Carryover effects and feeding behavior of Atlantic surfclams in response to climate change

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ABSTRACT

Temperature and food availability play large roles in bivalve energetics. Understanding bivalve responses to variability in temperature and food availability (i.e., phytoplankton), is important as climate change leads to ocean warming and changes in phytoplankton production. However, few studies address how changes in seasonal temperature regimes, such as an elevated fall or accelerated spring temperature regime affect bivalves via carryover effects, whereby response signals are detected months following temperature regime exposure. Few studies also address how bivalve feeding preferences may respond to variability in temperature and food availability. Here, controlled laboratory experiments simulated climate changed-induced fall and spring temperature regimes for Atlantic surfclams, *Spisula solidissima solidissima*. A variety of physiological responses were measured, including scope for growth, gonad development and feeding behavior, plus preferences for different phytoplankton groups. Carryover effects were observed where surfclams that experienced an elevated (+ 3.0 °C) fall temperature regime yielded enhanced gonad development the following spring (i.e., > 6 months later). An accelerated spring temperature regime (a more rapid temperature increase to 17 °C from 7 °C) also impacted surfclam scope for growth. Temperature was the primary driver of surfclam clearance rates, but food concentration was the primary driver of surfclam feeding preferences. Surfclams displayed preferential selection of diatoms and chlorophytes over cryptophytes and cyanobacteria, but increased food availability led to decreased selection of diatoms and a relative increase in the uptake of cyanobacteria. These results suggest that climate change induced alterations in food availability and seasonal temperature regimes may affect surfclam metabolism, reproduction and feeding preferences.

1. Introduction

Ocean warming (OW) is a prime feature of climate change. Of typical concern for marine organisms is increasing summer temperatures, as summer typically represents a period when an organism is most likely to eclipse thermal thresholds or hit critical thermal maxima (Jansen et al., 2007; Madeira et al., 2015; Richard et al., 2012). Summer temperatures are also important for reproduction, particularly for broadcast spawning marine invertebrates, as gametogenesis can increase with temperature, until thresholds are reached (Bayne, 1975), often yielding summer spawning events (Lubet, 1994; Porter, 1971). Therefore, many laboratory experiments interested in assessing OW impacts on marine organisms employ approaches where organisms are chronically exposed to a discrete increase in summer temperature (Hornstein et al., 2018). While it is important to understand the impacts of discrete temperature increases on organisms, it is also important to understand the impacts of changing temperature regimes during various seasons. For example, understanding the impact of an accelerated spring temperature regime (i.e., a spring during which water temperature increases more rapidly) on an organism that reproduces in the summer may provide insight regarding OW effects on processes related to obtaining and storing energy for growth and reproduction (Bhaud et al., 1995; Brockington and Clarke, 2001). However, few studies have assessed the impacts of OW-induced seasonal temperature regime changes on marine fauna (but see Fischer and Thatje, 2008; Schmalenbach and Franke, 2010).

Changes in seasonal temperature regimes may produce lagged biological responses after exposure, analogous to carryover effects whereby past environmental conditions may impact present biological states (Norris, 2005; O'Connor et al., 2014). Carryover effects may be considered from multiple timespans, that is, within- and between-

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generation carryover effects, as well as within- and between- life stage carryover effects (Donelan et al., 2023; O'Connor et al., 2014). Although within generation carryover effects, sometimes referred to as legacy effects, occur at relatively shorter time scales, they may be particularly important when considering delayed impacts of seasonal temperature regimes, as previously described (Donelan et al., 2023; Neylan et al., 2023).

Bivalves are of particular interest regarding climate change impacts. Not only do bivalves provide many ecosystem services and valuable fisheries (Beaumont et al., 2007; Grabowski et al., 2012; van der Schatte Olivier et al., 2020), but they are ectothermic organisms for which energy acquisition is closely tied to temperature (Kittner and Riisgård, 2005; McLusky, 1972; Riisgård and Seerup, 2003). Furthermore, many bivalves, including the Atlantic surfclam *Spisula solidissima solidissima*, are broadcast spawners that build up gonad reserves for at least one season to allow for successful summer spawning (Hornstein, 2010; Ropes, 1968). Surfclams are found in continental shelf waters in the northwest Atlantic and rarely experience salinities below 28 parts per thousand (Castagna, 1973). Adult growth declines when temperatures eclipse 20 °C, with complete mortality occurring at temperatures >28 °C (Hornstein et al., 2018; Munroe et al., 2016; Spruck et al., 1995). Subsequently, surfclams are known to be thermally sensitive and have displayed negative responses to OW in the northwest Atlantic (Hennen et al., 2018; Munroe et al., 2016; Narváez et al., 2015). However, the impact of dynamic (i.e., accelerated or elevated) spring and fall temperature regimes on surfclams is unknown. Therefore, surfclams represent an ideal species to assess impacts of OW-induced seasonal temperature regime changes, as previously described.

Linked to how ectotherms may respond to OW is food availability and/or feeding behavior. For suspension feeding bivalves, food often comes in the form of seston, and more specifically (although not exclusively) phytoplankton. Previous studies have demonstrated that harmful OW effects on bivalves can be offset by increased energy acquisition (Cheng et al., 2018; Cole et al., 2016; Czaja Jr. et al., 2023; Kang et al., 2016). Additionally, climate change may alter phytoplankton production, and subsequently, bivalve food quality and quantity. It is therefore important to consider how changes in food availability may affect bivalves. While the impacts of food variability on bivalve ecophysiology have been studied for nearly half a century (Bayne, 1975; Bayne and Newell, 1983), few studies have assessed how changes in food availability may affect bivalve feeding preferences. Bivalve feeding preferences and their governing mechanisms also have been studied for nearly a century (Dean, 1887; Hunt, 1925); however, how such preferences may change in response to climate change and environmental variability is relatively unknown (Vargas et al., 2013). This is particularly important as future phytoplankton community structures are expected to shift, potentially from diatom-dominated communities, which bivalves preferentially clear, to nanoplankton dominated communities, which are not preferentially cleared (Dean, 1887; Hunt, 1925; Møhlenberg and Riisgård, 1978), likely due to stratification-induced nutrient limitations (Hare et al., 2007; Henson et al., 2021; Rahman et al., 2020).

A series of seasonal lab experiments and measurements, also including field deployment to assess seasonal carryover effects, was conducted to address four specific objectives (Supp. Fig. 1). The first two objectives of this study were to test if an elevated fall temperature regime (objective one) and/or an accelerated spring temperature regime (objective two), both implemented via lab manipulations, affect the physiology of surfclams. The third objective of this study was to explore whether fluctuations in temperature and food availability can regulate surfclam clearance rate (CR). Finally, the fourth objective was to detect feeding preferences (or lack of) in surfclams based on phytoplankton groups, while also considering if feeding preferences change with temperature and food availability. Together, these objectives test the hypothesis that seasonal temperature regimes, as altered by climate change, and food availability variability will affect surfclam

ecophysiology, namely metabolic activity and feeding behavior.

2. Materials and methods

2.1. General design

These objectives were accomplished via two laboratory experiments. The first experiment examined seasonal carryover (measured six months after treatment exposure) effects to a warmer fall (~3.0 °C > ambient temperatures) by simulating an ambient fall temperature regime, a warm fall temperature regime, and measuring surfclam physiological responses the following spring (i.e., objective one). For the second experiment, physiological responses to an accelerated spring (i.e., a more rapid increase in temperature from 7 to 17 °C) were assessed by simulating an ambient spring temperature regime, an accelerated spring temperature treatment, and measuring surfclam physiological responses after 45 and 30 days, respectively (i.e., objective two). Throughout the first (fall) experiment, tank level CR was monitored to assess if natural fluctuations in temperature and food availability can be related to CR (i. e., objective three). Throughout the second (spring) experiment, clearance, ingestion and rejection rates of different phytoplankton groups were monitored to assess if natural fluctuations in temperature and food availability can be related to surfclam feeding preferences (i.e., objective four).

2.2. Objective one design (Fall temperature regime)

For the fall experiment, the physiological effects of a warm fall were tested by simulating two fall temperature regime treatments: ambient and warm fall temperature (~3.0 °C above ambient) regimes. Adult surfclams (9.69 ± 0.65, cm in length, average ± stdv,) were retrieved from local fishermen on October 10, 2020. Surfclams were caught near Moriches, NY (40.716332°N, 72.893426°W). They were housed in two flow-through tanks at Stony Brook University's Southampton Marine Station (Southampton, NY) from October 10 to December 21, 2020. The flow-through line delivered raw seawater from the adjacent Old Fort Pond. Tank A contained 40 surfclams and experienced ambient, flow-through temperatures to simulate an ambient fall temperature regime. Tank B contained 40 surfclams and experienced elevated, manipulated, flow-through temperatures (~3.0 °C > ambient) to simulate a warm fall temperature regime (Fig. 1A). Temperatures were controlled via a titanium plate heat exchange system (conceptually similar to counter current heat exchange) such that a boiler applies heat to freshwater, which then applies heat to natural seawater. Ten days were allowed for acclimation before temperature regime exposure began. Surfclams were placed in PVC clam holders to remain upright (Supp. Fig. 2). Tanks were cleaned to remove accumulated sediment and particles every other day. Onset Hobo temperature loggers were placed in each tank to record temperatures every 60 min. Following treatment exposure in the lab, surfclams were deployed on December 21, 2020 in the field in a total eight of oyster bags (10 clams/bag), yielding $N = 4$ per treatment such that the oyster bag is the experimental unit. Field exposure was conducted so that surfclams experienced uniform, natural winter and spring conditions. Oyster bags were deployed in Three Mile Harbor, East Hampton, NY (41.026856°N, 72.180749°W). This site was chosen as it provides easy access via the East Hampton Town Shellfish Hatchery, experiences consistent, high salinities (relative to other local harbors) and experiences high flow, which not only simulates natural surfclam habitat, but prevents winter freezing and maintains high food availability (pers. comm. John -Barley- Dunne). Nevertheless, since this location does not represent a true natural surfclam habitat, interpretations are limited to between-treatment outcomes, and limit extrapolation of outcomes that may be affected by environmental differences between a typical surfclam habitat and the study site. Surfclams were collected from the field the following spring on May 23, 2021 (i.e. ~6 months post field deployment). Following collection, physiological
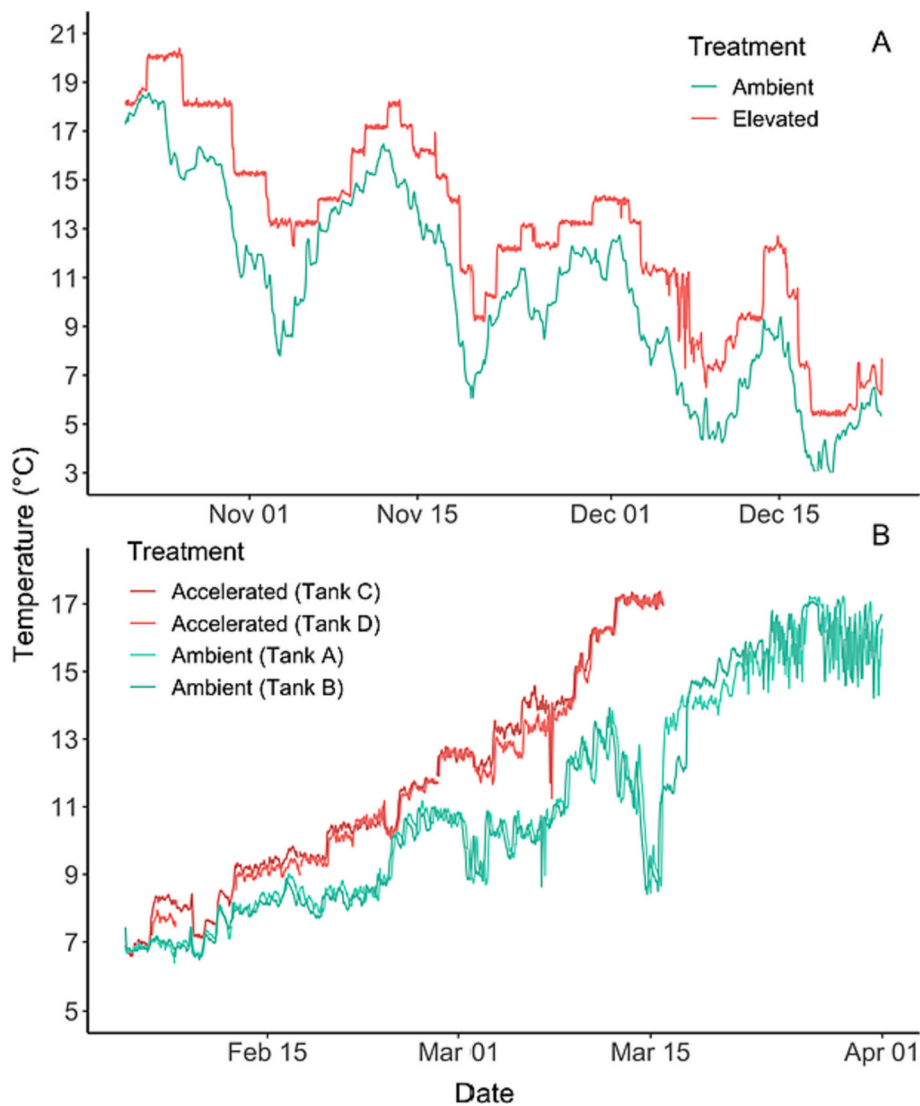
Fig. 1. Temperature trends from two tanks from the fall experiment simulating ambient and elevated fall temperature regimes (A), and from four tanks from the spring experiment simulating ambient and accelerated spring temperature regimes (B).

measurements including survival percent (for each of four oyster bags per temperature treatment), condition indices (CI, for eight surfclams per temperature treatment), scope for growth (SFG, for six surfclams per temperature treatment), biochemical content of different tissues (for six surfclams per temperature treatment) and gonad stages (for eight surfclams per temperature treatment) were assessed (detailed below).

2.3. Objective two design (spring temperature regime)

For the spring thermal experiment, the physiological effects of an accelerated spring were tested by simulating two spring temperature treatments: ambient and accelerated spring temperature (i.e., a more rapid increase in temperature from 7 to 17 °C) regimes. These temperature regimes were chosen as NOAA buoy data (buoy 44,025) show that over the last 28 years, the average number of days in spring by which the temperature increased from 7 °C to 17 °C was 45 days and the shortest number of days for the same temperature increase was 30 days. Adult surfclams (9.44 ± 0.51, cm in length, avg. ± stdv) were retrieved from local fishermen on January 28, 2021. Surfclams were caught near Cape Cod, MA (42.141546°N, 70.203434°W). They were housed in four flow-through tanks, (Tanks A, B, C and D) each containing eight surfclams, at Southampton Marine Station (Southampton, NY) from January 28 to

March 29, 2021, yielding two tanks per temperature treatment. Tanks A and B experienced an ambient increasing spring temperature regime of about 1.0 °C every 4.5 days over 45 days (Fig. 1B). Tanks C and D experienced an accelerated increasing spring temperature regime of about 1.0 °C every 3.0 days over 30 days (Fig. 1B). Treatment exposure began on February 14, 2021 and ended on March 292,021 for the ambient treatment and on March 14, 2021 for the accelerated treatment. Two weeks were allowed for acclimation before temperature regime exposure began. Husbandry practices from objective one were applied to objective two. On the second to last day of the experiment (i.e., day 44 for surfclams from Tanks A and B and day 29 for surfclams from Tanks C and D), surfclams were measured for SFG (for ten surfclams per temperature treatment). On the last day of the experiment (i.e., following SFG assays), surfclams were dissected for condition indices (for 14 surfclams per temperature treatment), biochemical content of different tissues (for six surfclams per temperature treatment) and for gonad stages (for 14 surfclams per temperature treatment).

2.4. Physiological responses

To calculate SFG, respiration rate (RR), filtration rate (FR), absorption efficiency (AbE) and ammonia excretion (AmE) were measured.

Each assay (other than AbE) contained replicate controls without surf-clams to measure background oxygen loss, particle settlement, and ammonia production. RR was measured using Pyroscience Oxygen Sensor Spots. Surfclams were placed in individual, sealed two-liter plastic containers with UV-treated filtered (1 μm) seawater at room temperature (~17 °C). Oxygen sensor spots continuously measured oxygen concentrations for the entire period (1 to 2 h). Water homogeneity was ensured by manually, gently swirling containers every ten minutes. RR was calculated as the average oxygen loss per hour and was standardized to ash free dry weight (AFDW). Surfclams from the fall experiment began respiring within 15 min after placement into containers (as shown by real time sensor spot data inspection). These surfclams also drew down oxygen levels to levels <4.0 mg O_2/l after nearly 60 min. Therefore, fall RR assays lasted one hour. However, surfclams from the spring experiment began respiring later, and drew down oxygen at a lower rate. Therefore, spring RR assays lasted two hours, and RR was calculated from oxygen concentrations starting at 60 min and ending at 120 min. For SFG calculations, oxygen loss was transformed into energy calories assuming 1 mg O_2 = 3.38 cal (Elliott and Davison, 1975).

Immediately after RR assays, FR and AbE were measured by placing individual surfclams in five-liter plastic containers with natural seawater. Plastic containers were placed in the holding (flow-through) tanks so that the holding tanks could function as temperature-controlled baths. FR assays lasted three hours and five ml water samples were collected every 30 min. Water samples were fixed with 1% glutaraldehyde and stored at 4 °C until FlowCam analysis to measure particle concentrations. FlowCam samples were run with a FC300-FV FlowCell, a 4× objective lens, a flow rate of 0.1 ml/ 20 s (run for 0.2 ml) and a minimum particle length of two microns. Water homogeneity was ensured via magnetic stir bars. FR was standardized to AFDW and was calculated as ml/h as follows:

$$FR = V/t^* \ln (C_0/C_t).$$

where V is the volume of water on the container, t is time in hours, C_0 is initial particle concentration and C_t is end particle concentration (Coughlan, 1969; Shumway et al., 1985). Surfclams from the fall experiment gaped and began clearing water 15 to 30 min after being placed in containers. Surfclams also substantially drew down particle concentrations after 90 min. Therefore, for the fall experiment, particle concentrations at 30 and 90 min were used for FR calculations. However, surfclams from the spring experiment gaped and began clearing water 30 to 60 min after being placed in containers. Surfclams also drew down particle concentrations at slower rates than the fall experiment. Therefore, particle concentrations at 60 and 180 min were used for spring calculations. Water samples were not taken for caloric analysis. Therefore, to convert FR to calories per hour (for SFG calculations), a caloric content of 7.9 cal/l was assumed. This was assumed as Carlson (1978) found an average caloric content of 7.9. calories/l in natural water samples taken during the spring from Flax Pond, NY. While this assumption limits interpretations of the absolute values of SFG, it still allows for relative comparisons between treatments.

AbE was measured during FR assays. At the start and end of FR assays, 20 ml water samples were taken for measurements on available food. Feces were collected, using a pipette, also at the end FR assays. Samples were immediately filtered on weighed and pre-combusted (4 h at 450 °C in a muffle furnace) glass fiber filters and washed with a 6% solution of ammonium formate. Samples were dried at 50 °C for at least 72 h, weighed, and then combusted in a muffle furnace for 4 h at 450 °C and reweighed. AbE was calculated as follows:

$$AbE = (F - E)/[(1 - E) (F)].$$

where F is the AFDW:dry weight ratio (i.e., fraction of organic matter) in available food samples and E is the same ratio but for feces samples.

AmE was also measured during FR assays. At the start of FR assays, 20 ml water samples were taken for measurements on initial ammonia concentrations and then again at the end of FR assays for final ammonia concentrations. Ammonia concentrations were determined colorimetrically via the Megazyme Ammonia Assay Kit. For SFG calculations, energy loss due to AmE was transformed into energy units assuming 1 mg NH_4 = 5.94 cal (Elliott and Davison, 1975; Han et al., 2008). SFG was then calculated as follows and reported as cal/h:

$$SFG = (FR^* AbE) - (RR + AmE).$$

Following SFG assays, surfclams were measured, weighed, shucked and dissected for remaining physiological assays. Condition indices (CIs) were calculated as follows:

$$CI = ((dry \ meat \ weight/wet \ shell \ weight)^* 100).$$

Lipid composition was measured on gonad, gill, mantle and adductor muscle tissue. Lipids were measured gravimetrically via the Folch method (Folch et al., 1957). Glycogen was measured colorimetrically via the Sigma-Aldrich MAKO16 Glycogen Assay Kit on mantle tissue.

Visceral mass cross sections were taken for histology (gonad development) assessments. Tissues were placed in cassettes and fixed in formalin before being embedded in paraffin wax and sectioned (5 μm thickness). Sections were mounted on slides and stained with hematoxylin and eosin. Slides were then assessed to determine the gonad stage for each surfclam. Classification of gonad stages was based on Kim and Powell (2004). However, because of low sample sizes, a broader classification scheme was used for statistical analyses (see upcoming section) that grouped all gonad developmental stages as D and all spawning stages as S. Although it should be noted that only stage D2 was observed, and only S1 and S2 were observed.

2.5. Objective three design (feeding rates)

From October 28, 2021 to December 2, 2021 during the fall experiment, water samples were taken approximately every three days from the intake and outtake pipes of both flow-through tanks, as representative samples of available food and remaining food following feeding, respectively. By measuring the difference in particle concentrations between the intake and outtake pipes, the tank-level clearance rate (i.e., the difference in particle concentrations between both pipes) was estimated. Tank level clearance rate was quantified according to Filgueira et al. (2006) as follows:

$$Tank \ Level \ Clearance \ Rate = f^* [(C_i - C_0/C_i)].$$

where f is the flow rate through the tank in liters/h, and C_i and C_o are the particle concentrations of the inflow and outflow, respectively. Multiple measurement occasions occurred on an individual day, generally once each hour for three hours. For each measurement occasion, five 20-ml water samples were taken from each of the intake and outtake pipes. Preliminary analyses suggested that the running mean of particle concentrations leveled off at replicates of five samples (i.e., less than five samples yielded particle concentrations means that may not accurately represent the true value) (Supp. Fig. 3). Samples were fixed in 1% glutaraldehyde for FlowCam measurement of particle concentrations (see previous section for details of FlowCam particle count measurements). Measurements were repeated through time (every three days for approximately 30 days) allowing for natural fluctuations in both temperature and food availability in each tank. Temperature and food availability were quantified and noted for each sampling occasion. Food availability was quantified as the total particle concentration from the first intake sample. These measurements allowed for assessing if environmental factors (temperature and food availability) can predict tank level clearance (see upcoming statistical analyses section). Control measurements ($N = 3$ per tank) without surfclams in tanks were taken at the end of the experiment to account for background particle loss.

Particle loss (1.5–7.7%) was subtracted from observed clearance rates.

2.6. Objective four design (feeding preferences)

Throughout March of the spring experiment, approximately every four days, three to four surfclams from the ambient spring temperature regime were placed in individual containers (same as FR assays) filled with natural seawater for approximately three hours. This yielded three to four surfclams per trial, with six total trials (individual surfclams were only used for one trial). Water samples were taken from each container at time zero and after three hours. Pseudofeces were also collected after three hours. Water and pseudofeces (homogenized) samples were immediately run on a FACSCalibur flow cytometer (BD BioSciences, San Jose, California, USA). For each sample, 60 μl were analyzed for particle counts of different phytoplankton groups using 488-nm argon and 635 nm diode lasers for excitation. Flow cytometer gating for quantifying the relative abundances of difference phytoplankton groups was conducted according to Allam et al. (2021). Briefly, parameters of FL2 at 585 nm for phycoerythrin, FL3 at 675 nm for chlorophyll *a* and FL4 at 695 nm for phycocyanin allowed for identification of the broad phytoplankton groups of diatoms, chlorophytes, cryptophytes and cyanobacteria. For each phytoplankton group, the relative percent of that phytoplankton group to all phytoplankton particles was calculated. By quantifying the percent contribution of each phytoplankton group for water samples and pseudofeces samples, electivity indices (EI) were calculated to examine relative ingestion or rejection of different phytoplankton groups as follows:

$$EI = -[(P-S)/((P+S)-(2PS))]$$

where P is the proportion of the phytoplankton group of interest in pseudofeces samples and S is the proportion of the phytoplankton group of interest in water samples (Baker and Levinton, 2003; Jacobs, 1974). With this approach, EI values range between −1.0 and 1.0 where a negative value indicates phytoplankton group rejection, a positive value indicates phytoplankton group preferential ingestion and a value of zero represents no preference. The temperature and total available phytoplankton for each trial were also recorded. In addition to calculating EI values, Clearance Index (ClrI) values were calculated to detect if surfclams were selectively clearing phytoplankton groups. The same formula as EI calculations was used for ClrI calculations, but instead of P representing the proportion of the phytoplankton group of interest in pseudofeces, P represents the proportion of the phytoplankton group of interest remaining in the water after three hours of surfclam feeding activity.

2.7. Objective one and two (carryover effects) statistical analyses

For objective one, a *t*-test was used to evaluate the effect of fall temperature regime survival percent post field deployment. A nested ANOVA was used to evaluate the effect of fall and spring temperature regime on physiological responses including CI, SFG (and all four related metrics), lipid content (four tissue types) and glycogen content (mantle only). A Bonferroni correction was applied yielding an alpha level of 0.0045 (0.05/11) to account for nonindependence of 11 ANOVAs on individual physiological responses. For fall experiments, oyster bags were used as a nested factor, and for spring experiments, tanks were used as a nested factor. Diagnostic plots revealed departures from normality for survival percent, AbE, AmE, RR and fall biochemical contents. Therefore, an arcsine transformation was performed on survival percent and AbE (proportion data) values and a log+1 transformation was performed on values for remaining responses. To assess whether temperature regime affected gonad stage, a chi squared test was used.

2.8. Objective three and four (feeding behavior) statistical analyses

For objective three, mixed effects linear models were used to assess whether temperature, food availability, both variables and their interaction can best predict tank level CR, for each individual tank. Tanks were modeled individually to assess if outcomes differed between fall temperature treatments. Temperature and food availability were used as fixed factors, and date was used as a random factor to account for multiple CR measurements on the same date. The data also resembled time series data, as CR was typically measured every three to four days for one month. Therefore, temporal autocorrelation was considered. However, plots of residuals as a function of the time series displayed no clear temporal autocorrelation patterns (Supp. Fig. 3). Residual and quantile-quantile plots showed no significant deviations from normality and homoscedasticity for Tank A (Supp. Fig. 4A). However, such plots revealed nonlinearity in the residuals for Tank B (Supp. Fig. 4B). Therefore, a quadratic effect for temperature was added to the model to remove the hump shape in the residuals (Supp. Fig. 4C). The Akaike information criterion (AIC) and AIC weights were used to determine which model (i.e., temperature, food availability or both factors) was the best model for each tank given the data (Burnham and Anderson, 2004), such that the model with the lowest AIC and highest AIC weight was considered the best model given the data.

For objective four, to assess if surfclams exhibited phytoplankton selection preferences, a one-sample *t*-test was used (on average EI values for each phytoplankton group for each sampling occasion) to test the null hypothesis that selection of a particular phytoplankton group was equal to zero (i.e., no preference) (Baker and Levinton, 2003). A Bonferroni correction was applied yielding an alpha level of 0.0125 (0.05/4) to account for nonindependence of four *t*-tests on individual phytoplankton groups. To test the hypothesis that EI values differed between phytoplankton groups, a repeated measures ANOVA (as surfclams were measured repeatedly through time) was used to assess if phytoplankton group had a significant effect on EI values. Tukey's multiple comparison test was used to determine significant differences in EI values between individual phytoplankton groups. Weighted linear models were used to predict the average EI values (average of each day, as multiple trials were performed on multiple surfclams per day) for each phytoplankton group as functions of temperature and food availability. Interactions were not included due to low sample sizes ($N = 6$). Weights of the inverse variance of average EI values were used to give more weight to averages that were less variable. Weighted linear models were used in the same manner as the previous objective to determine which set of predictor variables (i.e., temperature and/or food availability) may best predict EI values. All preceding approaches were then repeated for ClrI values. Diagnostic plots confirmed that in general, EI and ClrI linear models did not experience substantial departures from normality and homogeneity of variance (Supp. Figs. 5 to 8). All analyses were conducted in R version 4.0.2 (Core, R., Team, 2020).

3. Results

3.1. Temperature regime and carryover effects

Fall temperature regimes generally matched the intended temperature difference of 3.0 °C (Fig. 1A), with an average temperature of 10.83 °C for the ambient treatment and an average temperature of 13.25 °C for the elevated treatment. Surfclam survival the following spring after 6 months of field deployment (following fall temperature regime exposure in the lab) was generally low (23.2, ± 15.1%, average ± stdev), with no significant differences between fall temperature treatments (Supp. Table 1, Supp. Fig. 9). No significant effects of fall temperature regime were found for CI, SFG (and all four related metrics), and all biochemical contents (Supp. Table 1, Fig. 2, Supp. Fig. 10). The chi-squared test revealed that gonad stages significantly varied with fall temperature treatment ($p = 0.0498$, Chi-squared = 6, df = 2,
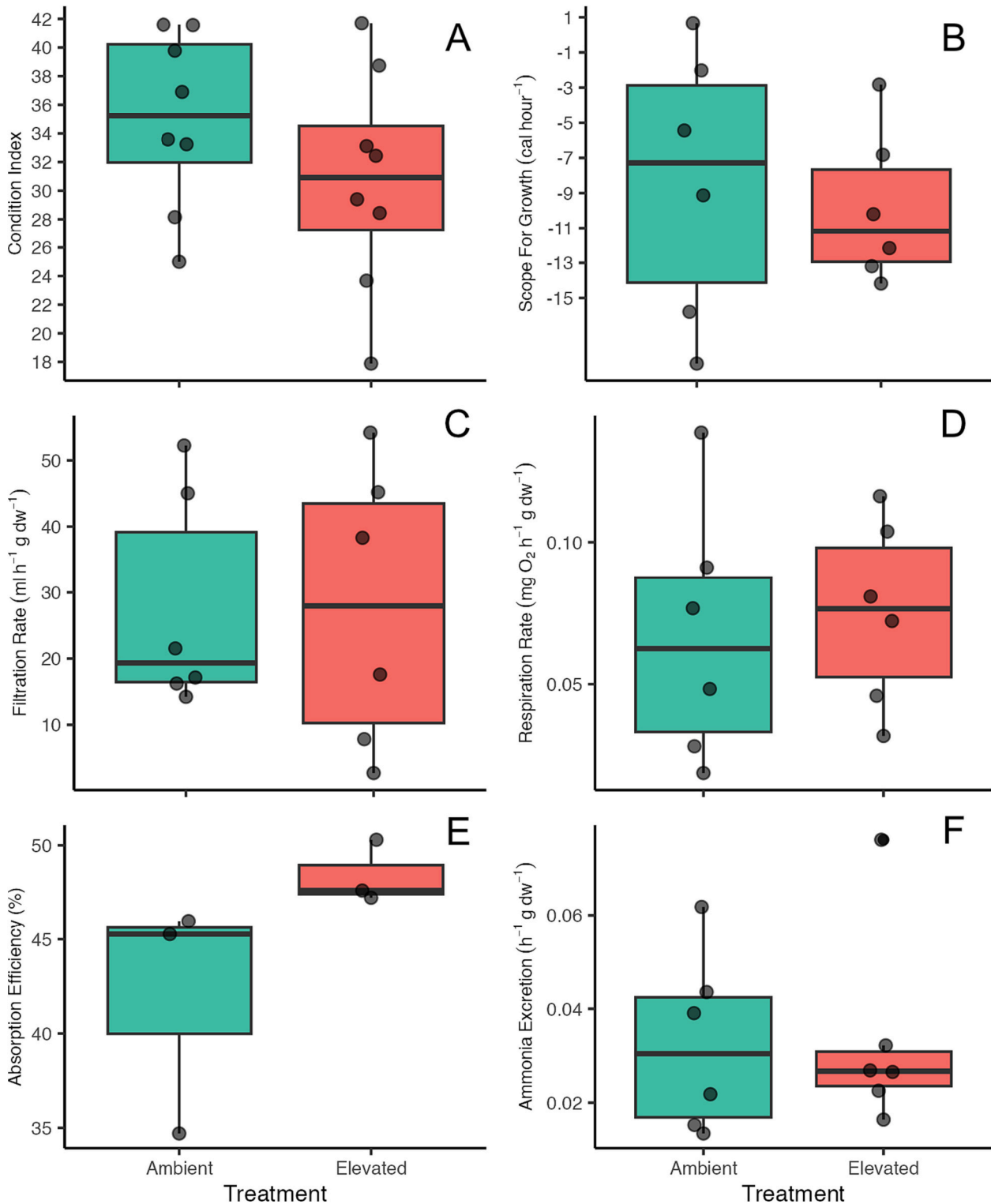
Fig. 2. Condition Index (A) and metabolic responses (B—F) from two treatments from the fall experiment. Metabolic responses include Scope for Growth (B), Filtration Rate (C), Respiration Rate, (D) Absorption Efficiency (E), and Ammonia Excretion (F). All rate responses are standardized to grams of dry tissue weight per hour. N = 6 for each treatment for each response, other than Condition Index (N = 8) and Absorption Efficiency (N = 3, due to lack of fecal production from multiple surfclams). No significant differences were detected.

Fig. 3A). More specifically, 50% of surfclams were in spawning stages for the elevated fall temperature treatment, but no surfclams were in spawning stages for the ambient fall temperature treatment (Fig. 3A).

Spring temperature regimes matched the intended temperature increases of 1.0 °C per day over 30 days for the accelerated treatment and

of 1.0 °C over 45 days for the ambient treatment (Fig. 1B). FR and SFG were significantly higher in the accelerated treatment than the ambient treatment (Supp. Table 1, Fig. 4). No significant effects of spring temperature regime were found for CI, RR, AmE and all biochemical contents (Supp. Table 1, Fig. 4, Supp. Fig. 10). The chi-squared test revealed
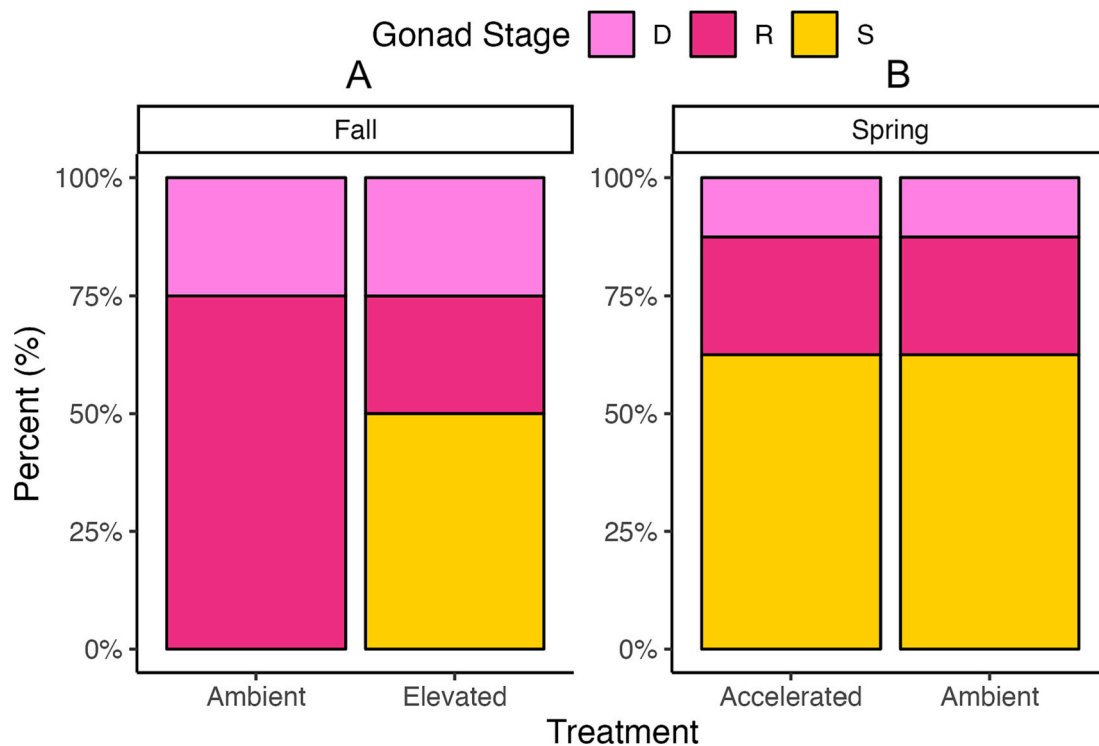
Fig. 3. Stacked boxplot of percent of surfclams displaying different gonad stages. Gonad stages come from two treatments from the fall experiment (left, ambient [N = 8] and elevated [N = 8] temperature regimes) and two treatments from the spring experiment (right, ambient [N = 14] and accelerated temperature regime [N = 14]). Gonad stages include Developing (D), Ripe (R), and Spawning (S).

that gonad stage did not vary with spring temperature treatment (p = 1.0, Chi-squared = 0, df = 2, Fig. 3B).

3.2. Feeding behavior responses

Throughout the fall experiment, tank level CR values were variable through time for the elevated treatment, ranging from 0 to 19 l/h (total of 40 surfclams, Fig. 5) Values were less variable through time for the ambient treatment, ranging from 0 to 11 l/h (total of 40 surfclams, Fig. 5). Temperature alone (without food availability) yielded the model with the lowest AIC and the highest AIC weight of all candidate models considered for predicting tank level CR for both fall temperature tanks (Supp. Table 2).

From the spring experiment, EI values for all four phytoplankton groups were significantly different than zero, indicating preferential selection and rejection (Fig. 6, Supp. Table 3). EI values for diatoms, chlorophytes and cryptophytes were consistently positive, indicating preferential selection and EI values for cyanobacteria were consistently negative, indicating preferential rejection (Fig. 6). A significant effect of phytoplankton group on EI values was detected (F$_{3,15}$ = 50.53, p = 4.5e-8), indicating different preferential selection among phytoplankton groups. Tukey's test revealed that EI values for diatoms and chlorophytes were significantly greater than that of cryptophytes and cyanobacteria, and EI values for cryptophytes were significantly greater than that of cyanobacteria (Fig. 6, Supp. Table 4). For chlorophytes, food availability alone (without temperature) yielded the model with the lowest AIC and highest AIC weight for predicting EI values (Table 1). For cryptophytes, the model with food availability alone produced the lowest AIC and highest AIC weight, however, temperature alone also produced a relatively low AIC and high AIC weight (Table 1). Both chlorophytes and cryptophytes yielded negative relationships with food availability (Table 1). For diatoms and cyanobacteria, food availability combined with temperature yielded the model with the lowest AIC and highest AIC weight, however, the models with temperature alone also

produced moderately high AIC weights, specifically for cyanobacteria (Table 1). Diatom EI values had negative relationships with both food availability and temperature and cyanobacteria EI values had a positive relationship with food availability but negative relationship with temperature (Table 1).

ClrI values for all phytoplankton groups were variable within and across dates, yielding weaker patterns relative to that of EI values (Fig. 7). Nevertheless, mean ClrI values were significantly different from zero for diatoms (Fig. 7, Supp. Table 3). ClrI values for diatoms were consistently positive, indicating preferential clearing (Fig. 7). A significant effect of phytoplankton group on ClrI values was not detected (F$_{3,15}$ = 2.629, p = 0.088). For chlorophytes, cyanobacteria and diatoms, temperature alone (without food availability) yielded the model with the lowest AIC and highest AIC weight for predicting ClrI values (Table 2). However, for chlorophytes, food availability alone also produced a relatively low AIC and high AIC weight (Table 2). Temperature yielded a positive relationship with ClrI values for chlorophytes and diatoms, but a negative relationship for cyanobacteria (Table 2). For cryptophytes, food availability alone (without temperature) yielded the model with the lowest AIC and highest AIC weight, including a positive relationship between cryptophyte ClrI values and food availability (Table 2).

4. Discussion

4.1. Responses to climate change

Simulated warming impacts on fall and spring temperature regimes had moderate effects on surfclam metabolic responses via seasonal carryover effects. Specifically, evidence was found to suggest that an elevated fall temperature regime may yield seasonal carryover effects with more rapid gonad development the following spring. An accelerated spring temperature regime may also yield short-term thermal carryover effects with increased scope for growth following temperature
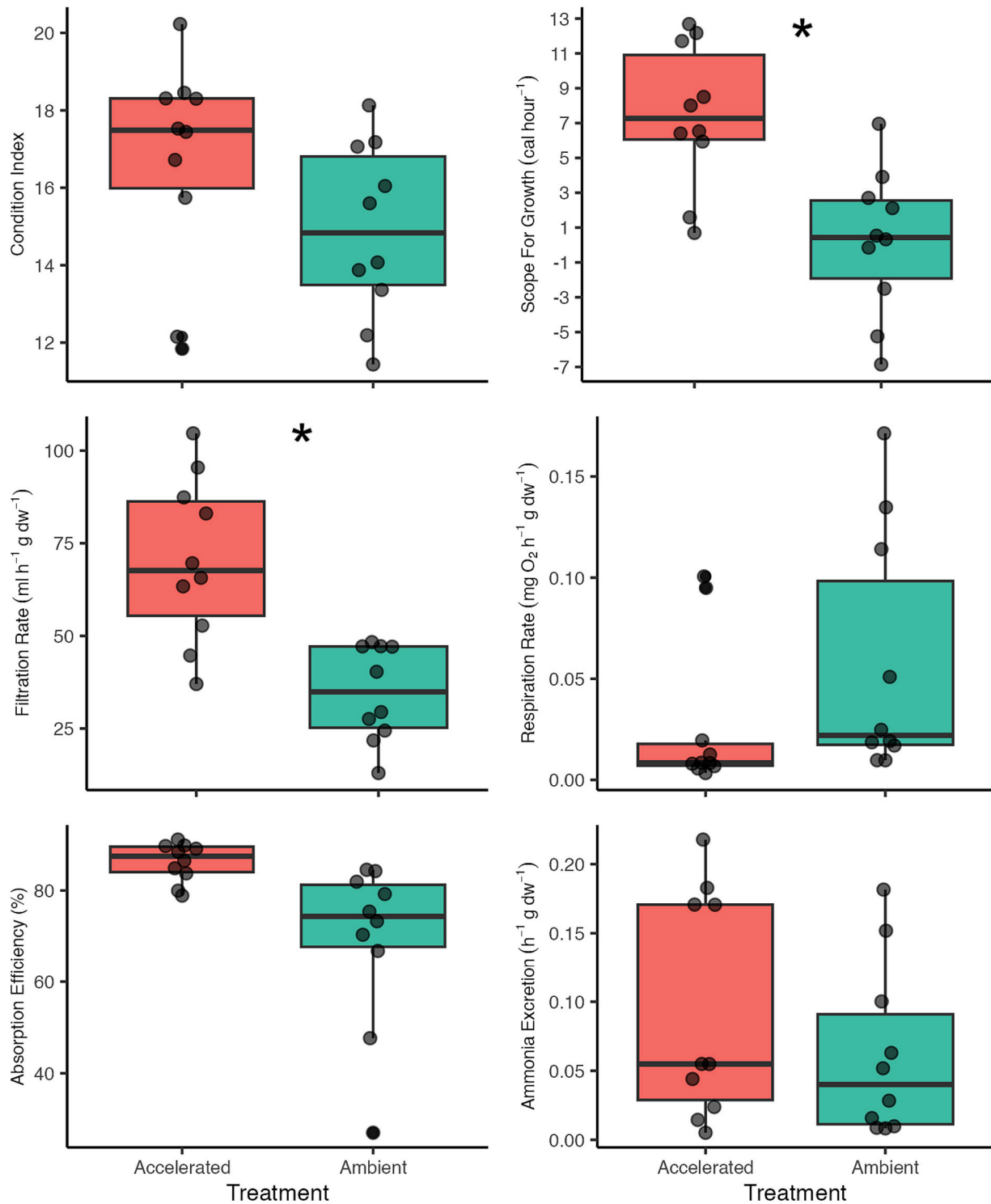
Fig. 4. Condition Index (A) and metabolic responses (B—F) from two treatments from the spring experiment. Metabolic responses include Scope for Growth (B), Filtration Rate (C), Respiration Rate (D), Absorption Efficiency (E), and Ammonia Excretion (F). All rate responses are standardized to grams of dry tissue weight per hour. $N = 10$ for each treatment for each response, other than Condition Index ($N = 14$). * denote significant differences.

regime exposure. Feeding behavior experiments showed that both clearance rate and phytoplankton prey preferences may be driven by temperature and food availability fluctuations. Temperature is more important than food availability for predicting surfclam clearance rates and surfclams may prefer diatoms and chlorophytes, but reject cyanobacteria. Furthermore, both temperature and food availability may affect phytoplankton preferences, with food availability playing a larger role in ingestion preferences and temperature playing a larger role in

clearing preferences. More specifically, increased food availability may decrease preferential ingestion of diatoms, chlorophytes and crypto-phytes and increased temperature may increase preferential clearing of diatoms and decrease clearing of cyanobacteria.

4.2. Thermal carryover effects

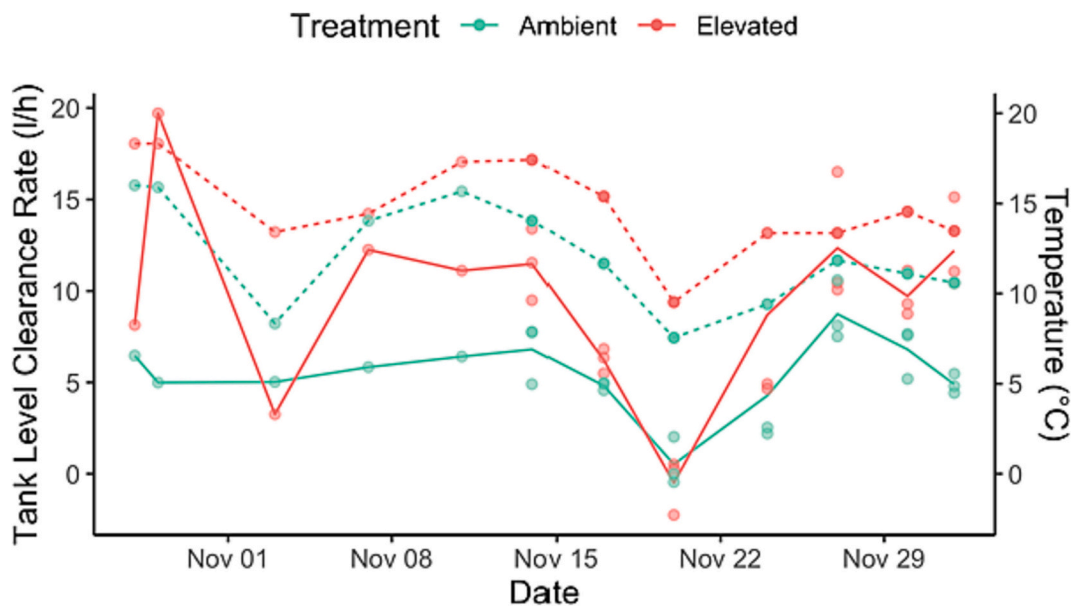The fall experiment revealed moderate gonad development

Fig. 5. Line plot displaying tank level clearance rate (solid lines, liters/h, left y-axis) through time for the fall experiment. Clearance rate points represent mean ($n =$ 3) values for each trial. Temperature through time (dashed lines, °C, right y-axis) for each temperature regime treatment is also displayed. Lines for tank level clearance rate go through the average value for each day. Individual data points for tank level clearance rate are also plotted, as after November 13, multiple measurements were taken each day.
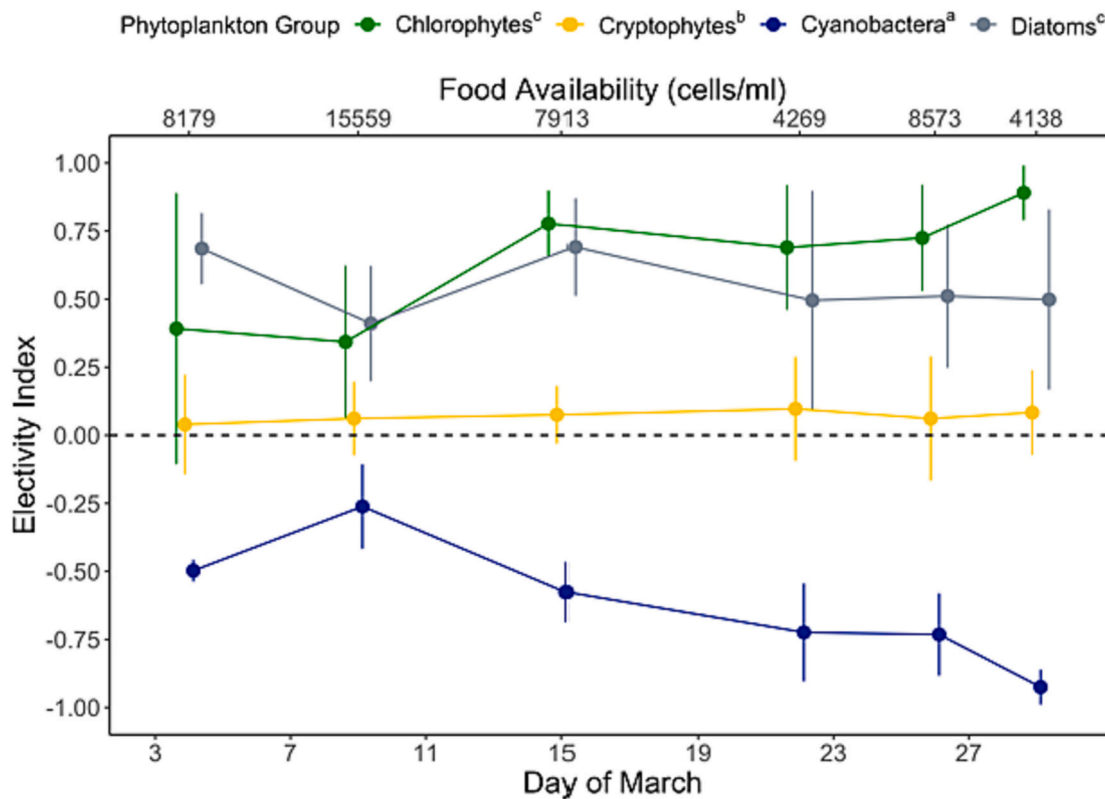

Fig. 6. Line plot displaying Electivity Index (EI) values, for each phytoplankton group, for each of six trials (dates) that occurred through March (spring experiment). Points represent mean (n = 3) EI values for each trial and vertical lines display standard deviation of the mean. The mean food availability, in cells/ml, corresponding with the date of each trial, is displayed on the secondary (top) x-axis. Different letters for different phytoplankton groups represent significant differences in mean EI values.

carryover effects, but minimal SFG carryover effects of an elevated fall temperature regime on surfclams the following spring. The latter outcome is not entirely surprising. A known thermal threshold for surfclams is 20 °C, after which, surfclam metabolic activity and growth is negatively impacted (Hornstein et al., 2018; Munroe et al., 2016). Fall temperatures during the present study never eclipsed 20 °C, therefore, surfclams were likely not encountering thermally stressful conditions. It is possible that if temperatures eclipsed 20 °C, decreased metabolic

Table 1

Output for linear regressions that model Electivity Index (EI) values for each phytoplankton group as a function of each environmental predictor variable (temperature or food availability), or both combined. AIC weights are displayed below AIC values in parentheses. Bolded models denote the highest AIC weight model for that phytoplankton group. $N = 6$ for each model.

| Phytoplankton Group	Model	AIC (AIC weights)	Multiple R^2	Adjusted R^2	Predictor Variable	Predictor p-value	Predictor Slope
Chlorophytes	Temp + Food	−3.62 (0.0)	0.730	0.550	Temp Food	0.798 0.084	−4.5e-3 −4.2e-5
	Temp	1.31 (0.03)	0.142	−0.073	Temp	0.462	0.017
	Food	**−5.47** (0.97)	**0.723**	**0.654**	**Food**	**0.032**	**−4.0e-5**
Cryptophytes	Temp + Food	−27.27 (0.0)	0.369	−0.052	Temp Food	0.704 0.375	1.1e-3 −1.9e-6
	Temp	−27.42 (0.32)	0.141	−0.073	Temp	0.463	0.002
	Food	**−28.93** (0.68)	**0.332**	**0.165**	**Food**	**0.232**	**−2.5e-6**
Cyanobacteria	**Temp + Food**	**−11.97** (0.52)	**0.972**	**0.953**	**Temp** **Food**	**0.023** **0.022**	**−3.7e-2** **4.5e-5**
	Temp	−2.04 (0.48)	0.795	0.744	Temp	0.017	−0.062
	Food	−2.20 (0.0)	0.800	0.750	Food	0.016	7.3e-5
Diatoms	**Temp + Food**	**−13.37** (0.83)	**0.893**	**0.822**	**Temp** **Food**	**0.024** **0.054**	**−3.4e-2** **−2.1e-5**
	Temp	−6.76 (0.17)	0.550	0.438	Temp	0.091	−0.031
	Food	−3.59 (0.0)	0.238	0.047	Food	0.327	−1.7e-5
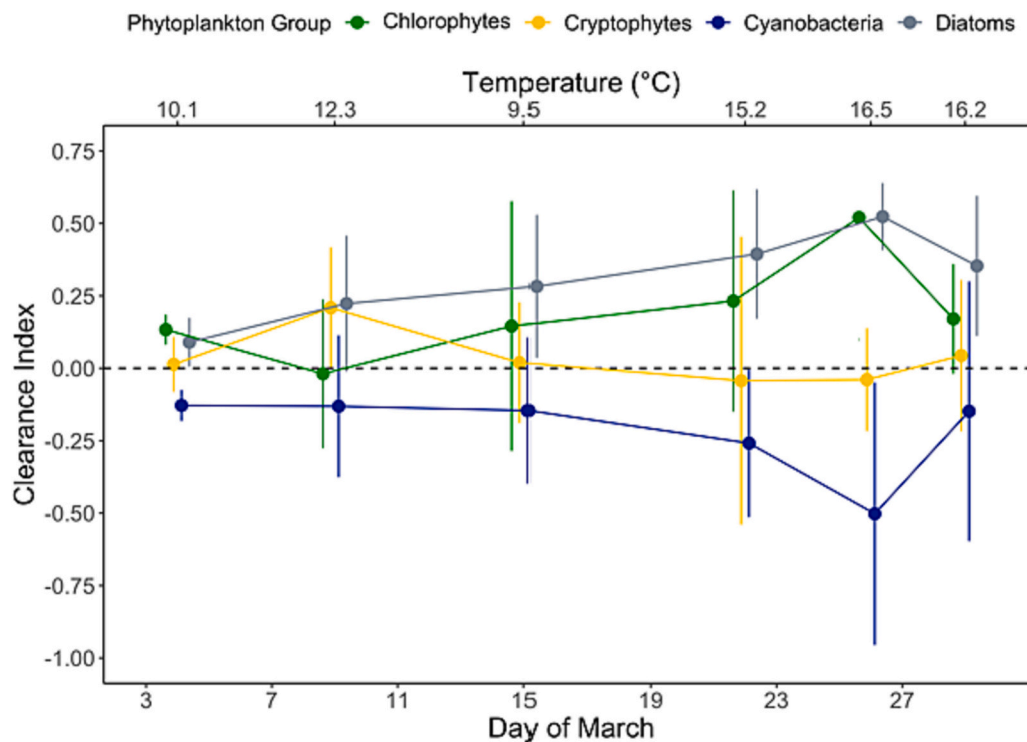
Fig. 7. Line plot displaying Clearance Index (ClrI) values, for each phytoplankton group, for each of six trials (dates) that occurred through March (spring experiment). Points represent mean (n = 3) ClrI values for each trial and vertical lines display standard deviation of the mean. The mean temperature (°C) corresponding with the date of each trial, is displayed on the secondary (top) x-axis. No significant differences in mean ClrI values between phytoplankton groups were detected.

activity the following spring may have been observed. This hypothesis is supported by other studies documenting decreased metabolic activity of marine invertebrates, via carryover effects, after being exposed to stressful temperature regimes (Donelan et al., 2023; Harianto et al., 2021).

While results suggested minimal carryover effects in response to an

elevated fall temperature regime, an elevated fall temperature regime yielded more surfclams reaching the spawning stage at the end of the proceeding May. Increased FR during the fall leading to increased energy acquisition may have permitted increased energy allocation for gametogenesis, providing a potential mechanism for elevated fall temperatures yielding enhanced gonad production (MacDonald and

Table 2
Output for linear regressions that model Clearance Index values for each phytoplankton group as a function of each environmental predictor variable (temperature or food availability), or both combined. AIC weights are displayed below AIC values in parentheses. Bolded models denote the highest AIC weight model for that phytoplankton group. $N = 6$ for each model.

Phytoplankton Group	Model	AIC (AIC weights)	Multiple R^2	Adjusted R^2	Predictor Variable	Predictor p-value	Predictor Slope
Chlorophytes	Temp + Food	−2.31 (0.0)	0.296	−0.173	Temp	0.557	1.2e-2
					Food	0.638	−9.8e-6
	Temp	−3.79 (0.54)	0.233	0.041	Temp	0.333	0.016
	Food	−3.50 (0.46)	0.195	−0.007	Food	0.381	−1.5e-5
Cryptophytes	Temp + Food	−9.60 (0.0)	0.548	0.246	Temp	0.752	−3.1e-3
					Food	0.168	1.8e-5
	Temp	−7.17 (0.11)	0.053	−0.183	Temp	0.660	−0.005
	Food	−11.34 (0.89)	0.529	0.412	Food	0.101	1.8e-5
Cyanobacteria	Temp + Food	−7.75 (0.00)	0.604	0.400	Temp	0.129	−2.8e-2
					Food	0.904	1.6e-6
	Temp	−9.71 (0.93)	0.602	0.502	Temp	0.070	−0.029
	Food	−4.39 (0.07)	0.032	−0.210	Food	0.733	5.8e-6
Diatoms	Temp + Food	−6.58 (0.0)	0.912	0.854	Temp	0.011	6.1e-2
					Food	0.704	−6.3e-6
	Temp	−8.24 (1.0)	0.907	0.884	Temp	0.003	0.060
	Food	6.00 (0.0)	0.006	−0.243	Food	0.884	−6.8e-6

Thompson, 1986). These results have interesting implications for the surfclam fishery, as they suggest elevated fall temperatures may yield faster gonad development the following spring, and therefore earlier spawning. In the northeast U.S., surfclams occasionally produce a fall spawn, following the primary late spring/early summer spawn (Ma et al., 2006; Ropes, 1968; Weissberger and Grassle, 2003). If surfclams were to produce a primary spawn even earlier in the spring, that may allow for enhanced gonad development from late spring through the summer (i.e., after the primary spawn), assuming summer maxima do not exceed optimal temperatures for surfclams. This may allow for a potentially stronger fall spawn. Increased spawning output in the fall may increase total annual surfclam recruitment, a process that has been in decline for surfclams in recent decades due to climate change (Czaja et al., 2023). Although speculative, such effects may represent a potential positive impact of climate change on bivalve fisheries. It should be noted that such changes may yield negative consequences (e.g., increased exposure to predators during the vulnerable young-of-the-year stage). It should also be noted that experimental surfclams used in this study were deployed in a shallow coastal embayment that certainly warms faster than normal surfclam habitat. Therefore, while warming falls may still result in faster gonad development the following spring in normal surfclam habitat, such shifts will likely be lagged compared to this experiment.

The spring temperature regime experiment revealed that accelerated spring temperatures increased FR and SFG. Increases in FR may allow for increased energy acquisition before high summer temperature, potentially providing an energetic buffer against stressful summer conditions (Kang et al., 2022). Regarding SFG effects, trends in individual growth may produce similar trends in population growth, suggesting that future OW-induced accelerated spring temperature regimes can have positive effects on the surfclam fishery (Narváez et al., 2015; Thomas and Bacher, 2018). However, similar to the fall temperature regime experiment, such a positive outcome may only be experienced until temperatures surpass 20 °C. Few studies have assessed short term carryover effects of spring temperature regimes on marine invertebrates (see previous references), providing limited context for discussion. However, these results align with previous data regarding surfclam responses to spring temperatures. More specifically, Hornstein (2010) found that

during the spring of 2008, surfclam condition indices and biochemical contents were generally higher than that of 2009. Furthermore, spring sea surface temperature during 2008 increased from 10 °C to 20 °C over approximately 1.0 month, whereas, spring sea surface temperature during 2009 increased from 10 °C to 20 °C over approximately 1.5 months. It is therefore tempting to conclude that an accelerated spring temperature regime can be related to the observed increased condition indices and biochemical contents, which would align with the results of the present study. However, to firmly draw such conclusions, data from multiple years would be needed and additional factors (e.g., food availability, and as the present study mentions, temperatures during the preceding fall) should be considered. While temperature regime treatment comparison outcomes have implications for the natural environment, as previously described, caution should also be taken when extrapolating absolute values of responses to the natural environment and replication limitations should be considered. Specifically, survival in the field (following exposure to fall temperature treatments) was low, likely due to unnatural conditions of being physically constrained in an oyster bag. Additionally, SFG values were low and negative, likely due to caloric content assumptions of available food. Nevertheless, these experiments highlight potentially positive outcomes of OW-induced seasonal temperature regime changes.

While carryover effects of climate change conditions to the proceeding generation are frequently studied for marine invertebrates (Chi et al., 2021; Leung and McAfee, 2020; Ross et al., 2016 (and see references within); Uthicke et al., 2021), within generation and within life stage carryover effects receive less attention (see previous references). Although some recent within generation carryover effect studies include Long et al. (2023) who assessed ocean acidification carryover effects from the embryo stage to the larval stage for Alaskan snow crabs and Shen et al. (2022) who assessed hypoxia carryover effects from the larval stage to the grow out stage for Pacific abalone. This study therefore highlights that within generation carryover effects, and within life stage carryover effects, should receive increased consideration for future studies.

4.3. Feeding behavior responses

Results suggest that for surfclams, temperature may be more important than food availability in predicting CR. There is a vast literature documenting bivalve CR in response to climate change and environmental variability, specifically variability in temperature and food availability (see Bayne, 1993; Cranford et al., 2011 and references therein; Riisgård, 2001). Accordingly, results from the present experiments are not very surprising. Results also suggest that surfclams display feeding preferences for diatoms and a lack of preference for cyanobacteria. Accordingly, there is a vast literature documenting bivalve feeding preferences and their governing physiological mechanisms (Dean, 1887; Hunt, 1925; Møhlenberg and Riisgård, 1978). Many studies have found that bivalves display pre-ingestive selection for phytoplankton of larger sizes and superior nutritional quality, including diatoms (Beninger and Decottignies, 2005; Beninger et al., 2008; Hedberg et al., 2021), with external organic compound coatings playing large roles in selection (Pales Espinosa et al., 2022; Pales-Espinosa et al., 2016). However, very few studies assess how climate change and environmental variability may affect mollusk preferences for different phytoplankton, although Vargas et al. (2013) found that under ocean acidification conditions, *Concholepas concholepas* larvae ingested more cyanobacteria and less diatoms.

Results revealed that temperature and food availability play substantial roles in feeding preferences, with higher food availability leading to increased selection for cyanobacteria and decreased selection of diatoms, chlorophytes and cryptophytes and with higher temperatures leading to decreased selection for diatoms and cyanobacteria. These results may have implications for climate change impacts on bivalve feeding behavior. For example, climate change may lead to decreased primary production in continental shelf waters, which based on results from the present study, could lead to increased selection for diatoms, chlorophytes and cryptophytes (Henson et al., 2021). It is possible that as food becomes scarce, marine invertebrates employ more discriminate feeding behavior to select for preferred food items of higher nutritional quality (Navarro et al., 2003; Purroy et al., 2018).

In contrast, OW may lead to decreased selection for both diatoms and cyanobacteria. Contrary to the previously postulated food scarcity hypothesis, under thermal stress, marine invertebrates may employ less discriminate feeding behavior (Mitterwallner et al., 2021; Sotka and Giddens, 2009). This response may allow bivalves to combat temperature-induced metabolic stress by increasing net energy acquisition, regardless of the nutritional quality of the phytoplankton that may be ingested (Jørgensen, 1990), even though such mechanisms may be counterproductive as food selection usually serves to increase energy gain. These speculatory evolutionary mechanisms may present opportunities for further research, particularly in a climate change context.

The present study showed that temperature may affect variability in phytoplankton preferences by surfclams. However, the temperatures observed in the present study fall within the preferred range of surfclams, as surfclams respond negatively to temperatures >20 °C (Hornstein et al., 2018). Therefore, future studies may consider assessing particle or phytoplankton preferences in temperature ranges that exceed optimal thermal windows to aid in predicting how bivalves, and the economic and ecological services that they provide, may respond to climate change. For example, elevated temperatures may disrupt regulation or synthesis of proteins involved in bivalve particle selection, thereby having negative impacts on energy acquisition on bivalves, which may have cascading effects on their economic and ecological services (Niemisto et al., 2021). Additionally, relationships between surfclam feeding preferences and environmental variability were assessed with relatively low sample sizes, producing limitations for the present study. Future studies assessing climate change impacts on bivalve feeding preferences should consider increased sample sizes and increased experiment durations. Nevertheless, it is interesting to consider how climate change impacts on feeding behavior and diet may

cascade to population level effects. For example, changes in bivalve feeding activity may lead to changes in lipid and fatty acid content, thereby affecting energy devoted towards reproduction and ultimately recruitment (Bridier et al., 2023). Such population level consequences are speculative, but linking changes in feeding behavior to population level changes may also provide avenues for future research.

5. Conclusions

Assessing carryover effects and feeding preferences in response to temperature and food availability variability is becoming increasingly important as climate change warms the oceans and alters primary production. This study contributes to a better understanding of bivalve physiological responses to variability in temperature and food availability while focusing on within generation carryover effects and phytoplankton prey preferences in a climate change context. Results suggest that for Atlantic surfclams, an elevated fall temperature regime may accelerate gonad development the following spring through seasonal carryover effects. This outcome may present an example of positive climate change impacts on bivalve populations, as accelerated gonad development may allow for increased reproductive output and recruitment (Shephard et al., 2010; Weitere et al., 2009). Results also suggest that an accelerated spring temperature regime may lead to increased metabolic activity in surfclams. This outcome highlights another potential positive impact of climate change, as increased metabolic rates can lead to increased growth at the individual organism level, and potentially population level (Thomas and Bacher, 2018). Ingestion preference measurements also provide insight on surfclam diets, and surfclams, like many other bivalves, may prefer diatoms and chlorophytes over cyanobacteria. Furthermore, results suggest that variation in environmental factors including temperature and food availability, may affect surfclam feeding preferences, with food availability playing a larger role in ingestion preferences and temperature playing a larger role in clearing preferences. Such changes in feeding behavior may also affect growth at the individual and potentially population level (Fearman et al., 2009). The impacts of climate change on bivalve feeding preferences remains an understudied niche of bivalve ecophysiology, but may present an opportunity to unravel a deeper understanding of bivalve feeding behavior and to predict future bivalve responses to climate change.

CRediT authorship contribution statement

Raymond Czaja: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. **Emmanuelle Pales Espinosa:** Funding acquisition, Investigation, Methodology, Project administration, Resources, Writing – review & editing. **Robert M. Cerrato:** Formal analysis, Funding acquisition, Methodology, Resources, Writing – review & editing. **Bassem Allam:** Conceptualization, Data curation, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare no competing interests.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi. org/10.1016/j.jembe.2024.152002.

References

Allam, S., Allam, B., Pales Espinosa, E., 2021. Regulation of mucosal lectins in the oyster Crassostrea virginica in response to food availability and environmental factors. J. Molluscan Stud. 87.

Baker, S.M., Levinton, J.S., 2003. Selective feeding by three native north American freshwater mussels implies food competition with zebra mussels. Hydrobiologia 505, 97–105.

Bayne, B., 1975. Reproduction in Bivalve Molluscs under Environmental Stress. Physiological Ecology of Estuarine Organisms. University of South Carolina Press, Columbia, pp. 259–277.

Bayne, B.L., 1993. Feeding physiology of bivalves: time-dependence and compensation for changes in food availability, bivalve filter feeders. In: Estuarine and Coastal Ecosystem Processes. Springer, pp. 1–24.

Bayne, B., Newell, R., 1983. Physiological Energetics of Marine Molluscs, The Mollusca. Elsevier, pp. 407–515.

Beaumont, N., Austen, M., Atkins, J., Burdon, D., Degraer, S., Dentinho, T., Derous, S., Holm, P., Horton, T., Van Ierland, E., 2007. Identification, definition and quantification of goods and services provided by marine biodiversity: implications for the ecosystem approach. Mar. Pollut. Bull. 54, 253–265.

Beninger, P.G., Decottignies, P., 2005. What makes diatoms attractive for suspensivores? The organic casing and associated organic molecules of Coscinodiscus perforatus are quality cues for the bivalve Pecten maximus. J. Plankton Res. 27, 11–17.

Beninger, P.G., Valdizan, A., Cognie, B., Guiheneuf, F., Decottignies, P., 2008. Wanted: alive and not dead: functioning diatom status is a quality cue for the suspension-feeder Ecology and Evolution. J. Plankton Res. 30, 689–697.

Bhaud, M., Cha, J., Duchene, J., Nozais, C., 1995. Influence of temperature on the marine fauna: what can be expected from a climatic change. J. Therm. Biol. 20, 91–104.

Bridier, G., Olivier, F., Grall, J., Chauvaud, L., Sejr, M.K., Tremblay, R., 2023. Seasonal lipid dynamics of four Arctic bivalves: Implications for their physiological capacities to cope with future changes in coastal ecosystems. Ecol. Evol. 13, e10691.

Brockington, S., Clarke, A., 2001. The relative influence of temperature and food on the metabolism of a marine invertebrate. J. Exp. Mar. Biol. Ecol. 258, 87–99.

Burnham, K.P., Anderson, D.R., 2004. Multimodel inference: understanding AIC and BIC in model selection. Soc. Methods Res. 33, 261–304.

Carlson, D.M., 1978. The ecological role of zooplankton in a Long Island salt marsh. Estuaries 1, 85–92.

Castagna, M., 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.

Cheng, M.C., Sarà, G., Williams, G.A., 2018. Combined effects of thermal conditions and food availability on thermal tolerance of the marine bivalve, Perna viridis. J. Therm. Biol. 78, 270–276.

Chi, X., Shi, D., Ma, Z., Hu, F., Sun, J., Huang, X., Zhang, L., Chang, Y., Zhao, C., 2021. Carryover effects of long-term high water temperatures on fitness-related traits of the offspring of the sea urchin Strongylocentrotus intermedius. Mar. Environ. Res. 169 (105), 371.

Cole, V.J., Parker, L.M., O'Connor, S.J., O'Connor, W.A., Scanes, E., Byrne, M., Ross, P. M., 2016. Effects of multiple climate change stressors: ocean acidification interacts with warming, hyposalinity, and low food supply on the larvae of the brooding flat oyster Ostrea angasi. Mar. Biol. 163, 125.

Core, R., Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Coughlan, J., 1969. The estimation of filtering rate from the clearance of suspensions. Mar. Biol. 2, 356–358.

Cranford, P.J., Ward, J.E., Shumway, S.E., 2011. Bivalve filter feeding: variability and limits of the aquaculture biofilter. Shellfish Aquacult. Environ. 81–124.

Czaja Jr., R., Beal, B., Pepperman, K., Espinosa, E.P., Munroe, D., Cerrato, R., Busch, E., Allam, B., 2023. Interactive roles of temperature and food availability in predicting habitat suitability for marine invertebrates. Estuar. Cost. Shelf Sci. 108, 515.

Czaja, R.E., Hennen, D., Cerrato, R.M., Lwiza, K., Pales-Espinosa, E., O'Dwyer, J., Allam, B., 2023. Using LASSO regularization to project recruitment under CMIP6 climate scenarios in a coastal fishery with spatial oceanographic gradients. Can. J. Fish. Aquat. Sci. 80, 1032–1046.

Dean, B., 1887. The food of the oyster, its conditions and variations. In: Suppl. to 2nd Rept. Oyster Investigations, New York, NY, pp. 49–87.

Donelan, S.C., Ogburn, M.B., Breitburg, D., 2023. Legacy of past exposure to hypoxia and warming regulates an ecosystem service provided by oysters. Glob. Chang. Biol. 29, 1328–1339.

Elliott, J., Davison, W., 1975. Energy equivalents of oxygen consumption in animal energetics. Oecologia 19, 195–201.

Fearman, J.-A., Bolch, C.J., Moltschaniwskyj, N.A., 2009. Energy storage and reproduction in mussels, Mytilus galloprovincialis: the influence of diet quality. J. Shellfish Res. 28, 305–312.

Filgueira, R., Labarta, U., Fernandez-Reiriz, M.J., 2006. Flow-through chamber method for clearance rate measurements in bivalves: design and validation of individual chambers and mesocosm. Limnol. Oceanogr. Methods 4, 284–292.

Fischer, S., Thatje, S., 2008. Temperature-induced oviposition in the brachyuran crab Cancer setosus along a latitudinal cline: aquaria experiments and analysis of field-data. J. Exp. Mar. Biol. Ecol. 357, 157–164.

Folch, J., Lees, M., Sloane Stanley, G.H., 1957. A simple method for the isolation and purification of total lipids from animal tissues. J. Biol. Chem. 226, 497–509.

Grabowski, J.H., Brumbaugh, R.D., Conrad, R.F., Keeler, A.G., Opaluch, J.J., Peterson, C. H., Piehler, M.F., Powers, S.P., Smyth, A.R., 2012. Economic valuation of ecosystem services provided by oyster reefs. Bioscience 62, 900–909.

Han, K.N., Lee, S.W., Wang, S.Y., 2008. The effect of temperature on the energy budget of the Manila clam, Ruditapes philippinarum. Aquac. Int. 16, 143–152.

Hare, C.E., Leblanc, K., DiTullio, G.R., Kudela, R.M., Zhang, Y., Lee, P.A., Riseman, S., Hutchins, D.A., 2007. Consequences of increased temperature and CO2 for phytoplankton community structure in the Bering Sea. Mar. Ecol. Prog. Ser. 352, 9–16.

Harianto, J., Aldridge, J., Torres Gabarda, S.A., Grainger, R.J., Byrne, M., 2021. Impacts of acclimation in warm-low pH conditions on the physiology of the sea urchin Heliocidaris erythrogramma and carryover effects for juvenile offspring. Front. Mar. Sci. 7 (588), 938.

Hedberg, P., Albert, S., Nascimento, F.J., Winder, M., 2021. Effects of changing phytoplankton species composition on carbon and nitrogen uptake in benthic invertebrates. Limnol. Oceanogr. 66, 469–480.

Hennen, D.R., Mann, R., Munroe, D.M., Powell, E.N., 2018. Biological reference points for Atlantic surfclam (Spisula solidissima) in warming seas. Fish. Res. 207, 126–139.

Henson, S.A., Cael, B., Allen, S.R., Dutkiewicz, S., 2021. Future phytoplankton diversity in a changing climate. Nat. Commun. 12, 5372.

Hornstein, J., 2010. The Impact of Environmental Factors on the Physiology of the Atlantic surfclam, Spisula Solidissima. State University of New York at Stony Brook.

Hornstein, J., Espinosa, E.P., Cerrato, R.M., Lwiza, K.M., Allam, B., 2018. The influence of temperature stress on the physiology of the Atlantic surfclam, Spisula solidissima. Comp. Biochem. Physiol. A Mol. Integr. Physiol. 222, 66–73.

Hunt, O., 1925. The food of the bottom fauna of the Plymouth fishing grounds. J. Mar. Biol. Assoc. U. K. 13, 560–599.

Jacobs, J., 1974. Quantitative measurement of food selection. Oecologia 14, 413–417.

Jansen, J.M., Pronker, A.E., Kube, S., Sokolowski, A., Sola, J.C., Marquiegui, M.A., Schiedek, D., Bonga, S.W., Wolowicz, M., Hummel, H., 2007. Geographic and seasonal patterns and limits on the adaptive response to temperature of European Mytilus spp. and Macoma balthica populations. Oecologia 154, 23–34.

Jørgensen, C.B., 1990. Bivalve filter feeding: hydrodynamics, bioenergetics, physiology and ecology. Olsen & Olsen.

Kang, H.Y., Lee, Y.-J., Choi, K.-S., Park, H.J., Yun, S.-G., Kang, C.-K., 2016. Combined effects of temperature and seston concentration on the physiological energetics of the Manila clam Ruditapes philippinarum. PLoS One 11, e0152427.

Kang, H.Y., Seong, J., Kim, C., Lee, B.G., Lee, I.T., Kang, C.-K., 2022. Seasonal energetic physiology in the ark shell Anadara kagoshimensis in response to rising temperature. Front. Mar. Sci. 9 (981), 504.

Kim, Y., Powell, E.N., 2004. Surfclam histopathology survey along the Delmarva mortality line. J. Shellfish Res. 23, 429–442.

Kittner, C., Riisgård, H.U., 2005. Effect of temperature on filtration rate in the mussel Mytilus edulis: no evidence for temperature compensation. Mar. Ecol. Prog. Ser. 305, 147–152.

Leung, J.Y., McAfee, D., 2020. Stress across life stages: Impacts, responses and consequences for marine organisms. Sci. Total Environ. 700 (134), 491.

Long, W.C., Swiney, K.M., Foy, R.J., 2023. Direct, carryover, and maternal effects of ocean acidification on snow crab embryos and larvae. PLoS One 18, e0276360.

Lubet, P., 1994. Reproduction in molluscs. Aquacult.: Biol. Ecol. Cult. Spec. 138–173.

Ma, H., Grassle, J.P., Rosario, J.M., 2006. Initial recruitment and growth of surfclams (Spisula solidissima Dillwyn) on the inner continental shelf of New Jersey. J. Shellfish Res. 25, 481–489.

MacDonald, B., Thompson, R., 1986. Influence of temperature and food availability on the ecological energetics of the giant scallop Placopecten magellanicus: III. Physiological ecology, the gametogenic cycle and scope for growth. Mar. Biol. 93, 37–48.

Madeira, D., Mendonça, V., Dias, M., Roma, J., Costa, P.M., Larguinho, M., Vinagre, C., Diniz, M.S., 2015. Physiological, cellular and biochemical thermal stress response of intertidal shrimps with different vertical distributions: Palaemon elegans and Palaemon serratus. Comp. Biochem. Physiol. Par A Mol. Inegr. Physiol. 183, 107–115.

McLusky, D.S., 1972. The effect of temperature on the oxygen consumption and filtration rate of Chlamys (Aequipecten) opercularis (L.)(Bivalvia). Ophelia 10, 141–154.

Mitterwallner, V., Suci, A.N.N., Zamani, N., Lenz, M., 2021. Exposure to moderately elevated temperatures changes food preferences in the tropical marine herbivore Haliotis squamata. Mar. Biol. 168, 110.

Møhlenberg, F., Riisgård, H.U., 1978. Efficiency of particle retention in 13 species of suspension feeding bivalves. Ophelia 17, 239–246.

Munroe, D., Narváez, D., Hennen, D., Jacobson, L., Mann, R., Hofmann, E., Powell, E., Klinck, J., 2016. Fishing and bottom water temperature as drivers of change in maximum shell length in Atlantic surfclams (Spisula solidissima). Estuar. Cost. Shelf Sci. 170, 112–122.

Narváez, D.A., Munroe, D.M., Hofmann, E.E., Klinck, J.M., Powell, E.N., Mann, R., Curchitser, E., 2015. Long-term dynamics in Atlantic surfclam (Spisula solidissima) populations: the role of bottom water temperature. J. Mar. Syst. 141, 136–148.

Navarro, J.M., Labarta, U., Fernández-Reiriz, M.J., Velasco, A., 2003. Feeding behavior and differential absorption of biochemical components by the infaunal bivalve Mulinia edulis and the epibenthic Mytilus chilensis in response to changes in food regimes. J. Exp. Mar. Biol. Ecol. 287, 13–35.

Neylan, I.P., Swezey, D.S., Boles, S.E., Gross, J.A., Sih, A., Stachowicz, J.J., 2023. Within- and transgenerational stress legacy effects of ocean acidification on red abalone (*Haliotis rufescens*) growth and survival. Glob. Chang. Biol. e17048.

Niemisto, M., Fields, D.M., Clark, K.F., Waller, J.D., Greenwood, S.J., Wahle, R.A., 2021. American lobster postlarvae alter gene regulation in response to ocean warming and acidification. Ecol. Evol. 11, 806–819.

Norris, D.R., 2005. Carry-over effects and habitat quality in migratory populations. Oikos 109, 178–186.

O'Connor, C.M., Norris, D.R., Crossin, G.T., Cooke, S.J., 2014. Biological carryover effects: linking common concepts and mechanisms in ecology and evolution. Ecosphere 5, 1–11.

Pales Espinosa, E., Eckstein, M., Allam, B., 2022. Density of compatible ligands on the surface of food particles modulates sorting efficiency in the blue mussel *Mytilus edulis*. Front. Mar. Sci. 9 (882), 356.

Pales-Espinosa, E., Cerrato, R.M., Wikfors, G.H., Allam, B., 2016. Modeling food choice in the two suspension-feeding bivalves, *Crassostrea virginica* and *Mytilus edulis*. Mar. Biol. 163, 40.

Porter, R.G., 1971. Reproductive cycle of the soft-shell clam, *Mya arenaria*, at Skagit Bay, Washington. Fish. Bull. 72, 648.

Purroy, A., Najdek, M., Isla, E., Župan, I., Thébault, J., Peharda, M., 2018. Bivalve trophic ecology in the Mediterranean: Spatio-temporal variations and feeding behavior. Mar. Environ. Res. 142, 234–249.

Rahman, M., Henderson, S., Miller-Ezzy, P., Li, X., Qin, J., 2020. Analysis of the seasonal impact of three marine bivalves on seston particles in water column. J. Exp. Mar. Biol. Ecol. 522 (151), 251.

Richard, J., Morley, S.A., Thorne, M.A., Peck, L.S., 2012. Estimating long-term survival temperatures at the assemblage level in the marine environment: towards macrophysiology. PLoS One 7, e34655.

Riisgård, H.U., 2001. Comment: Physiological regulation versus autonomous filtration in filter-feeding bivalves: Starting points for progress. Ophelia 54, 193–209.

Riisgård, H.U., Seerup, D.F., 2003. Filtration rates in the soft clam *Mya arenaria*: effects of temperature and body size. Sarsia 88, 416–428.

Ropes, J.W., 1968. Reproductive cycle of the surf clam, *Spisula solidissima*, in offshore New Jersey. Biol. Bull. 135, 349–365.

Ross, P.M., Parker, L., Byrne, M., 2016. Transgenerational responses of molluscs and echinoderms to changing ocean conditions. ICES J. Mar. Sci. 73, 537–549.

Schmalenbach, I., Franke, H.-D., 2010. Potential impact of climate warming on the recruitment of an economically and ecologically important species, the European lobster (*Homarus gammarus*) at Helgoland, North Sea. Mar. Biol. 157, 1127–1135.

Shen, Y., Gan, Y., Xiao, Q., Huang, Z., Liu, J., Gong, S., Wang, Y., Yu, W., Luo, X., Ke, C., 2022. Divergent Carry-Over Effects of Hypoxia during the Early Development of Abalone. Environ. Sci. Technol. 56, 17,836–17,848.

Shephard, S., Beukers-Stewart, B., Hiddink, J.G., Brand, A.R., Kaiser, M.J., 2010. Strengthening recruitment of exploited scallops *Pecten maximus* with ocean warming. Mar. Biol. 157, 91–97.

Shumway, S.E., Cucci, T.L., Newell, R.C., Yentsch, C.M., 1985. Particle selection, ingestion, and absorption in filter-feeding bivalves. J. Exp. Mar. Biol. Ecol. 91, 77–92.

Sotka, E.E., Giddens, H., 2009. Seawater temperature alters feeding discrimination by cold-temperate but not subtropical individuals of an ectothermic herbivore. Biol. Bull. 216, 75–84.

Spruck, C.R., Walker, R.L., Sweeney, M.L., Hurley, D.H., 1995. Gametogenic cycle in the non-native Atlantic surf clam, *Spisula solidissima* (Dillwyn, 1817), cultured in the coastal waters of Georgia. Gulf Caribb. Res. 9, 131–137.

Thomas, Y., Bacher, C., 2018. Assessing the sensitivity of bivalve populations to global warming using an individual-based modeling approach. Glob. Chang. Biol. 24, 4581–4597.

Uthicke, S., Patel, F., Petrik, C., Watson, S.A., Karelitz, S.E., Lamare, M.D., 2021. Cross-generational response of a tropical sea urchin to global change and a selection event in a 43-month mesocosm study. Glob. Chang. Biol. 27, 3448–3462.

van der Schatte Olivier, A., Jones, L., Vay, L.L., Christie, M., Wilson, J., Malham, S.K., 2020. A global review of the ecosystem services provided by bivalve aquaculture. Rev. Aquac. 12, 3–25.

Vargas, C.A., De La Hoz, M., Aguilera, V., Martín, V.S., Manríquez, P.H., Navarro, J.M., Torres, R., Lardies, M.A., Lagos, N.A., 2013. CO2-driven ocean acidification reduces larval feeding efficiency and changes food selectivity in the mollusk *Concholepas concholepas*. J. Plankton Res. 35, 1059–1068.

Weissberger, E., Grassle, J., 2003. Settlement, first-year growth, and mortality of surfclams, *Spisula solidissima*. Estuar. Cost. Shelf Sci. 56, 669–684.

Weitere, M., Vohmann, A., Schulz, N., Linn, C., Dietrich, D., Arndt, H., 2009. Linking environmental warming to the fitness of the invasive clam *Corbicula fluminea*. Glob. Chang. Biol. 15, 2838–2851.