. *Palaeontology* **28**, 1–34.

Powell EN, Klinck JM, Hofmann EE, Wilson-Ormond EA and Ellis MS (1995) Modeling oyster populations. V. Declining phytoplankton stocks and the population dynamics of American oyster (*Crassostrea virginica*) populations. *Fisheries Research* **24**, 199–222.

Powell EN, Kraeuter JN and Ashton-Alcox KA (2006) How long does oyster shell last on an oyster reef? *Estuarine, Coastal and Shelf Science* **69**, 531–542.

Powell EN, Mann R, Ashton-Alcox KA, Kim Y and Bushek D (2016) The allometry of oysters: spatial and temporal variation in the length–biomass relationships for *Crassostrea virginica*. *Journal of the Marine Biological Association of the United Kingdom* **96**, 1127–1144.

Quayle DB (1988) Pacific oyster culture in British Columbia. *Canadian Bulletins of Fisheries and Aquatic Sciences* **218**, 241.

R Core Team (2023) *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rainier JS and Mann RL (1992) A comparison of methods for calculating condition index in eastern oysters *Crassostrea virginica* (Gmelin, 1791). *Journal of Shellfish Research* **11**, 55–58.

Rick TC, Reeder-Myers LA, Hofman CA, Breitburg D, Lockwood R, Henkes G, Kellogg L, Lowery D, Luckenbach MW, Mann R, Ogburn MB, Southworth M, Wah J, Wesson J and Hines AH (2016) Millennial-scale sustainability of the Chesapeake Bay Native American oyster fishery. *Proceedings of the National Academy of Sciences* **113**, 6568–6573.

Rothschild B, Ault J, Goulletquer P and Héral M (1994) Decline of the Chesapeake Bay oyster population: a century of habitat destruction and overfishing. *Marine Ecology Progress Series* **111**, 29–39.

Scharping R, Plough L, Meritt D and North E (2019) Low-salinity tolerance of early-stage oyster larvae from a mesohaline estuary. *Marine Ecology Progress Series* **613**, 97–106.

Seed R (1976) Ecology. In Bayne BL (ed.), *Marine Mussels: Their Ecology and Physiology*. Cambridge: Cambridge University Press, pp. 13–66.

Serb JM, Alejandrino A, Otárola-Castillo E and Adams DC (2011) Morphological convergence of shell shape in distantly related scallop species (Mollusca: Pectinidae). *Zoological Journal of the Linnean Society* **163**, 571–584.

Shumway S (1996) Natural environmental factors. In Kennedy VS, Newell RIE and Eble AF (eds), The Eastern Oyster *Crassostrea virginica*. College Park: Maryland Sea Grant College, pp. 467–513.

Smith GF, Roach EB and Bruce DG (2003) The location, composition, and origin of oyster bars in mesohaline Chesapeake Bay. *Estuarine, Coastal and Shelf Science* **56**, 391–409.

Smith RS, Lusk B and Castorani MCN (2022) Restored oyster reefs match multiple functions of natural reefs within a decade. *Conservation Letters* **15**, e12883.

Sousa R, Vasconcelos J and Riera R (2020) Weight–length relationships of four intertidal mollusc species from the northeastern Atlantic Ocean and their potential for conservation. *Molluscan Research* **40**, 363–368.

Southworth M and Mann RL (2020) The status of Virginia's public oyster resource 2019. *Virginia Institute of Marine Science, William & Mary* 52.

Southworth M, Harding JM, Wesson JA and Mann R (2010) Oyster (*Crassostrea virginica*, Gmelin 1791) population dynamics on public reefs in the Great Wicomico River, Virginia, USA. *Journal of Shellfish Research* **29**, 271–290.

Speiser DI and Johnsen S (2008) Comparative morphology of the concave mirror eyes of scallops (Pectinoidea). *American Malacological Bulletin* **26**, 27–33.

Tamburri MN, Finelli CM, Wethey DS and Zimmer-Faust RK (1996) Chemical induction of larval settlement behavior in flow. *The Biological Bulletin* **191**, 367–373.

Tamburri MN, Luckenbach MW, Breitburg DL and Bonniwell SM (2008) Settlement of *Crassostrea ariakensis* larvae: effects of substrate, biofilms, sediment, and adult chemical cues. *Journal of Shellfish Research* **27**, 601–608.

Telesca L, Michalek K, Sanders T, Peck LS, Thyrring J and Harper EM (2018) Blue mussel shell shape plasticity and natural environments: a quantitative approach. *Scientific Reports* **8**, 2865.

Tokeshi M, Ota N and Kawai T (2000) A comparative study of morphometry in shell-bearing molluscs. *Journal of Zoology* **251**, 31–38.

Turner EJ, Zimmer-Faust RK, Palmer MA, Luckenbach M and Pentchef ND (1994) Settlement of oyster (*Crassostrea virginica*) larvae: effects of water flow and a water-soluble chemical cue. *Limnology and Oceanography* **39**, 1579–1593.

Waldbusser GG, Steenson RA and Green MA (2011) Oyster shell dissolution rates in estuarine waters: effects of pH and shell legacy. *Journal of Shellfish Research* **30**, 659–669.

Waldbusser GG, Powell EN and Mann R (2013) Ecosystem effects of shell aggregations and cycling in coastal waters: an example of Chesapeake Bay oyster reefs. *Ecology* **94**, 895–903.

Wickham H (2016) *ggplot2: Elegant Graphics for Data Analysis*. New York: Springer-Verlag.

Zuur A, Ieno EN, Walker N, Saveliev AA and Smith GM (2009) *Mixed Effects Models and Extensions in Ecology with R*. New York, NY: Springer-Verlag.