



In-situ valve opening response of eastern oysters to estuarine conditions

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Received: 5 January 2024 / Accepted: 16 July 2024 / Published online: 9 August 2024
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Abstract

High-frequency recordings of valve opening behavior (VOB) in bivalves are often used to detect changes in environmental conditions. However, generally a single variable such as temperature or the presence of toxicants in the water is the focus. A description of routine VOB under non-stressful conditions is also important for interpreting responses to environmental changes. Here we present the first detailed quantitative investigation of the in-situ VOB of eastern oysters (*Crassostrea virginica*) to environmental variables typically not considered stressful. The VOB of eight individuals was monitored for seven weeks in a Louisiana estuary. We examined the relationships between VOB metrics (variance in mean % max opening among oysters, the probability of an oyster being closed, and the rate of valve closure), and temperature, salinity, chlorophyll-a (chl-a) concentration, the rate of change in those environmental variables, and the rate of change in water depth. Relationships were analyzed through statistical models including rates of change over 0, 0.25, 1-, 6-, 12-, and 24-hours. All the responses were best explained by the 12-hour time step model. The interaction effect between salinity and the rate of change of salinity had the greatest impact on variance in oysters' behavior. Oysters closed faster at higher salinities and were more likely to be closed at lower chl-a concentrations. Significant interactions were found between many environmental variables, indicating a high level of complexity of oyster behavior in the natural environment. This study contributes to a better understanding of the impact of environmental conditions on oyster behavior and can help inform predictive tools for restoration initiatives and fisheries practices.

Keywords Behavior · *Crassostrea virginica* · Salinity · Temperature · Chlorophyll-a · Valvometry

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Communicated by P. Ramey-Balci.

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Introduction

The eastern oyster, *Crassostrea virginica*, is an important species for habitat formation and ecosystem function in estuaries along the Atlantic and Gulf of Mexico coasts of North America. Like many other bivalves, they live most of their life attached to a substrate (rock, congener shell, wood piling, etc.) and are exposed to changes in environmental conditions that some mobile organisms may be able to avoid. Eastern oysters can tolerate large ranges and changes in temperature (Shumway 1996; Comeau et al. 2012; Marshall et al. 2021a), salinity (Shumway and Koehn 1982; Casas et al. 2018a; Marshall et al. 2021b), and dissolved oxygen (DO; Stickle et al. 1989; Coxe et al. 2023) and can survive starvation periods of several months (Comeau et al. 2012). With a wide geographical distribution, different populations can live in highly contrasting environmental conditions both in terms of average values and range of daily or

seasonal variations (Beseres Pollack et al. 2011; Casas et al. 2018b). When changes occur rapidly and beyond the oysters' capacity to osmoconform in time, oysters close their valves to seclude themselves from the surrounding water. For instance, oysters typically close when salinity drops too rapidly or when it falls below a certain threshold to avoid cellular damage caused by osmotic pressure changes (Hand and Stickle 1977; Shumway 1996; Casas et al. 2018a). The capacity of oysters to behaviorally respond to changes and the rate of change in environmental conditions through valve closure may be critical to their resilience in a changing coastal environment (Cloern et al. 2016). However, valve closure may also impact metabolism through a reduction in energy input from feeding and less energy efficient anaerobic pathways.

Bivalves open their valves to perform essential physiological functions such as feeding, respiration, reproduction, and excretion. When closed, the shell offers protection from predators and adverse environmental conditions. For a century, scientists have increasingly studied the valve opening behavior (VOB) of bivalves for two purposes: to better understand bivalve tolerance to ranges of environmental conditions or their rate of change (e.g., Shumway 1977a, b) and to use them as sentinels of environmental variability (Vereycken and Aldridge 2023). However, while past works have contributed to the description of the impact of single or a few environmental variables on VOB at the same time, analyses of the response of bivalves and oysters in particular to multiple environmental factors co-occurring in natural conditions are scarce. Knowledge is also lacking on the response of oysters to conditions within their tolerance range, i.e., 'normal' conditions. Many studies have focused on identifying thresholds of VOB response of oysters at the extreme of the tolerance range such as winter temperatures (Comeau et al. 2012; Clements et al. 2018), low pH (Clements et al. 2018), or hypoxic events (Coffin et al. 2021; Coxe et al. 2023); however, few reports exist of their behavior over long periods and under more average conditions. A better understanding of how oysters respond to a variety of changes in their natural environment will provide valuable information for the interpretation of VOB in both ecophysiological and environmental monitoring studies.

Valvometry techniques have evolved since the pioneering work of Nelson (1922), but research has continuously shown that the valve movements of oysters in response to environmental factors are complex. Oysters exhibit high inter-individual variability, which may be due to the generally low number of monitored individuals or failure to account for interactive effects. Valve closures of bivalves have been linked to tidal cycles (Nelson 1922; Sow et al. 2011), algal concentration (Higgins 1980), algal toxins (Nagai et al. 2006; Tran et al. 2010; Lavaud et al. 2021),

chemical compounds (Kramer and Foekema 2001; Hartmann et al., 2016), acidification (Clements et al. 2018; Lassoued et al. 2021), dissolved oxygen concentration (DO; Porter and Breitbart 2016; Coffin et al. 2021), parasitic infections (Chambon et al. 2007), and sound (Charifi et al. 2017; Hubert et al. 2023). Most studies carried out in the field have related valve opening to a single factor. However, in the natural environment, oysters can experience multiple changes in conditions simultaneously, and the potential effect and interaction of multiple variables on the VOB of oysters and bivalves in general have rarely been studied (Hubert et al. 2023).

In this study, we aimed to describe the VOB of eastern oysters under typical environmental conditions in southeastern Louisiana, USA. A tray containing eight oysters was deployed under natural conditions and oyster valve movements were continuously recorded along with multiple environmental variables. We quantified the respective effects of water temperature, salinity, chlorophyll-a concentration, DO concentration, depth, their rate of change and their possible interactions on oyster VOB over a 7-week period. We hypothesized that interactions between environmental variables would be important drivers of oyster VOB. To test this assumption, we analyzed the data to determine how each environmental variable and their interactions may influence (i) inter-individual variability in VOB, (ii) the probability of oysters being closed, and (iii) the strength of the response through the rate of valve closure.

Materials and methods

Study site, oysters, and environmental variables

Oysters used in this study were the progeny of wild oysters (i.e., diploids) from Calcasieu Lake (29°47'6.00"N, 93°55'5.02"W) spawned during the summer of 2019 at the Louisiana Sea Grant Oyster Research Farm (LASGRF) in Grand Isle, LA (see Bodenstein et al. 2023 for details of larvae rearing). Once the spat height reached 6 mm, they were transferred to baskets on the longline system at the LASGRF. In January 2020 market-sized oysters (> 75 mm shell height) were transferred to Louisiana Universities Marine Consortium's (LUMCON) De Felice Marine Center in Cocodrie, LA (29°15'14.10"N; 90°39'49.70"W). On 9 March 2021, shell height was measured for eight oysters, which were individually tagged, equipped with a valvometry system (see next section), and evenly placed in a tray box formed of two trays (50 × 50 × 10 cm each) securely tightened with cable ties to protect the oysters from predation. The trays were suspended horizontally from a pier located 42 m south of LUMCON's environmental monitoring station so that the

oysters were continuously submerged approximately 0.3 m off the bottom at 2 m depth (high tide). The study area is within a coastal saltmarsh dominated by a network of small bays connected by channels and is under the influence of the Gulf of Mexico to the South and runoff from various bayous (i.e., streams) in the North. Temperature (°C), salinity, chlorophyll-a concentration ($\mu\text{g L}^{-1}$), DO concentration (mg L^{-1}), and water depth (m) were recorded every fifteen minutes (0.25 h) by LUMCON's environmental monitoring station located in a channel of western Terrebonne Bay (29°15.20'N, 90°39.80'W; data available at <https://lumcon.edu/environmental-monitoring/>).

Valve opening measurement

The oysters were equipped with a valvometry system (Nagai et al. 2006; Comeau et al. 2012) to monitor valve movements. UV light curing glue was used to attach a coated Hall element sensor (HW-300a, Asahi Kasei Corp, Chiyoda-ku, Tokyo, Japan; 0.5 g) to one valve at the maximum distance from the hinge (i.e., the ventral margin). A small magnet (4.8 mm diameter \times 0.8 mm height; 0.1 g) was glued to the other valve, opposite the Hall sensor. Valve movements, measured by variation in the magnetic field between the sensor and the magnet (in μV), were recorded every 1 s using dynamic strain recording devices (DC 204R, Tokyo Sokki Kenkyujo Co., Shinagawa-ku, Tokyo, Japan). Every two weeks, the tray box was cleaned of fouling organisms and the oysters were checked to ensure that the sensors were still securely attached. The monitoring ended on 25 April 2021, at which point the oysters were notched, the adductor muscle was cut, and small calibration wedges (1–6 mm) were inserted between the valves at the ventral margin to derive a voltage versus gap calibration curve ($R^2 > 0.90$) and convert voltage measurements into valve opening distances (VOD) for each individual oyster.

Valvometry data analysis

Data pre-processing

The valve opening distance (VOD) and shell height (SH) were combined to calculate the opening angle (OA) via the following equation: $\text{OA} = \arcsin(0.5 \times \text{VOD}/\text{SH}) \times 100$ (adapted from Wilson et al. 2005). There was detectable drift in voltage measurements over the course of the study, likely due to shell growth, which resulted in unrealistic measurements of opening angles (i.e., < 0 or $> 100\%$ of percent of maximum opening). To correct for this the maximum and minimum angle openings for each oyster were calculated over a centered rolling 48-hour window. This window was chosen after visual inspection of the data confirmed that all

oysters completely opened and completely closed multiple times within any given 48-hour window. Drift-corrected values were then used to convert each OA to the percent of maximum (% max) opening over that 48-hour window so that when an oyster was completely open % max = 100 and when an oyster was completely closed % max = 0.

Oyster VOB data (% max) were matched to environmental data, which were collected every 15 min, using the date and time of the measurements. For example, environmental variables were measured at 00:00:00 and 00:15:00 on 9 March 2021, and the time between these two readings was designated as environmental interval 1. Oyster % max values recorded at or between 0:00:00 and 0:14:59 on 9 March 2021, were assigned to the environmental interval 1. To avoid pseudo-replication, % max values were summarized for each environmental interval into three variables: the mean of % max (hereafter mean % max) for that environmental interval, the percentage of time closed during that environmental interval – where closed was defined as % max $\leq 10\%$, and percent of time fully open during that environmental interval – where fully open was defined as % max $\geq 80\%$. Finally, we identified individual closure events for each oyster. These closure events were identified through a 5-step process. First, the change in % max values from the previous second was calculated. Second, the change was classified as positive (i.e., the valve opening became larger), negative (i.e., the valve opening narrowed), or no change. Third, consecutive periods of change in the same direction were combined. Fourth, the total % change in opening was calculated for all negative change groups by subtracting the % max value from the last second of the group from the % max value from the first second of the group. The rate of closure was then calculated by dividing this total % change by the number of seconds within the group. Finally, negative change groups were identified as a closure event if the total change in % max was $\geq 40\%$.

Initial visual inspection of the environmental data and oyster VOB indicated that oyster behavior may be related to the rate of change of temperature, salinity, chlorophyll-a concentration, and DO concentration. Therefore, for each of these environmental variables five additional variables were calculated: change from the previous 15-min time step (i.e., measurement recorded on the previous environmental interval), the rate of change over the past hour, as well as the rate of change over the past 6, 12, and 24 h. The rates of change were calculated using the equation:

$$\frac{v_t - v_{t-x}}{v_{t-x}} \times 100$$

where v_t is the environmental variable value (temperature, salinity, or DO) for the current environmental interval and

v_{t-x} is the environmental variable value of the previous time interval with $x = 0.25, 1, 6, 12,$ or 24 h.

In many systems, oyster VOB is tightly coupled to tidal cycles. However, in our study system, water depth varies both with tidal cycles and in response to on- and off-shore winds. As a result, behavioral rhythms associated with the ebb and flow of tides are regularly disrupted. Therefore, rather than accounting for tidally linked behaviors using a cyclical model, as several other studies have done (Tran et al. 2011), we included the rate of change in water depth as an explanatory variable in all models. This rate of change was calculated as described above, except only at the 6-hour interval.

Inter-individual variability in oyster behavior

Inter-individual correlations in oyster behavior (mean % max) was assessed in two ways. First, to assess if oyster behavior was correlated across the time series, we used variance ratio analysis (Schluter 1984) using the codyn package (Hallett et al., 2016). Significance was assessed by comparing the observed value to a null distribution generated via bootstrapping, where each oyster's time series started at randomly assigned starting points (Hallett et al. 2014). Second, to determine whether environmental variables contributed to inter-individual variation, we calculated the variance between the mean % max values of all oysters in each environmental interval. We then fit 6 separate mixed effects models to test for a relationship between the variance in mean % max among oysters (% max²) and environmental variables in the current environmental interval and their rates of change at the 5 different time steps described above (0.25, 1, 6, 12, and 24 h). All models included the rate of change in water depth at the 6-hour interval as a proxy for tides and included all possible two-way interactions between all environmental variables and their rates of change as fixed effects (Table S2-S4). The oyster tray box was cleaned, and oysters were measured three times throughout the study. The period of time between each cleaning was considered a deployment. All the models also included deployment as a random variable.

All models were checked for multicollinearity using the `check_collinearity` function in the `performance` package in

R (Lüdecke et al. 2021). Any model terms with moderate or high values of multicollinearity were removed from the model. In all cases, including both DO and chlorophyll-a concentrations (and their rates of change) introduced multicollinearity to the model. Since DO concentrations never reached critical values ($> 4 \text{ mg L}^{-1}$ throughout the monitoring; Table 1), DO and its associated rate of change variables were removed from all models. All predictor variables were scaled to adjust for variables having different ranges. The residuals of all models were examined to ensure compliance with model assumptions. Models were compared using the corrected Akaike information criterion (AICc) and all models within $2\Delta \text{AICc}$ were considered well supported.

Environmental drivers of the rate of closure

To assess whether environmental conditions drove the rate of oyster closure, the dataset was filtered to retain only oysters and intervals where closure events occurred (see Sect. 2.3.1 for details). Multiple closure events within a single environmental interval did not occur. The relationship between the rate of oyster closure (absolute value of the slope) and environmental variables was assessed using mixed effects models with oyster ID as a random variable and a Beta distribution with logit link within the `glmmTMB` package (Brooks et al. 2017). The same models were assessed as with variability in oyster behavior and model residuals were examined using the `DHARMA` package (Hartig 2020). To meet model assumptions, the log of the rate of oyster closure was ultimately used as the response variable. Model fit was again compared using AICc.

Environmental drivers of oyster closure

To assess whether environmental conditions drove whether or not oysters closed their valves, the larger dataset was subset to include only periods where an oyster was fully opened or closed. The probability of an oyster being closed was assessed using logistic regression with oyster ID as a random variable via the `glmmTMB` package (Brooks et al. 2017). The same models were assessed as with the rate of valve closure. Model residuals were examined using the `DHARMA` package (Hartig 2020). Model fit was again compared using the Akaike Information Criterion corrected for small sample size (AICc).

Table 1 Summary of the environmental conditions experienced by oysters over the course of the seven-week study

Environmental variable	Minimum	Maximum	Mean	Standard deviation
Chlorophyll-a ($\mu\text{g L}^{-1}$)	3.73	25.30	10.10	3.70
Dissolved Oxygen (mg L^{-1})	4.11	11.50	7.32	1.30
Salinity	3.23	23.90	12.20	5.70
Temperature ($^{\circ}\text{C}$)	14.00	26.40	20.60	2.90

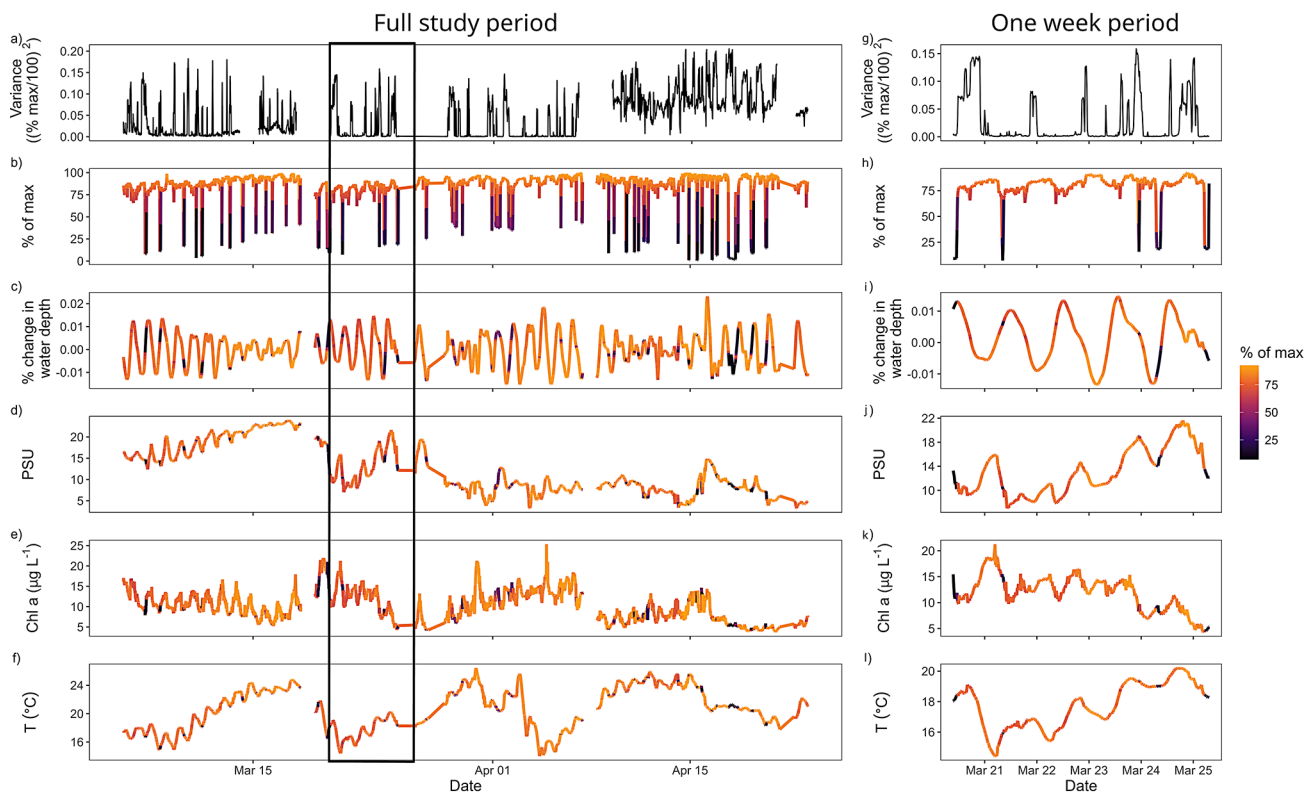


Fig. 1 Dynamics of the variance between oyster % max values of the 8 oysters monitored (a, g), % max of a single individual (b, h; per-second measures of % max averaged over the 15 min environmental intervals), % change in water depth (c, i), salinity (d, j), chlorophyll a

concentration (Chl a; e, k), and temperature (f, l) over the entire study period (left) and over one week (right) between 9 March and 26 April 2021. PSU = practical salinity unit

Table 2 The percentages of time each oyster spent closing, fully closed (consistently < 10% of max opening during the 15-minute interval), opening, partially open (mean valve angle was > 10% and less than 80% of max opening during the 15-minute interval, and oyster was not actively opening or closing), or fully open (consistently > 80% of max opening during the 15-minute interval) and their average rate of closure (% per second)

Oyster	Closing	Fully closed	Opening	Partially open	Fully open	Average rate of closure
1	40.40	4.65	37.14	8.73	9.04	5.32
2	41.89	1.62	42.60	8.51	5.33	3.92
3	41.89	2.53	44.50	4.34	6.74	20.4
4	41.00	2.98	38.47	3.68	13.82	5.08
5	42.18	2.48	39.28	3.63	12.43	7.04
6	36.80	9.90	39.10	7.29	6.87	3.11
7	42.57	1.36	40.85	4.62	10.60	3.70
8	38.13	2.40	42.94	4.13	12.41	6.25

Results

Environmental conditions and summary of oyster behavior

Throughout the 48 days of the study, environmental conditions varied, but would not be expected to induce a significant stress response in oysters (Table 1; Fig. 1). DO concentration was negatively correlated with water temperature and positively correlated with chlorophyll-a concentration (Table S1). As a result, DO concentration was

removed from further analyses. Oysters spent most of their time either opening or closing their valves (Table 2) rather than in a fully open or fully closed position. Seven of the eight oysters we studied spent more time fully opened than fully closed, and all 8 oysters spent more time either fully or partially open than fully closed (Table 2). When oysters were closing their valves, they did so with an average closure rate of 9.7% per second ($\pm 12.1\%$, sd).

Table 3 Model comparison table for models examining the role of environmental drivers on variance in oysters' behavior. Any model within 2 Δ Akaike Information Criterion corrected for small sample size (AICc) of the best fit model was considered well supported. ModelLik = relative likelihood; AICcWt = akaike weights; LL = log-likelihood; Cum.Wt = cumulative Akaike weights

Model	K	AICc	Δ AICc	ModelLik	AICcWt	LL	Cum.Wt
12 h	25	-117976.8	0.0	1	1	59013.4	1
24 h	25	-117610.9	365.8	0	0	58830.5	1
6 h	25	-117342.9	633.9	0	0	58696.5	1
1 h	25	-115724.2	2252.6	0	0	57887.1	1
0.25 h	25	-115296.4	2680.4	0	0	57673.2	1
0 h (no history)	9	-114826.9	3149.9	0	0	57422.5	1

Table 4 Model comparison table for models examining the role of environmental drivers on the rate of oyster closure. Any model within 2 Δ Akaike Information Criterion corrected for small sample size (AICc) of the best fit model was considered well supported. ModelLik = relative likelihood; AICcWt = akaike weights; LL = log-likelihood; Cum.Wt = cumulative Akaike weights

Model	K	AICc	Δ AICc	ModelLik	AICcWt	LL	Cum.Wt
12 h	25	-1965.7	0.00	1.00	0.95	1008.9	0.95
24 h	25	-1959.6	6.11	0.05	0.04	1005.8	0.99
6 h	25	-1955.4	10.31	0.01	0.01	1003.7	1.00
1 h	25	-1948.5	17.18	0.00	0.00	1000.3	1.00
0.25 h	25	-1943.1	22.59	0.00	0.00	997.56	1.00
0 h (no history)	9	-1916.7	48.94	0.00	0.00	967.51	1.00

Table 5 Model comparison table for models examining the role of environmental drivers on the probability of an oyster being closed. Any model within 2 Δ Akaike Information Criterion corrected for small sample size (AICc) of the best fit model was considered well supported. ModelLik = relative likelihood; AICcWt = akaike weights; LL = log-likelihood; Cum.Wt = cumulative Akaike weights

Model	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
12 h	24	3216.3	0.0	1	1	-1584.0	1
6 h	24	3429.5	213.2	0	0	-1690.6	1
24 h	24	3444.5	228.3	0	0	-1698.1	1
1 h	24	3592.8	376.6	0	0	-1772.3	1
0.25 h	24	3674.9	458.6	0	0	-1813.3	1
0 h (no history)	8	3756.7	540.4	0	0	-1870.3	1

Inter-individual variation in oyster behavior

Oyster behavior was significantly correlated among individuals throughout the course of the study (Observed Variance Ratio: 3.3, null mean and 95% confidence intervals: 1, 0.92–1.1). Despite this overall correlation between oyster behavior, variance in mean % max among oysters varied over the course of the study (Fig. 1a). The 12-hour time step model was the best model to explain changes in variance in oyster behavior (Table 3). Overall, this model explained a large proportion of the variance between oysters ($R^2=0.48$). However, the fixed effects alone explain a much lower proportion ($R^2=0.07$).

Rate of valve closure

The 12-hour time step model was the best model to explain how quickly oysters closed their valves (Table 4). Overall, this model explains the variability in closing rate well (Conditional $R^2=0.60$).

Probability of an oyster being closed

The 12-hour time step model was the best model to explain the probability of an oyster being closed (Table 5). Overall, this model does a good job of explaining the probability of an oyster being closed (Tjur's $R^2=0.56$) and the fixed effects alone account for more than half of that probability (Tjur's $R^2=0.50$).

Environmental influence on oyster behavior

All the studied environmental variables influenced at least one aspect of valve opening behavior (Fig. 2a-c). The interaction between salinity and its rate of change had the largest effect on the variance among oysters' behavior (Fig. 2a). Salinity also had the greatest influence on the rate of valve closure (Fig. 2b). Chlorophyll-a concentration was the variable that had the largest effect size on the probability of an oyster being closed (Fig. 2c). The effects of all the environmental variables on the three aspects of oyster behavior we examined were modified, to some extent, by interactions.

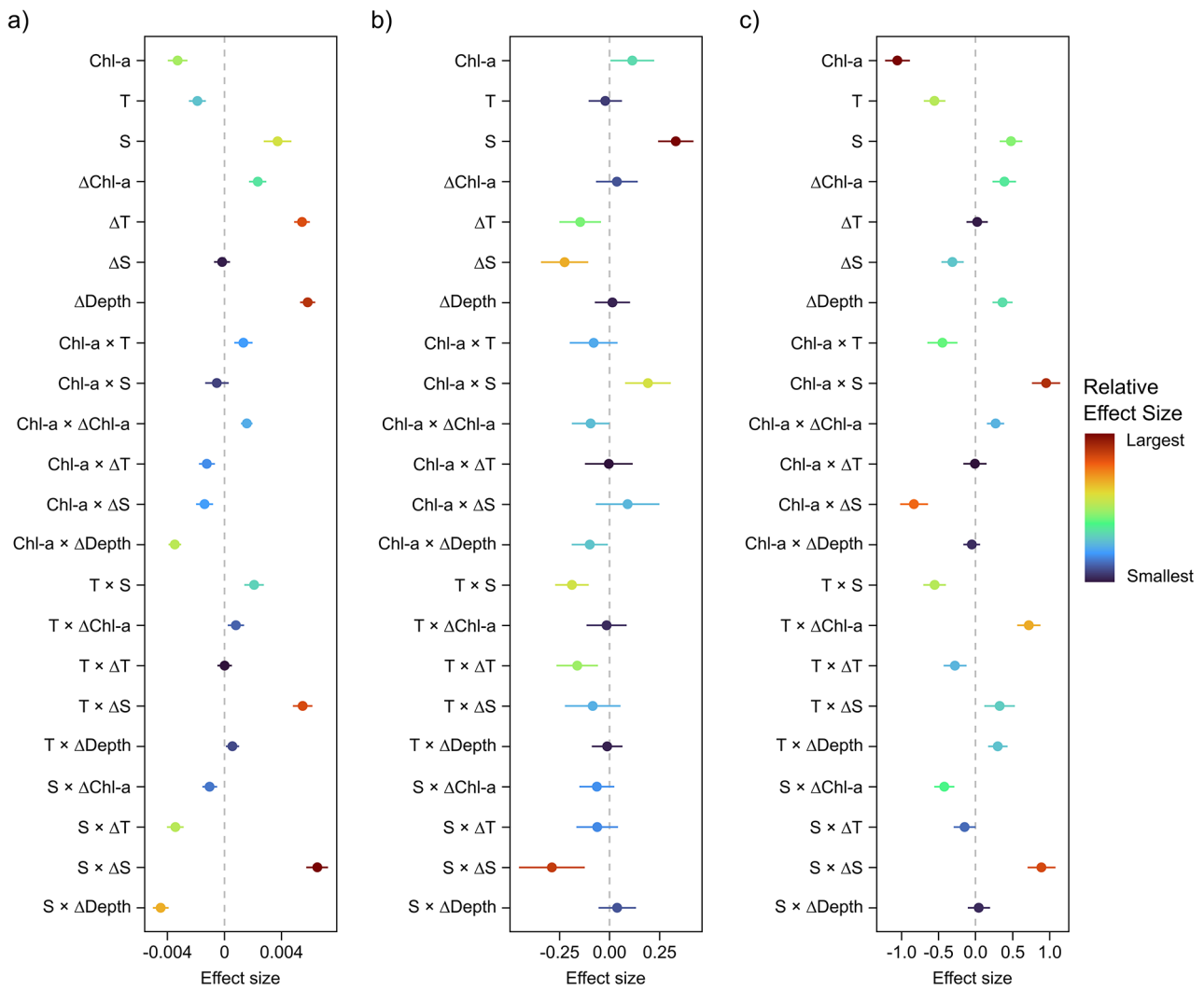


Fig. 2 Effect size (β terms from the best-fit models) of single- and two-way interactions of environmental predictors (salinity (S), temperature (T), chlorophyll-a (Chl-a), their rates of change (Δ), and the rate of change of water depth (Δ Depth)) on the variance in oyster behavior ((% max/100)²; a), rate of valve closure (b), and probability of an oys-

ter being closed (c). A positive effect size means that a higher value of the variable is associated with higher variability, more time spent closed, or a faster rate of closure. Error bars represent 95% confidence intervals. The color of each model term is scaled from smallest to largest effect size within each model

Below we describe only the interactions that alter the general pattern between the environmental variable and oyster behavior. The significant interactions that modify the intensity of the relationship between the environmental variables and oyster behavior but do not change the general pattern of response (Fig. 2a-c, Tables S2-4) are not discussed in the following sections.

Chlorophyll-a concentration

When considered on its own, higher chlorophyll-a (chl-a) concentrations ($\sim 25 \mu\text{g L}^{-1}$) decreased variance in oysters' behavior ($\beta = -0.0032$, 95% confidence interval (CI) = -0.0039 to -0.0026 , $t_{31000} = -9.20$, $p < 0.001$). Only the interaction with the rate of change of water depth altered

the direction of the relationship between the variance and chl-a concentration so that when water depth was decreasing (i.e., tide was ebbing) there was no relationship between chl-a concentration and variance in oysters' behavior ($\beta = -0.04$, 95% CI = 0.02 to 0.06 , $t_{31000} = -15.00$, $p < 0.001$; Fig. 3a). Oysters closed their valves more rapidly at higher chl-a concentrations than at lower concentrations ($\beta = 0.11$, 95% CI = 0.01 to 0.22 , $z = 2.05$, $p = 0.04$). This relationship is modified by salinity so that at lower salinities (~ 8) there is no relationship between closure rate and chl-a concentrations, but at higher salinities (~ 20) there is a strong positive relationship with oysters closing faster in higher chl-a concentrations ($\beta = 0.19$, 95% CI = 0.08 to 0.3 , $z = 3.34$, $p < 0.001$). Chl-a concentration had the largest effect of all variables on the probability of an oyster being closed with

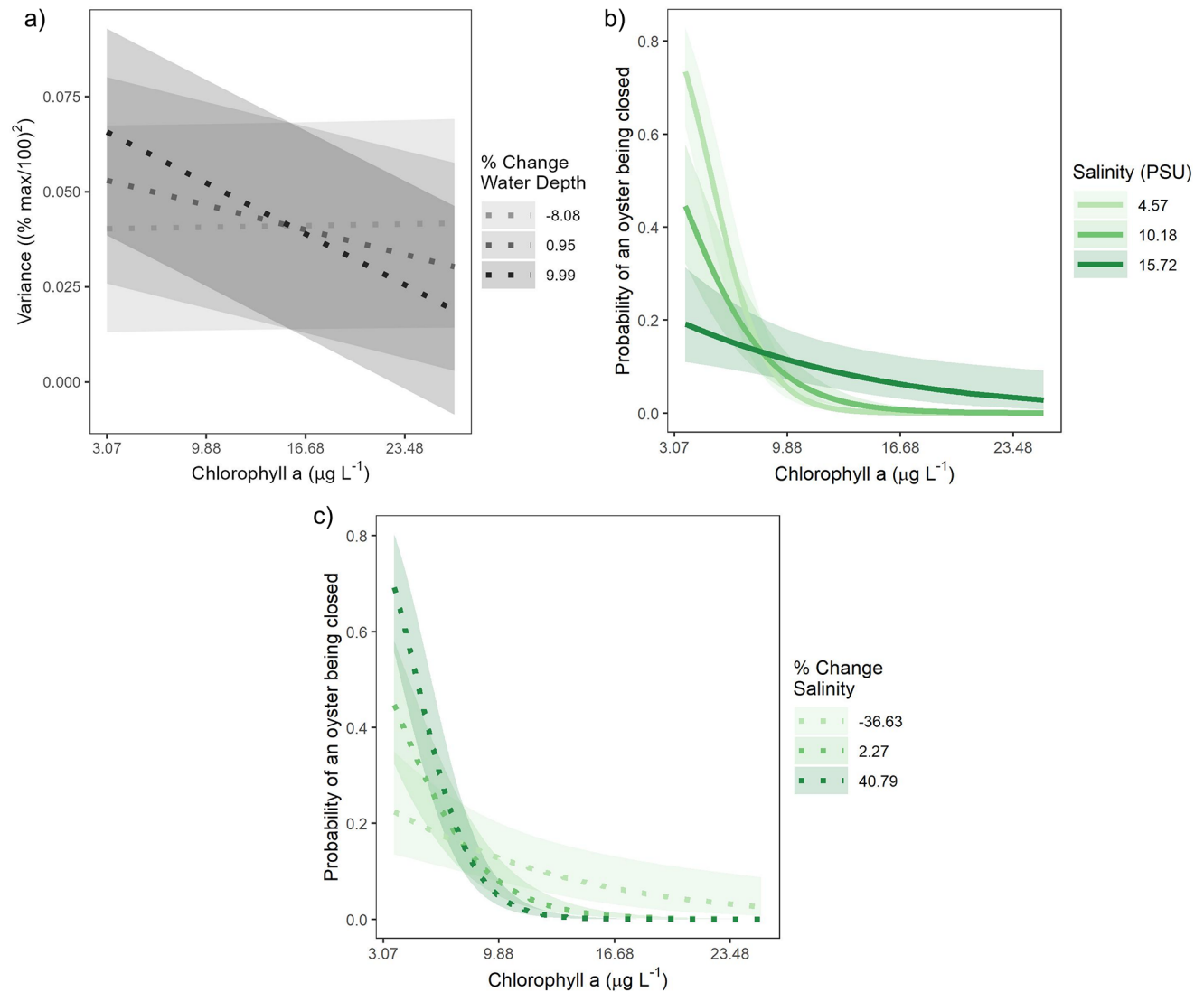


Fig. 3 Modeled interactions between chlorophyll-a (chl-a) concentration and the rate of change of water depth on the variance in oysters' behavior (a), and between chl-a concentration and salinity (b) and chl-a concentration and the rate of change of salinity (c) on the prob-

ability of an oyster being closed. Plotted values are conditional effects generated using the `ggpredict` function from the `ggeffects` package in R (Lüdtke 2018). PSU = practical salinity units. Shading represents the 95% confidence interval

oysters being more likely to be closed when chl-a concentration was low ($\sim 4 \mu\text{g L}^{-1}$; $\beta = -1.10$, 95% CI = -1.20 to -0.90 , $z = -12.00$, $p < 0.001$). This relationship was weaker at higher salinities (> 15 ; $\beta = 0.96$, 95% CI = 0.77 to 1.15 , $z = 9.80$, $p < 0.001$; Fig. 3b) or when salinity was rapidly decreasing ($\beta = -0.83$, 95% CI = -1.02 to -0.64 , $z = -8.60$, $p < 0.001$; Fig. 3c), as oysters were less likely to be closed at low chl-a concentrations under those conditions.

Rate of change of chlorophyll-a concentration Rising chl-a concentration increased variance among oysters ($\beta = 0.0023$, 95% CI = 0.0017 to 0.0029 , $t_{31000} = 7.60$, $p < 0.001$; Fig. 2a). Conversely, the rate of change in chl-a concentration did not significantly influence the rate of valve closure ($\beta = 0.036$,

95% CI = -0.069 to -0.142 , $z = 0.67$, $p = 0.5$; Fig. 2b). While rising chl-a concentration increased the probability that an oyster would be closed ($\beta = 0.39$, 95% CI = 0.23 to 0.55 , $z = 4.80$, $p < 0.001$; Fig. 2c), this relationship was dramatically reduced at high salinities ($\beta = -0.42$, 95% CI = -0.56 to -0.28 , $z = 6.00$, $p < 0.001$) and reversed when the water temperature was cooler ($\beta = 0.72$, 95% CI = 0.57 to 0.88 , $z = 9.00$, $p < 0.001$).

Temperature

Similar to chl-a concentrations, warmer temperatures ($\sim 26 \text{ }^\circ\text{C}$) decreased variance among oysters ($\beta = -0.0013$,

95% CI = -0.0025 to -0.0013 , $t_{31000} = -6.20$, $p < 0.001$). However, several other environmental variables influenced this relationship (Table S2). When salinity was higher, temperature had no effect on variance ($\beta = 0.0021$, 95% CI = 0.0014 to 0.0028 , $t_{31000} = 6.00$, $p < 0.001$; Fig. 4a) and when salinity was rapidly increasing, variance increased at warmer temperatures ($\beta = 0.0055$, 95% CI = 0.0048 to 0.0061 , $t_{31000} = 16.00$, $p < 0.001$; Fig. 4b). Temperature alone had no effect on the rate of valve closure ($\beta = -0.023$, 95% CI = -0.105 to 0.059 , $z = -0.54$, $p = 0.54$) but it did influence how salinity (Fig. 4c) and the rate of change of temperature (Fig. 4d) affect the rate of valve closure. At low temperatures (~ 14 °C), oysters closed more quickly in high salinities (> 20) than in low salinities (< 8), but at high temperatures (~ 26 °C), oysters closed at a similar rate, regardless of salinity ($\beta = -0.17$, 95% CI = -0.20 to -0.15 , $z = -13.00$, $p < 0.001$; Fig. 4c). The interactive effect of the rate of change of temperature was small, but significant ($\beta = 0.16$, 95% CI = 0.27 to -0.06 , $z = -3.6$, $p = 0.002$). Oyster closure rate decreased with increasing temperature when water temperatures were steady or rising, but when water temperatures were falling valve closure rates were higher at higher temperatures (> 23 °C) (Fig. 4d). Warmer temperatures also decreased the probability that an oyster would be closed ($\beta = -0.55$, 95% CI = -0.70 to -0.41 , $z = -7.5$, $p < 0.001$), but several other variables interacted with temperature to influence this pattern (Table S4). When salinity was low (< 5 ; Fig. 4e), or chl-a concentration was rapidly increasing (Fig. 4f), this pattern reversed, and the oysters were more likely to be closed at warmer temperatures. There was no relationship between water temperature and the probably that an oyster would be closed when temperatures were decreasing, or when salinity or water depth were increasing (Table S4).

Rate of change of temperature Rising temperatures increased variance among oysters ($\beta = 0.0054$, 95% CI = 0.0049 to 0.0060 , $t_{31000} = -19.00$, $p < 0.001$, Fig. 2a) and decreased the rate of valve closure ($\beta = -0.15$, 95% CI = -0.25 to -0.04 , $z = -2.77$, $p = 0.01$; Fig. 2b). The effect of rising temperatures on the rate of valve closure was modified by temperature, as discussed in the previous section. The rate of change in water temperature also had no direct effect on the probability of an oyster being closed (Table S4), but the interaction between the rate of change in water temperature and temperature did ($\beta = -0.28$, 95% CI = -0.43 to -0.12 , $z = -3.50$, $p < 0.001$). At lower temperatures, oysters were more likely to be closed when temperatures were

rising rapidly; the reverse was true when temperatures were warmer.

Salinity

At higher salinities (~ 23 and above) variance in behavior was higher ($\beta = 0.0037$, 95% CI = 0.0028 to 0.0047 , $t_{31000} = 7.60$, $p < 0.001$; Fig. 2a). The relationship between variance and salinity was significantly modified by the rate of change of salinity ($\beta = 0.0065$, 95% CI = 0.0057 to 0.0073 , $t_{31000} = 17.00$, $p < 0.001$; Fig. 5a) so that when salinity was decreasing oyster VOB was less variable at higher salinities than at lower salinities (~ 4). This constituted the largest effect on inter-individual variability (Fig. 2a). The rates of change of water depth ($\beta = -0.0044$, 95% CI = -0.0050 to -0.0039 , $t_{31000} = -16.00$, $p < 0.001$; Fig. 5b) and temperature ($\beta = -0.0034$, 95% CI = -0.0040 to -0.00285 , $t_{31000} = -12.00$, $p < 0.001$; Fig. 5c) also interacted significantly with salinity. There was no relationship between variance and salinity when water depth or temperature were rising. Oysters closed faster at higher salinities ($\beta = 0.33$, 95% CI = 0.24 to 0.42 , $z = 2.74$, $p < 0.001$; Fig. 2b) and this amounted to the largest effect on rate of valve closure. Finally, the probability of an oyster being closed was higher at higher salinities (Fig. 2c). This relationship was altered by chl-a concentration ($\beta = 0.96$, 95% CI = 0.77 to 1.15 , $z = 9.81$, $p < 0.001$; Fig. 5d) as well as the rates of change of chl-a concentration ($\beta = -0.42$, 95% CI = -0.56 to -0.28 , $z = -6.02$, $p < 0.001$; Fig. 5f) and salinity ($\beta = 0.89$, 95% CI = 0.71 to 1.08 , $z = 9.30$, $p < 0.001$, Fig. 5e) in opposite ways. At higher salinities, high (> 12 $\mu\text{g L}^{-1}$) or decreasing chl-a concentrations or rising salinities increased the probability that an oyster would be closed; at lower salinities, low (< 6 $\mu\text{g L}^{-1}$) or rising chl-a concentrations or decreasing salinities increased the probability that an oyster would be closed.

Rate of change of salinity The rate of change of salinity had no direct effect on variance among oysters ($\beta = -0.00015$, 95% CI = -0.00071 to 0.00041 , $t_{31000} = -0.52$, $p = 0.6$; Fig. 2a) but decreased the rate of valve closure ($\beta = -0.23$, 95% CI = -0.35 to -0.11 , $z = -3.75$, $p < 0.001$; Fig. 2b) and the probability that an oyster would be closed ($\beta = -0.31$, 95% CI = -0.46 to -0.16 , $z = -4.04$, $p < 0.001$; Fig. 2c). The rate of change of salinity interacted significantly with other environmental variables to influence variance (Table S2), the rate of valve closure (Table S3), and the probability

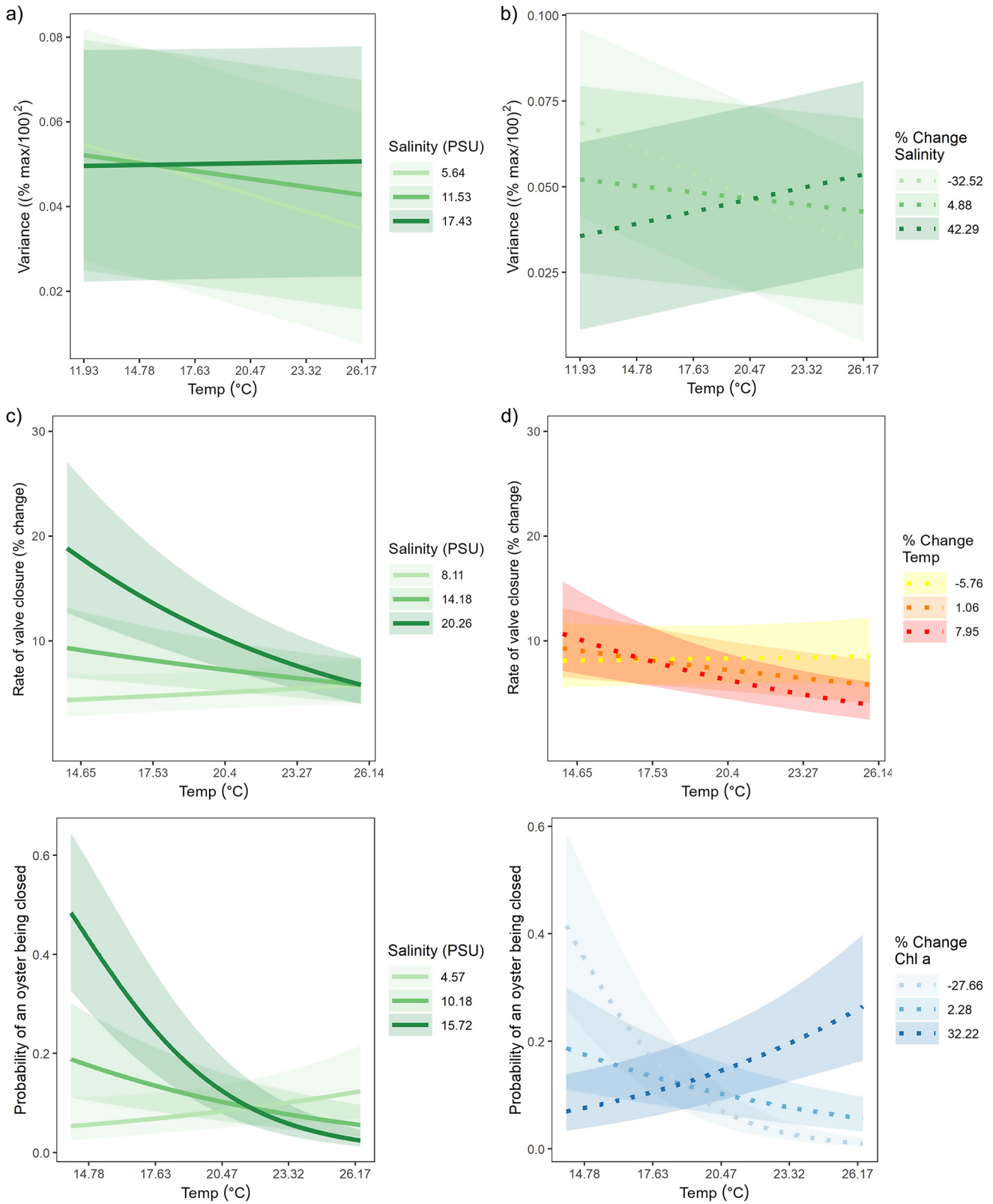


Fig. 4 Modeled interactions between temperature and salinity (a) and temperature and the rate of change of salinity (b) on the variance in oysters' behavior, between temperature and salinity (c) and temperature and the rate of change of temperature (d) on the rate of valve closure, and between temperature and salinity (e) and temperature and

the rate of change of chlorophyll-a concentration (f) on the probability of an oyster being closed. Plotted values are conditional effects generated using the `ggpredict` function from the `ggeffects` package in R (Lüdtke 2018). PSU = practical salinity units. Shading represents the 95% confidence interval

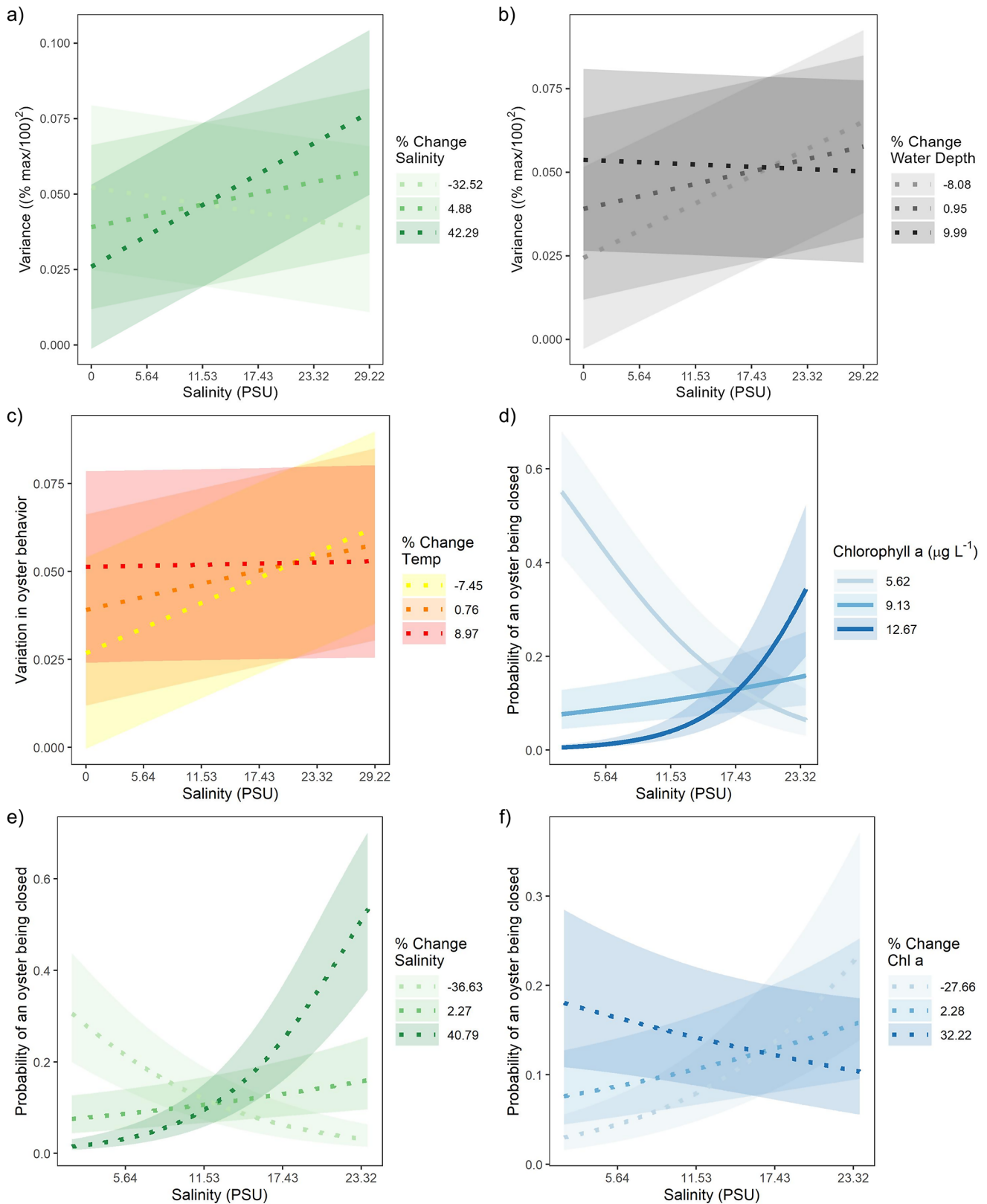


Fig. 5 Modeled interactions between salinity and its rate of change (a), salinity and the rate of change of water depth (b), and salinity and the rate of change of temperature (c) on the variance in oysters’ behavior, and between salinity and the chlorophyll-a (chl-a) concentration (d), salinity and its rate of change (e) and salinity and the rate of change

of chl-a concentration (f) on the probability of an oyster being closed. Plotted values are conditional effects generated using the ggpredict function from the ggeffects package in R (Lüdtke 2018). PSU=practical salinity units. Shading represents the 95% confidence interval

that an oyster would be closed (Table S4); all these interactions are described in the above sections.

Rate of change of water depth

Rising water depth increased variance among oysters ($\beta=0.0058$, 95% CI=0.0053 to 0.0063, $t_{31000}=22.00$, $p<0.001$; Fig. 2a) and the probability that an oyster would be closed ($\beta=-0.70$, 95% CI = -0.01 to -0.04 , $z=-4.80$, $p<0.001$; Fig. 2c), but had no effect on the rate of valve closure (Fig. 2b). The rate of change of water depth interacted significantly with other environmental variables to influence variance among oysters (Table S2), the rate of valve closure (Table S3), and the probability that an oyster would be closed (Table S4); all these interactions are described above.

Discussion

In this study, we present the first quantitative evaluation of the effects of multiple environmental variables on the VOB of eastern oysters under typical estuarine conditions in Louisiana, United States. The simultaneous and continuous monitoring of VOB and temperature, salinity, chlorophyll-a (chl-a) concentration, DO concentration, and the rate of change in these variables and in water depth allowed the characterization of the complexity of the response of oysters to fluctuations in surrounding environmental conditions. As VOB directly influences basic physiological functions such as respiration and feeding in bivalves, which in turn determine growth and reproduction success (Payton et al. 2017; Casas et al. 2018a; Tonk et al. 2023), our findings provide valuable insight into the interpretation of physiological data, the improvement of bioenergetic model simulations, and the management of fisheries and restoration initiatives.

Each of the four environmental variables examined and their rate of change influenced oyster VOB separately, but several significant two-way interactions between variables were found to influence the direction or the magnitude of these relationships. This highlights the complexity of the response of oysters to environmental factors, particularly as scientists in past decades have focused on relating VOB to single environmental conditions (Clements et al. 2018; Lassoued et al. 2021; Tran et al. 2010; Lavaud et al. 2021; Kramer and Foekema 2001; Hartmann et al., 2016; Chambon et al. 2007; Charifi et al. 2017; Hubert et al., 2023). Our study encompassed close to two months of continuous recording, corresponding to 4,608 data points for environmental factors and more than 4 million gape angle values for each oyster (averaged each 15 min to match the resolution

of the environmental data). No extreme or known thresholds that represent conditions outside of the eastern oyster's tolerance range where mortality is expected were observed: temperature remained well below 30 °C, salinity never fell below 3.0, and chl-a concentration never decreased below 3.7 $\mu\text{g L}^{-1}$ (Table 1). As such, these results are good indicators of conditions in which oysters are known to thrive in Louisiana. Moreover, despite being somewhat restricted in time, our monitoring captured the overall range and variability in average environmental conditions encountered throughout a year (Lowe et al., 2017).

Among the three VOB metrics analyzed (variance in oysters' behavior, rate of valve closure, and probability of an oyster being closed), variance in oysters' behavior was the least affected by environmental variation as shown by the lowest range of effect sizes on this metric (Fig. 2). This observation is noteworthy considering the relatively small sample size ($n=8$). Synchronism in valve opening in eastern oysters has previously been reported in relation to changes in temperature and light intensity (Comeau et al. 2012). Variance in oysters' behavior did increase when environmental variables tended toward physiologically stressful conditions. The interaction between salinity and its rate of change (Fig. 5a) had the largest effect on variance in oysters' behavior. Variation between individuals was more important at high salinity when salinity was increasing and at low salinity when salinity was decreasing. Conversely, low variance was observed at low salinity when salinity was increasing and at high salinity when salinity was decreasing. This pattern can be explained by the fact that the differences between the physiological capacity of individual oysters are likely to be revealed under conditions at the extremes of the species tolerance range. This is also evidenced by previous studies describing population differences in tolerance to various salinities in the northern Gulf of Mexico (Marshall et al. 2021b; Swam et al. 2022).

Salinity was also, by far, the main factor influencing the rate of valve closure in our study (Fig. 2b). This result underscores the role of salinity as a major driver of oyster ecophysiology even within a range of typical spring salinity conditions in southeastern Louisiana estuaries in which oysters generally thrive (3.2–23.9; Table 1; Fig. 1; Lowe et al., 2017). Salinity is a well-documented driver of the ecological and physiological responses of eastern oysters (Loosanoff 1953; Shumway 1996; Casas et al. 2018a; Marshall et al. 2021b; Swam et al. 2022), and field studies have indicated that low salinity events (<5) may cause mortality events in Louisiana or adjacent waters (La Peyre et al., 2013; Gledhill et al. 2020). In our study, oysters were less likely to be closed at lower salinities (<5) than at higher salinities (>17). This observation contradicts the expectation that oysters would close when exposed to lower salinity.

Moreover, as salinity remained above 3.2 and did not change abruptly over the course of this monitoring (which may not be outside the oyster's tolerance range), oysters may have acclimated to such gradual changes. This aligns with observations by Marshall et al. (2021b), who recorded no mortality from oysters gradually exposed to a salinity of 2. Slower rates of valve closure were also measured at low salinities, which could reflect negative effects of low salinity on cellular metabolism (through disruption of intracellular ion and acid base regulation), as was reported for gill ciliary activity (van Winkle 1972) and clearance rates (Casas et al. 2018a) at the same salinity (5). Additionally, the rate of closure may have been affected indirectly by salinity through the presence of predators around the cages. Oyster predators include black drums, mud and blue crabs, and shell drilling snails, which are usually more abundant at higher salinity (White and Wilson 1996; Brown and Richardson 1988; Brown et al. 2008).

Food availability is usually considered not limiting for oysters in southeast Louisiana given elevated phytoplankton concentrations (D'Sa 2014; Turner et al. 2019). Oysters closed their valves more rapidly at higher chl-a concentrations, possibly to unclog their gills. Despite high concentrations (mean of $10 \mu\text{g L}^{-1} \pm 3.7 \text{ sd}$), lower chl-a concentrations increased the probability of an oyster being closed ($\sim 4 \mu\text{g L}^{-1}$; Fig. 2c). Most bivalves typically close their valves or drastically reduce their gaping amplitude to decrease clearance rates at low chl-a concentrations (Strohmeier et al. 2009; Comeau et al. 2012; Tonk et al. 2023) to conserve energy. Furthermore, the interaction between chl-a concentration and salinity (Fig. 5d) also had a large effect on the probability of an oyster being closed (Fig. 2c). Oysters remained open at low salinity when chl-a concentration was high but not at low chl-a concentrations. This effect on VOB could be mechanistically linked to the energetic physiology of oysters through a trade-off between being open and feeding (accumulating energy) versus being closed to avoid osmotic stress and fast (depleting energy). As osmoconformers, salinity variations trigger a physiological response involving the transport or synthesis of amino acids and ions, which may incur high energy expenditure (although no clear quantitative data exist to our knowledge). Oysters generally close their valves for these physiological processes to take place gradually (Hand and Stickle 1977; McFarland et al. 2013). During these closing phases, no feeding occurs, which was identified as the main effect of low salinity on oysters' energy budgets (Lavaud et al. 2017). So, as salinity changes, valve closure could be controlled by the energetic status of oysters, which could determine whether they remain open to fuel the energetic demand from osmoconforming or close and rely on existing reserves. A similar mechanism was hypothesized in a bioenergetic

model to account for the impact of salinity on the energy budget of oysters in the region (Lavaud et al. 2017). Our results confirm this assumption. The probability of an oyster being closed even seemed to increase at median chl-a concentration (10%; Fig. 5d), suggesting a threshold in the balance between energy uptake and consumption despite the high food availability in these estuarine conditions. Adding support to this hypothesis is the fact that clearance rates are higher at high salinity (above 6–9; Casas et al. 2018a); as oysters trap more food (and non-food) particles through their gills, they may need to close to process and ingest large amounts of food at higher chl-a concentration. Recently, Ledoux et al. (2023) measured glycogen content along with the gaping response of mussels exposed to acoustic stress, but neither acute nor longer-term correlations were found. Further investigations of bivalve's responses to salinity could provide valuable insights into the suggested links between VOB and the energetic physiology of oysters.

In the analysis, we also explored the potential relationships between the measured environmental variables and the probability of oysters opening, but most monitored variables had little effect. This can be expected as the closing of valves secludes the animal from the surrounding water, making the organism unable to assess any change in environmental conditions. Some authors mentioned that once closed, bivalves may "test the water" before re-opening or re-open slowly (Kramer and Foekema 2001; Tran et al. 2010). The individual VOB dynamics in the present study clearly showed that oysters re-opened quickly (between consecutive 15-min intervals) and at wide angles when doing so (Figure S1), indicating that the animals did not slightly open their valves to evaluate environmental conditions before opening again. The main difference between our study and the previous work mentioned above is that we conducted our investigations under conditions thought to be within the physiological tolerances of the animals. Exposure to harsher conditions, such as toxic algae blooms, hurricanes or freshwater discharge from river diversions, may produce different results. Nevertheless, a closed oyster may well perceive thermal variations, as shell valves do not act as thermal barriers. This may also explain why the interactive effect of temperature and water depth had the strongest effect on the probability of opening. In another study on eastern oysters in Canada, Comeau et al. (2012) reported a correlation between temperature and valve re-opening after a long period of 'quiescence' over the winter. After being either closed or slightly open during the quiescent phase, the oysters abruptly awakened and opened to maximum angles when temperature rose. Further investigations, possibly including measurements of anaerobic metabolic products (e.g., alanine and succinate concentrations), could help to

better understand the factors leading to the re-opening of oysters following closure.

Because DO concentration and water depth were correlated with other variables analyzed, we did not investigate their role on oyster VOB in our analysis (but the role of the rate of change in water depth on oyster VOB was investigated, see Sect. 2.3.1). Like chl-a concentration, DO concentration did not reach any known threshold impacting oyster physiology, typically assumed around 2 mg L^{-1} (Porter and Breitbart 2016; Coxe et al., 2023). However, this threshold is known to vary with temperature, activity level, and exposure time (Deutsch et al., 2020; Seibel et al., 2021). Combining VOB and metabolic rate measurements could provide valuable insight into the effect of DO concentrations on VOB, particularly as increases in temperatures, hypoxic events, and freshwater runoff from river management are expected in the future (Rabalais and Turner 2019). The water depth in Louisiana estuaries is strongly impacted by winds and weather systems, which is illustrated by the broken cyclical pattern in this variable (Fig. 1) and could explain why we did not observe a clear tidal pattern in VOB. The monitoring of spawning activity could also provide valuable insight to interpret VOB (Payton et al. 2017), although such analysis is usually destructive. More studies of the VOB of oysters, and generally sessile bivalves, in relation with variations in environmental conditions could help to better identify thresholds (possibly population or geographically specific) in the physiological tolerance range of organisms triggering a behavioral response. Extreme or prolonged events affecting oyster off-bottom aquaculture could be managed through real-time warning systems as is being done with other bivalve species that trigger pollution alerts (Vereycken and Aldridge 2023). This knowledge can also be used as an input for bioenergetics models as VOB directly influences energy acquisition (Lavaud et al. 2017, 2021). As we aim to understand and explain the complex effects of environmental variables and their interactions on oyster VOB and ultimately on their life traits, such a mechanistic approach could be a valuable tool to integrate this complexity.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00227-024-04488-1>.

Acknowledgements We would like to thank Kim de Mutsert, two anonymous reviewers and an external reviewer for their comments. The authors thank Amanda Fontenot for providing verified environmental monitoring data. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Author contributions Funding for the study was acquired by Stephanie Archer, Megan La Peyre, and Jerome La Peyre. Study conceptualization and methodology were performed by Romain Lavaud, Stephanie

Archer, Megan La Peyre, Sandra Casas, and Jerome La Peyre. Formal analysis, data curation, visualization, and original draft writing were conducted by Romain Lavaud and Stephanie Archer. Software and resources were provided by Stephanie Archer. All authors contributed to the investigation and manuscript review and editing.

Funding Funding for this study included LA Sea Grant, the U.S. Geological Survey South Central Climate Adaptation Science Center, the Louisiana Department of Wildlife and Fisheries, the U.S. Geological Survey, LUMCON and the Louisiana Fish and Wildlife Cooperative Research Unit.

Data availability Data collected during this study may be shared upon reasonable request.

Declarations

Competing interests We declare no conflict of interest.

Animal welfare No ethics approval was needed for this study.

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