



## Interactive roles of temperature and food availability in predicting habitat suitability for marine invertebrates

Raymond Czaja Jr.<sup>a</sup>, Brian Beal<sup>b,c</sup>, Kyle Pepperman<sup>c</sup>, Emmanuelle Pales Espinosa<sup>d</sup>,  
Daphne Munroe<sup>e</sup>, Robert Cerrato<sup>d</sup>, Evan Busch<sup>b</sup>, Bassem Allam<sup>d,\*</sup>

<sup>a</sup> National Center for Ecological Analysis and Synthesis, University of California, Santa Barbara, Santa Barbara, CA, 93101, USA

<sup>b</sup> University of Maine at Machias, Machias, ME, 04654, USA

<sup>c</sup> Downeast Institute, Beals, ME, 04611, USA

<sup>d</sup> School of Marine and Atmospheric Sciences, Stony Brook University, Stony Brook, NY, 11790-5000, USA

<sup>e</sup> Haskin Shellfish Research Laboratory, Rutgers University, Port Norris, NJ, 08349, USA

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### ABSTRACT

Natural variability in habitat characteristics, including their interactions, can affect marine invertebrate development. Controlled laboratory experiments seek to assess responses to such variability. For marine invertebrates, responses to temperature are typically assessed but a continuous gradient of all temperatures that a species may encounter is not frequently used. For planktonic larvae of marine invertebrates, biotic factors such as food availability receive less attention due to difficulty in simulating planktonic biotic interactions in a controlled laboratory setting. Here, a laboratory experiment was used to quantify larval development (growth, pelagic larval duration and survival) of the Atlantic surfclam, *Spisula solidissima*, in response to a continuous range of temperatures and food (phytoplankton) concentrations, allowing quantification of thermal and food availability niches. A second experiment was conducted to quantify the thermal and food availability niches for recruit (post-settlement) surfclams. These experiments were uniquely designed to inform future climate change-based forecasting and habitat suitability modeling. Larval growth and survival increased with increased food availability, while pelagic larval duration decreased with increased food availability. Larval survival decreased with increased temperature, growth peaked near 22 °C and pelagic larval duration was lowest near 22 °C. For recruits, survival and growth increased with both temperature and food availability, but growth decreased at temperatures >22 °C. Broadly, results suggest potential food limitation for continental shelf bivalve larvae and demonstrate that natural variation in food availability may affect thermal tolerances. Results also suggest that throughout the range of the surfclam, high food and moderate temperature areas such as New York Bight and Georges Bank are ideal for larvae and early recruits, whereas low food and high temperature areas, including continental shelf waters in the southern Middle Atlantic Bight, are suboptimal for early life stages of surfclams. This framework may be used for habitat suitability modeling, from an energetic perspective, for other marine invertebrate taxa.

### 1. Introduction

For ectothermic organisms, two important habitat characteristics that may affect development (e.g., growth and survival during earlier life stages) include temperature and food availability. (Huey, 1991; Pepin, 1991). For suspension-feeding marine invertebrates, available food often comes in the form of plankton (Gili and Coma, 1998; Riisgård and Larsen, 2010). For marine planktotrophic larvae, food is often more restricted to smaller plankton, specifically nanophytoplankton (Raby

et al., 1997; Lindeque et al., 2015). Nanophytoplankton may be patchily distributed through space, thereby contributing to highly variable habitat characteristics that invertebrate larvae may encounter as they drift through the water column before settlement to the benthos (Thompson et al., 2012; Lawlor and Arellano, 2020). In addition to spatial variability, temporal variability in temperature and food availability (e.g., phytoplankton) should be considered, particularly as a function of climate change. Ocean warming (OW) impacts are well documented in the northwest Atlantic where bottom temperatures are

\* Corresponding author.

E-mail address: [bassem.allam@stonybrook.edu](mailto:bassem.allam@stonybrook.edu) (B. Allam).

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increasing at rates  $>1.0$  °C per decade (Friedland et al., 2020a, 2022). Another oceanographic symptom of OW is stratification (Li et al., 2020). In continental shelf waters, increased stratification limits surface nutrient availability, thereby constraining phytoplankton production (Winder and Sommer, 2012; Fu et al., 2016). In the northwest Atlantic, Henson et al. (2021) predicted a 10% decrease in total phytoplankton biomass by the end of the century. Such changes may impact food availability for herbivorous suspension feeders. Therefore, it is important to understand how natural variability in temperature and food availability may impact marine invertebrate development, specifically for larval stages in dynamic environments that may be sensitive to climate change (Przeslawski et al., 2008, 2015).

When assessing climate change impacts on marine invertebrates, it is important to consider interactive stressors, as they may act synergistically (Gobler et al., 2018; Poletto et al., 2018). From a physiological perspective, it is well documented that temperature and food availability can induce stress responses and changes in metabolic activity for marine invertebrates, including bivalves (Lesser et al., 2010; Fitzgerald-Dehoog et al., 2012; May et al., 2021). Feeding rate, which can affect growth rate, is dependent on temperature and food availability such that increased temperature may increase feeding (e.g., clearance) rate until a certain threshold, (e.g., Bayne, 1976; Riisgård and Seerup, 2003; Jihong et al., 2004; Kittner and Riisgård, 2005) and decreased food may increase clearance rate (Schulte, 1975; Widdows et al., 1979; Strohmeier et al., 2009). Furthermore, the interaction of low food availability and high temperature stressors may act synergistically to negatively impact metabolic activity and development of marine invertebrates (Cole et al., 2016; Silina, 2023). However, this knowledge base needs to be expanded upon in a climate change context, and for larval stages, as food availability impacts on adult invertebrates, namely bivalves, are more frequently studied than that of larvae (see previous references). While laboratory studies have shown that increased food availability (e.g., phytoplankton, or algae cell concentrations) can interact with temperature and impact bivalve growth and survival, such studies may have limited environmental applications, as food availability levels are based often on standard food levels under hatchery conditions (e.g., Martinez et al., 2000; Cheng et al., 2018). Therefore, it is important to consider whether climate change or environmentally relevant increases in temperature and decreases in food availability may hamper metabolic activity, and subsequently development, of marine invertebrates.

The Middle Atlantic Bight (MAB) and adjacent continental shelf waters in the northwest Atlantic not only host many commercially important species, but also experience large temporal and spatial variation in sea surface temperature (SST) and surface chlorophyll concentration (as a phytoplankton availability proxy) (Murawski et al., 2000; Chen et al., 2016; Friedland et al., 2020a). For example, average spring and summer chlorophyll concentrations in coastal Gulf of Maine and Georges Bank may reach 10  $\mu\text{g}/\text{l}$  but on shelf waters near the mid-Atlantic may drop below 1  $\mu\text{g}/\text{l}$  (Yoder et al., 2002). Chlorophyll concentrations within this range have been shown to affect growth of marine invertebrates (Paulay et al., 1985; Fotel et al., 1999), however, whether optimal food levels lie within this range of variability remains unknown for many, if not most MAB invertebrate larvae. Therefore, it is important to assess whether such food availability variability, coupled with temperature variability, may present limiting habitat characteristics. The Atlantic surfclam, *Spisula solidissima* is one of many commercially important invertebrate species in the environmentally variable MAB. While surfclams have traditionally yielded one of the largest fisheries in that region, landings have dropped in recent decades likely due to global change (Cargnelli, 1999; NEFSC, 2014; Narváez et al., 2015). The cumulative effects of climate change, including OW, are contributing to a variety of impacts on surfclam populations. These include, but are not limited to, offshore shifts in surfclam distributions (Weinberg, 2005; Timbs et al., 2019; Powell et al., 2020), low condition indices (Marzec et al., 2010), low scope for growth (Hornstein et al., 2018), slow growth rates (Munroe et al., 2016) and gonad abnormalities

(Kim and Powell, 2004). While these studies have documented observed and predicted OW impacts on adult surfclams, few efforts have assessed OW impacts on surfclam larvae and recruits. Recently, Czaja et al. (2023) found that New York Bight (NYB) surfclam larvae may benefit metabolically from a warming environment, but it is unclear how variations in temperature and food availability that impact earlier life stages of surfclams may affect the fishery. Quantifying effects of a wide range of temperature and food availability levels on surfclam development could allow for spatial predictions of habitat suitability (McManus et al., 2018). Assessing spatial and temporal shifts in habitat suitability for surfclams, and their larvae, may be particularly important as in surfclam habitat, OW rates are three times greater than the global average rate (Saba et al., 2016) and primary production changes including altered bloom phenology and intensity are occurring due to climate change (Friedland et al., 2015, 2023). This information may enhance management efforts for the surfclam fishery.

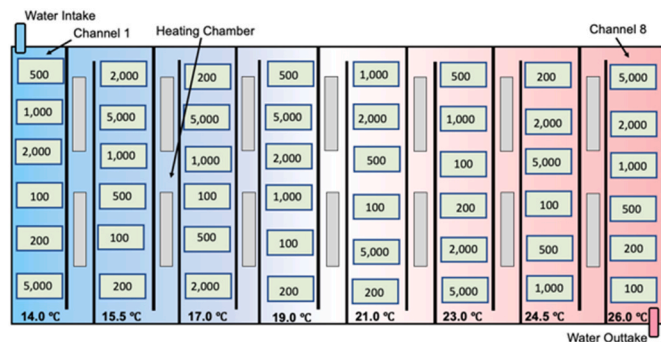
Metabolically, temperatures above 19 °C negatively impact adult surfclams, but temperatures above 23 °C negatively impact larval surfclams (Hornstein et al., 2018; Czaja et al., 2023), potentially making adults more vulnerable to OW. However, assessing interactive effects of OW and food availability on the fate and growth of larvae and recently-settled surfclams (i.e., recruits) provides multiple advantages from a logistical and ecological implications perspective. Adult bivalves consume a wide range of seston particles including detritus and zooplankton, whereas larvae and young recruits typically are restricted to nanophytoplankton (2–20  $\mu\text{m}$ ) (Raby et al., 1997; Lindeque et al., 2015), allowing for surface chlorophyll measurements to better represent food availability for larvae. Large datasets of surface temperature and food availability (e.g., chlorophyll) are available that can be used to support high resolution predictions regarding habitat suitability through time and space for larvae that occupy near-surface waters (Lee et al., 2019; Mondal et al., 2021). Surfclams have relatively long pelagic larval durations (PLD) of 20–35 days, increasing the likelihood of inadequate food supplies, and underscoring the potential relevance of food availability in larval development (Fay et al., 1983). Czaja et al. (2023) also found that climate change may prolong larval surfclam PLD, but higher resolution data is needed to better predict PLD changes due to climate change. Prolonged PLD, along with postponed metamorphosis, may also alter post-metamorphosis fitness, underscoring the importance of quantifying larval development variability due to environmental variability (Bayne, 1965; Pechenik and Eyster, 1989; Pechenik, 1990; Pechenik et al., 1998; Qian and Pechenik, 1998). Furthermore, to aid fisheries management, work has been conducted to model larval dispersal of surfclam larvae (Zhang et al., 2015, 2016). However, questions remaining regarding the impact of environmental variation on surfclam larval dispersal, potentially through PLD links. Quantifying development of surfclam larvae in response to the interactive effects of temperature and food availability can improve spatially explicit predictions that can help inform larval transport models.

This study hypothesizes that temperature, food availability and their interaction can predict surfclam development. The primary objective of this study was to quantify the thermal and food availability niches for larval surfclam development. This was done experimentally in the laboratory using an environmentally culturing gradient design, altering the design of Lawlor and Arellano (2020), where surfclam larvae were exposed to a wide range of temperature and food availability levels. Development responses, including survival, growth and PLD were quantified. As a secondary objective, a second experiment was conducted to quantify the thermal and food availability niches for surfclam recruits (1.5 months post settlement). These experiments were explicitly designed to allow for predictions and projections to be made regarding developmental responses to spatial and temporal changes in temperature and food availability.

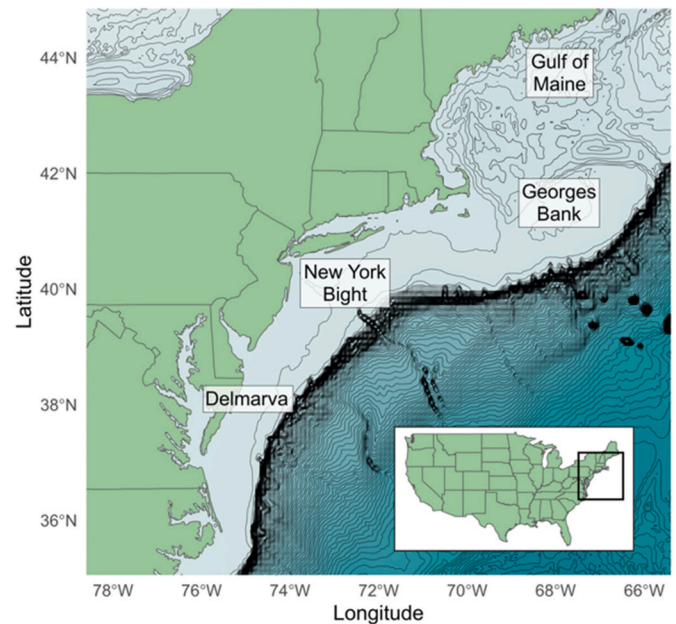
## 2. Methods

### 2.1. Experimental design

Experiments were conducted at the Downeast Institute in Beals, ME (44°28'49.26"N, 67°35'57.42"W). A PVC tank (279.4 cm × 87.4 cm × 25.4 cm deep) was used for both lab experiments. The tank functioned as a temperature-controlled water bath attached to a freshwater, recirculating system. The tank was divided into eight channels, each containing six experimental units (EU; N = 48), with seven heating chambers, each containing two 100-W heaters (controlled via InkBird digital temperature controllers), and an air bubbler to enhance circulation (Fig. 1). In other words, individual EUs (plastic 4-L containers) were separate, closed units such that organisms and water were not mixed among EUs. Cold water (supplied via a chiller as part of the recirculating system) entered the tank at the first channel and moved through channels, accumulating heat as it passed through the heating chambers. This configuration allowed for maintenance of eight target temperatures: 14, 15.5, 17, 19, 21, 23, 24.5 and 26 °C. Within each channel (i.e., target temperature group), each EU was assigned one of six target food availability levels (100, 200, 500, 1,000, 2000 and 5000 algae cells/ml). These temperatures and algal concentrations were chosen given the range that surfclam larvae experience based on documented spawning times and corresponding sea surface temperatures (Ropes, 1968; Mann, 1985; Yoder et al., 2002; Thomas et al., 2003; Hornstein, 2010; Li and He, 2014; Liu et al., 2021) extending from the northern Gulf of Maine to the southern edge of the MAB (Fig. 2). The bounds of these temperatures also consider OW impacts, such that 14 °C represents temperatures that surfclam larvae may experience present day further north (e.g., New England), and that 26 °C represents temperatures that surfclam larvae may experience in the future (under the Representative Concentration Pathway 8.5 scenario) further south (e.g., Delmarva) (Mann, 1985; Weissberger and Grassle, 2003; Alexander et al., 2018; Pörtner et al., 2019, 2022). The relationship between chlorophyll concentration and cell concentration was measured for each algal species (see next subsection) to identify cell concentrations corresponding to environmentally relevant chlorophyll concentrations. This relationship was measured using a UV-Vis Spectrophotometer at seven different cell concentrations for each algal species according to Lorenzen (1967), and then modeled using a linear regression (Appendix S1: Fig. S1, Appendix S2: Figs. S1–S2).



**Fig. 1.** Schematic of experimental system. Chilled freshwater enters the system at the intake, runs through eight channels and seven heating chambers, then exits the system at the outtake. Gray boxes in heating chambers represent 100 W heaters. Boxes (shaded light green) in channels represent experimental units (N = 48) containing larvae. Numbers in boxes represent target algae cell concentrations (cells/ml) for each experimental unit. Numbers at the bottom of each channel represent target temperatures (°C) for that channel. The same design was used for recruits with adjustments to target algae cell concentrations (cells/ml) (see text for more details). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)



**Fig. 2.** Bathymetry map displaying the distribution and region of interest for surfclam habitat characteristics. Gray lines denote depth contours every 50 m. Areas of historically high surfclam production and fishery activity are denoted including the Gulf of Maine, Georges Bank, New York Bight and Delmarva.

### 2.2. Husbandry and experiment maintenance

Adult surfclams were collected during low tide from an intertidal flat on Deer Isle, Maine (44°16'40.5"N, 68°40'48.9"W) on April 28, 2022, and spawning was induced on May 27, 2022. Spawning and fertilization were conducted according to standard commercial hatchery procedures (Helm et al., 2004). Briefly, spawning was induced via thermal shock (25 °C) after adults were held at 12 °C overnight. Sperm (five males) were pooled and added to eggs (one female) at 26 °C. At approximately 30 min post fertilization, during which gametes were homogenized every 5 min to gently resuspend eggs, fertilized eggs were removed from remaining male gametes, as approximately 95% of the eggs showed the presence of polar bodies. Larvae were maintained at standard hatchery conditions (23 °C) for four days before being added to individual EU within the experimental system. To limit heat shock, larvae assigned to each of the four coldest temperatures (14, 15.5, 17 and 19 °C) were acclimated to their target temperature at a rate of 1 °C/h, prior to their addition to the appropriate EU. Prior to addition to EUs, all larvae were gently homogenized and a mixture of all larvae was randomly assigned to each EU. Experimental units were stocked at 2 larvae/ml and with filtered seawater (1 µm; FSW) pumped into the lab from nearby Black Duck Cove (salinity = 31.00 ± 0.53, SD). This larval density, chosen based on the total estimated biomass of organisms that may feed on nanophytoplankton, was intended to simulate per unit volume of grazing pressure (Dagg et al., 1981; Sprung, 1984; Thompson et al., 2013; Vogt et al., 2013, see Appendix S1 for further explanation on grazing pressure calculations). Each EU received an air stone to supply light oxygen bubbling and maintain suspension of larvae. Experimental units were cleaned and water was replaced every 48 h. During each cleaning, larvae were graded using a 105 µm sieve. Hobo temperature loggers were placed in each channel within the experimental system to verify that large (i.e., >1.5 °C) deviations from target temperatures did not occur. Temperature within each EU was measured twice daily using a mercury thermometer. Salinity (31.0 ± 0.53 psu, ±SE) and pH (7.75 ± 0.12, ±SE) were maintained at ambient conditions. Dissolved oxygen (DO) levels remained nearly fully saturated, with an average DO of 7.67 ± 0.73 mg/l. Larval survival was monitored every 2–4 days for the first three weeks of the experiment to ensure no mass mortality events in



individual EUs.

### 2.3. Feeding regime

Larvae were fed a 1:1 ratio of the haptophyte *Tisochrysis lutea* and the diatom *Thalassiosira pseudonanna*. To maintain target algal concentrations, algae were added to each EU 6–8 times a day, typically beginning at 0800 and ending at 2000. Clearance rate trials were conducted to quantify algal cell loss rates at different temperatures and at different larval ages. Loss rates were used to determine amounts of algae to add to each EU to maintain target food availability levels. Clearance rate trials were conducted on larvae 5 days post fertilization (dpf) and 13 dpf and at six temperatures: 14, 15, 19, 23, 24 and 26 °C. Clearance rate trials occurred in triplicate for each temperature using 50 ml vials. Each vial contained 10 ml of FSW, 1000 larvae and an algal (*T. lutea*) concentration of 100,000 cells/ml. These concentrations were chosen to estimate loss (grazing + mortality) to be detected during microscope counts made over a 6-h period. The authors acknowledge that these concentrations are relatively high. However, high larval and algal concentrations were needed to detect quantifiable clearance rates. In other words, lower larvae and algae cell concentrations yielded algae losses and cell counts that were too variable or low to detect via microscopic counts over a 6-h period. Nevertheless, previous studies have found that bivalve larvae densities of 100 larvae/ml may not impact growth and feeding rate (Rico-Villa et al., 2008; Le et al., 2017). Additionally, results will show that these densities yielded clearance rates that not only align with those found in other studies, but successfully aided in determining algae additions. After sitting in a temperature-controlled bath for 6 h, 5 µl was sampled from each vial and the contents of each examined under a Nikon Eclipse TE2000-S inverted compound microscope (100x magnification) to quantify total remaining algae cells. This total was subtracted from initial ( $T_0$ ) cell counts to quantify algal cell loss rates that were then standardized to larva/hr. While this approach accounts for temperature and age dependent loss rates, it does not account for food availability dependent loss rates. Time and resource limitations prevented clearance rate trials from also incorporating food availability effects. For example, algal loss rates for EUs assigned to 5000 cells/ml may be higher than those assigned to 100 cells/ml, as studies have shown that changes in food availability can affect bivalve larvae feeding rates (Beiras and Camacho, 1994; Pérez-Camacho et al., 1994). Therefore, clearance rate trials were used to help inform algal additions, instead of absolute quantification of loss rates for each EU. During each algal addition, each EU received sufficient algae to replenish what was consumed over the previous 1–2 h. Overnight, “extra” algae were added such that the average algae concentration overnight aligned with the target algae concentrations. For example, if the target algae concentration was 1000 cells/ml, algae were added in excess at 2000 h such that at 0200 h (i.e., halfway through the night), algal concentrations would, theoretically, be drawn to the target concentration so that at 0800 h (i.e., the end of the night, and before the next feeding), algal concentrations would be near the target concentration. Filtered (40 µm) water samples from each EU were taken every 48 h (chosen randomly at a time between the first and last feedings of the day to represent average conditions) and fixed with 1% glutaraldehyde. Samples were then processed via flow cytometry to determine average algal concentration in each tank (i.e., to quantify how observed algal concentrations deviated from target algae concentrations). Samples were processed using a FACSCalibur flow cytometer (BD BioSciences, San Jose, California, USA). For each sample, 300 µl were analyzed for counts of each algae species using 488-nm argon and 635-nm red diode lasers for excitation. Counts for each algal species were based upon photosynthetic pigment auto-fluorescence (FL2, 585 nm for phycoerythrin; FL3, 670 nm for chlorophyll *a* and FL4 for allophycocyanin).

### 2.4. Larval development and statistical analyses

Beginning 20 dpf, 40 larvae were sampled (but replaced back to their respective EU following measurements) from each EU to detect settlement behavior (i.e., presence of an active foot). PLD was defined as the dpf in each EU when at least 50% of remaining larvae exhibit settlement behavior. It should be noted that surfclam larvae may maintain the pediveliger stage 0–2 days before metamorphosis (Ropes, 1980), therefore PLD may have been slightly underestimated. If larvae in an EU reached 50% settlement, survival rate was then quantified as the ratio of live larvae to live larvae plus remaining dead shell. It should be noted that larvae were graded using a 105 µm sieve. Therefore, survival rate does not account for larvae that died before reaching 105 µm, and it is possible that survival estimates slightly overestimate net survival. However, survival monitoring suggested low (<5%) mortality larvae smaller than 105 µm. Growth rate was quantified using a Nikon Eclipse TE2000-S inverted compound microscope (100x magnification) as the increase in larval length from the umbo/hinge to the outermost (i.e., ventral) shell edge (Appendix S1: Fig. S2) from 4 dpf (i.e., the day larvae were placed into the experimental system) to the end of PLD. Generalized additive models (GAMs), were used to predict larval PLD, growth and survival as functions of temperature, food availability and their interaction. GAMs were used as nonlinear relationships were expected based on previous studies finding quadratic relationships between larval growth and environmental variables (e.g., Tettelbach and Rhodes, 1981; Lawlor and Arellano, 2020). Cubic spline smoother were used and GAMs were restricted to four knots to prevent overfitting (Sagarese et al., 2014). For larval survival however, food availability was restricted to three knots, as four knots yielded potential overfitting (i.e., survival and food availability had a complex sine relationship when four knots were allowed). Averages of observed bi-daily temperature readings (via mercury thermometer) and observed food availability levels (via flow cytometry analyses on fixed water samples) were used as predictor variables in GAMs. Akaike information criterion (AIC) and AIC weights were used to determine which model (i.e., combination of all predictor variables, and their interaction, or an individual predictor variable) revealed the best fit for each response, such that the model with the highest AIC weight was considered the best fit model (Burnham and Anderson, 2004). GAMs also were used to quantify larval clearance rate as a function of a temperature. All analyses were conducted in R version 4.0.2 (2020-06-22) using base packages plus the packages “ggplot2” (Wickham, 2016), “mgcv” (Wood and Augustin, 2002) and “DHARMA” (Hartig, 2022).

### 2.5. Recruit experiment

The recruit experiment began on July 31, 2022 and ended after 21 days on 21 August. This experiment was nearly identical to the larval experiment as it used the same tank (see section 2.1); however, surfclam recruits 45 days post settlement were stocked in each EU. Prior to the experiment, recruits from the same spawning that yielded larvae for the larval experiment were held at standard hatchery conditions (23 °C). Fifty recruits were placed in each EU (bottom surface area of 152 cm<sup>2</sup>). This density was chosen to represent natural densities of year one surfclams, per square meter, observed in MAB waters (Weissberger and Grassle, 2003; Quijon et al., 2007). Clearance rate trials were also conducted for surfclam recruits to approximate the quantity of algal cells to be added to each EU to achieve target food availability levels. Recruit clearance rate trials were conducted in accordance with all details of larval clearance rate trials, except 10 recruits were added to each vial. Additionally, recruit clearance rates demonstrated linear relationships with temperature, therefore linear models were used instead of GAMs (Appendix S2: Figs. S3–S4). Survival was quantified as the percent of total remaining live recruits in each EU, and growth was calculated similarly to the larval experiment, using a dissecting microscope (Nikon SMZ1000).

### 3. Results

#### 3.1. Larval experiment

Observed temperatures for each EU aligned with target temperatures and showed minor variability, with the average temperature standard deviation being 0.32 °C (Appendix S1: Table S1). Observed algal concentrations, however, deviated from target levels and were highly variable with the average algal concentration standard deviation being 1978 cells/ml (Appendix S1: Table S2). The highest observed algal concentration was 28,520 cells/ml and the lowest was 36 cells/ml. Observed larval survival ranged from 100% (target 19 °C and 5000 cells/ml) to 2.6% (target 26 °C and 2000 cells/ml) (Appendix S1: Table S3). Observed larval growth ranged from 11.6 μm/day (target 19 °C and 5000 cells/ml) to 2.9 μm/m day (target 14 °C and 100 cells/ml) (Appendix S1: Table S3). Within individual EUs, larval growth standard deviation ranged from 0.64 to 3.45 μm (N = 25). Observed PLD ranged from 22 days (target 19 °C and 5000 cells/ml) to 39 days (target 14 °C and 500 cells/ml) (Appendix S1: Table S3). Larvae in two EUs (target 100 and 200 cells/ml at 14 °C) did not reach 50% settlement by experiment termination (40 dpf) (Appendix S1: Table S3). For reference, surfclam larvae raised in the DEI hatchery for commercial sale (from the same broodstock used for this experiment) yielded an average survival, growth and PLD of 95%, 12 μm/day and 22 days, respectively.

Models that included temperature, food availability and their interaction were the best fit models given the data for all larval responses, as these models yielded the highest AIC weight for each response (Table 1). Although it should be noted for larval growth, the AIC weight delta between the model with an interaction and the model without an interaction was 0.08, suggesting relatively minor interactive effects for growth (Table 1). Temperature and food availability yielded relatively low deviance explained for survival (Table 1). Survival generally decreased with increasing temperature and increased with increasing food availability (Fig. 3, Appendix S1: Figs. S3–4A). Highest survival occurred near 14 °C and 7000 cells/ml and lowest survival occurred near 26 °C and 3000 algae cells/ml (Fig. 3).

The growth model had substantially higher deviance explained than the survival model (Table 1). Growth increased with increasing

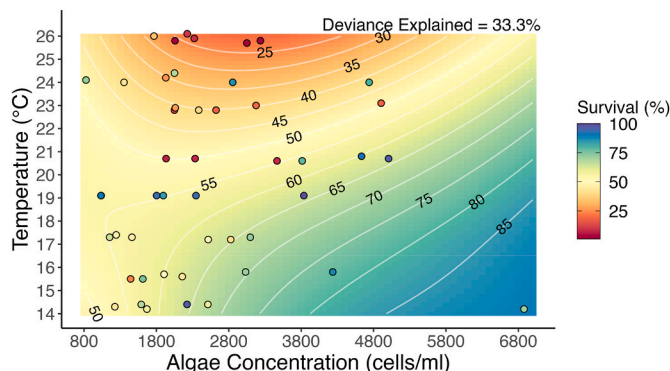


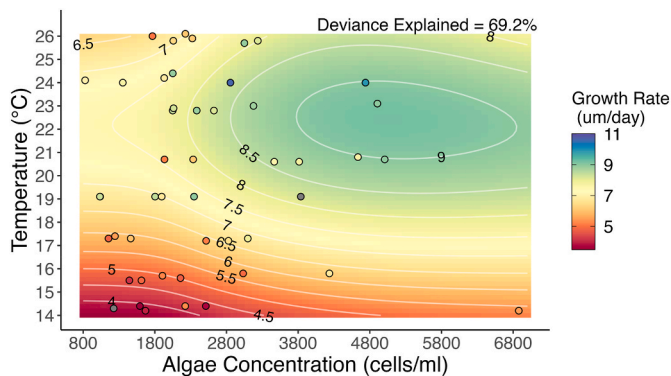
Fig. 3. Contoured heat map displaying larval survival (%) as a function (generalized additive model) of temperature (°C) and algae concentration (cells/ml). Circles represent observed data points. Circle colors correspond with legend values. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

temperature until 22–23 °C, and then decreased with increasing temperature (Fig. 4, Appendix S1: Fig. S3B). Growth generally increased with increasing food availability (Appendix S1: Fig. S4B); however, food availability had a slightly higher impact on growth at higher temperatures than at lower temperatures (Fig. 4). Fastest growth occurred at ~22.5 °C and 5500 algae cells/ml and slowest growth at 14 °C and 800 cells/ml (Fig. 5). Of all larval responses, PLD had the highest deviance explained (Table 1). PLD decreased with increasing temperature until 22 °C, and then increased with increasing temperature (Fig. 4, Appendix S1: Fig. S3C). PLD decreased with increasing food availability (Fig. 4, Appendix S1: Fig. S4C). The lowest and highest PLD occurred near 22 °C and 7000 algal cells/ml and near 14 °C and 800 algae cells/ml, respectively (Fig. 5). Larval clearance rates ranged from ~60 to 150 algae cells/larva/hour (Appendix S1: Fig. S5). Temperature yielded a significant relationship ( $p = 0.0095$ ) for clearance rates for 5-day old larvae, but not for 13-day old larvae ( $p = 0.0800$ , Appendix S1: Table S4). Clearance rate for 5-day old larvae increased with increasing temperature until approximately 20–21 °C, and then decreased with

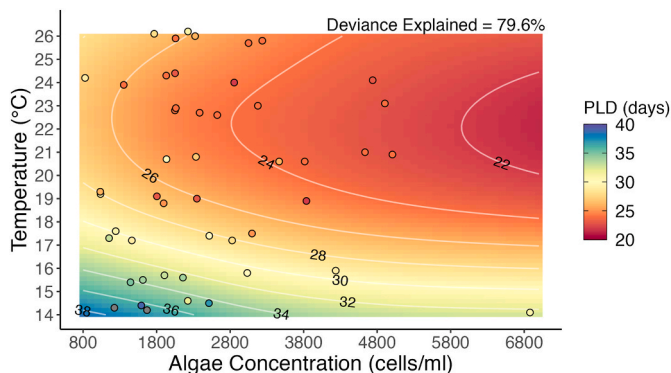
Table 1

Output for each candidate model (generalized additive models) for each larval response: larval survival, larval growth, and pelagic larval duration (PLD). Akaike information criterion (AIC) and AIC weights (in parentheses below AIC values) were used to select the best fit model given the data, in bold. Edf = estimated degrees of freedom.

Response	Candidate Model Variables	AIC	Temp p-value	Food p-value	Interaction p-value	Temp edf	Food edf	Interaction edf	Adjusted R <sup>2</sup>	Deviance Explained (%)
Larval Survival	<b>Temperature + Food + Temperature × Food</b>	456.9 (0.51)	0.0007	0.040	0.075	1.39	1.63	1.07	0.28	33.3
	Temperature + Food	458.2 (0.27)	0.0006	0.185	n/a	1.54	0.53	n/a	0.24	27.0
	Temperature	458.6 (0.22)	0.0007	n/a	n/a	1.56	n/a	n/a	0.22	24.7
	Food	468.8 (0.01)	n/a	n/a	n/a	n/a	1.81	n/a	0.04	7.82
Larval Growth	<b>Temperature + Food + Temperature × Food</b>	155.7 (0.54)	1.2e-8	0.003	0.040	2.37	0.80	1.052	0.66	69.2
	Temperature + Food	156.1 (0.46)	9.2e-11	0.0002	n/a	2.36	1.25	n/a	0.66	68.2
	Temperature	168.5 (0.01)	1.2e-9	n/a	n/a	2.48	n/a	n/a	0.54	56.8
	Food	192.1 (0.01)	n/a	0.0008	n/a	n/a	2.67	n/a	0.26	29.9
Larval PLD	<b>Temperature + Food + Temperature × Food</b>	205.1 (0.60)	2.6e-15	4.8e-5	0.22	2.49	1.36	1.16	0.77	79.6
	Temperature + Food	205.9 (0.40)	2e-16	1.31	n/a	2.48	1.31	n/a	0.76	78.1
	Temperature	220.3 (0.01)	5.1e-14	n/a	n/a	2.41	n/a	n/a	0.66	68.2
	Food	263.2 (0.01)	n/a	0.016	n/a	n/a	1.77	n/a	0.14	17.0



**Fig. 4.** Contoured heat map displaying larval growth rate (microns/day) as a function (generalized additive model) of temperature (°C) and algae concentration (cells/ml). Circles represent observed data points. Circle colors correspond with legend values. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)



**Fig. 5.** Contoured heat map displaying pelagic larval duration (PLD, days) as a function (generalized additive model) of temperature (°C) and algae concentration (cells/ml). Circles represent observed data points. Circle colors correspond with legend values. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

increasing temperature (Appendix S1: Fig. S5). However, for 13-day old larvae, clearance rate increased with increasing temperature until 22–23 °C and then reached a plateau (Appendix S1: Fig. S2).

**Table 2**

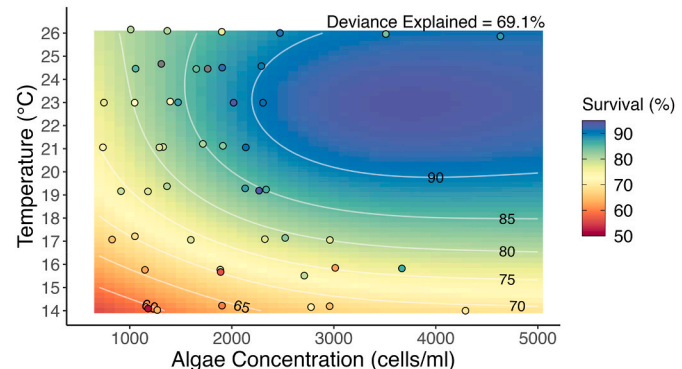
Output for each candidate model (generalized additive models) for each recruit response: recruit survival and recruit growth. Akaike information criterion (AIC) and AIC weights (in parentheses below AIC values) were used to select the best fit model given the data, in bold. Edf = estimated degrees of freedom.

Response	Candidate Model Variables	AIC	Temp <i>p</i> -value	Food <i>p</i> -value	Interaction <i>p</i> -value	Temp edf	Food edf	Interaction edf	Adjusted R <sup>2</sup>	Deviance Explained (%)
Recruit Survival	<b>Temperature + Food + Temperature × Food</b>	321.0 (0.56)	1.9e-11	0.0001	0.060	2.10	1.61	0.72	0.66	69.1
	Temperature + Food	321.4 (0.44)	3.5e-13	3.0e-5	n/a	2.26	1.76	n/a	0.65	68.2
	Temperature	339.6 (0.01)	3.0e-8	n/a	n/a	1.96	n/a	n/a	0.47	49.4
	Food	368.0 (0.01)	n/a	0.187	n/a	n/a	0.71	n/a	0.02	3.78
Recruit Growth	<b>Temperature + Food + Temperature × Food</b>	130.2 (0.62)	0.016	0.200	0.024	1.99	0.38	1.46	0.28	33.4
	Temperature + Food	131.6 (0.30)	0.002	0.071	n/a	2.27	1.17	n/a	0.25	30.3
	Temperature	134.2 (0.08)	0.006	n/a	n/a	2.15	n/a	n/a	0.19	22.3
	Food	142.4 (0.01)	n/a	0.31	n/a	n/a	1.49	n/a	0.02	5.25

**3.2. Recruit experiment**

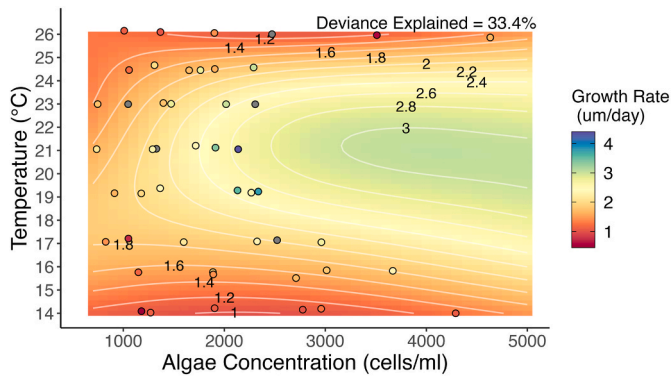
Similar to the larval experiment, target temperatures were met for the recruit experiment, but observed food availability levels deviated from target levels (Appendix S1: Tables S5–S6). The highest observed algae concentration was 8516 cells/ml and the lowest was 10 cells/ml (Appendix S1: Tables S5–S6). Observed recruit survival ranged from 98% (target 24.5 °C and 1000 cells/ml) to 56% (target 15 °C and 200 cells/ml) (Appendix S1: Table S7). Observed recruit growth ranged from zero (multiple treatments) to 4.35 μm/day (target 21 °C and target 5000 cells/ml) (Appendix S1: Table S7). Within individual EUs, recruit growth standard deviation ranged from 0.43 to 6.10 μm (N = 40).

Models including temperature, food availability and their interaction were the best fit models given the data for both recruit survival and growth (Table 2). Although it should be noted for recruit survival, the AIC weight delta between the model with an interaction and the model without an interaction was 0.12, supporting relatively minor interactive effects for survival (Table 1). The survival model had moderately high deviance explained (Table 2), with survival increasing as temperature and food availability increased (Fig. 6, Appendix S1: Figs. S6–7A). Highest survival occurred near 24.5 °C and 4000 cells/ml and lowest survival occurred near 14 °C and 900 cells/ml (Fig. 6). The growth model had lower deviance explained (Table 2). At low food availability levels, growth increased with increasing temperature until ~18 °C, and then decreased with increasing temperature (Fig. 7, Appendix S1:



**Fig. 6.** Contoured heat map displaying recruit survival as a function (generalized additive model) of temperature (°C) and algae concentration (cells/ml). Circles represent observed data points. Circle colors correspond with legend values. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)





**Fig. 7.** Contoured heat map displaying recruit growth as a function (generalized additive model) of temperature ( $^{\circ}\text{C}$ ) and algae concentration (cells/ml). Circles represent observed data points. Circle colors correspond with legend values. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

(Figs. S6–7B). However, at high food availability levels, growth increased with increasing temperature until  $\sim 21^{\circ}\text{C}$ , and then decreased with increasing temperature (Fig. 7, Appendix S1: Figs. S6–7B). Growth increased with increasing food availability until  $>2000$  cells/ml (Fig. 7, Appendix S1: Figs. S6–7B). Fastest growth occurred near  $21^{\circ}\text{C}$  and  $4000$  cells/ml, while slowest growth occurred near the lowest possible food availability at either the highest or the lowest temperature (Fig. 7). Overall, recruit clearance rates ranged from  $\sim 14,000$  to  $33,000$  algae cells/recruit/hour. Temperature yielded a significantly positive relationship for clearance rates for recruits of both ages (45 dps,  $p = 2.7e-7$  and 55 dps,  $p = 0.001$ , Appendix S1: Table S4, Fig. S8).

## 4. Discussion

### 4.1. Temperature and food availability relationships

While many studies have assessed the interactive impacts of temperature and food availability on marine invertebrate development, few studies have done so with larval stages and using explicitly stated, environmentally relevant, food availability ranges (Martinez et al., 2000; Cole et al., 2016; Cheng et al., 2018). Assessing larval responses may be particularly important, as poor larval habitat (i.e., stressful temperature and food availability levels) may contribute to decreased larval supplies, delayed metamorphosis (but see Pechenik et al., 1996 as an example of when food availability stress stimulates metamorphosis) and/or latent effects that carryover to benthic life stages (Pechenik, 1990, 2006; Elkin and Marshall, 2007; Bohn et al., 2013). Here, the present experiments used an environmentally culturing gradient design to find that environmentally relevant changes in temperature and food availability (due to spatial variability as well as climate change induced variability) can significantly impact survival, growth and PLD of early stage surfclams. These results highlight that the relatively understudied interaction of temperature and food availability, in a climate change context, may negatively impact marine invertebrate development, with cascading impacts on larval processes and potentially fisheries production.

For larvae, increased temperatures decreased survival and increased food availability increased survival. However, for recruits, increased temperature and food availability both increased survival. It is peculiar that larval and recruit stages yielded opposite survival-temperature relationships, that is, a negative relationship for larvae and positive relationship for recruits. While this could be due to differential habitat use (e.g., near surface water for larvae vs bottom water for recruits), this also could be due to experimental design artifacts (further discussed in upcoming sections). Larval growth rate peaked near  $22\text{--}23^{\circ}\text{C}$  under high algae concentrations and larval clearance rate peaked or plateaued near

$21\text{--}22^{\circ}\text{C}$ . Recruit growth also peaked near  $22^{\circ}\text{C}$  and at the highest algae concentrations, although recruit clearance rate continuously increased with temperature. Following growth trends, PLD was lowest near  $22\text{--}23^{\circ}\text{C}$  and PLD decreased with increased algae concentrations. These results suggest that temperatures  $>23^{\circ}\text{C}$  hamper metabolic activity, specifically for larvae, for whom changes in feeding may be driving changes in growth, as temperature thresholds for growth aligned with that of clearance rate. For most responses for both life stages, food availability impacts were greater at moderate or high temperatures. This not only highlights the importance of the temperature-food availability interaction, but suggests that in a climate change context decreased food availability may worsen the impacts of OW.

### 4.2. Larval processes

Only one previous study has assessed potential food availability impacts on larval surfclam processes. Specifically, Mann (1985) found that in southern New England, surfclam larval concentrations were not significantly linked to chlorophyll concentrations. However, multiple lab experiments have found that increasing food availability increases bivalve larvae development (e.g., growth) for other species (Przeslawski et al., 2012; Cole et al., 2016). Whether food and larvae concentrations used in these experiments are environmentally relevant remains unclear. Few studies have investigated the relationship between bivalve larval development and explicitly-stated, environmentally relevant variation in food availability. Typically, such studies are modeling simulations of energy budgets (Bos et al., 2006; Rico-Villa et al., 2010) demonstrating that as simulated food availability increases, simulated growth increases, suggesting that food limitation may exist for bivalve larvae. Results from the larval experiment align well with these modeling studies and show that environmentally relevant variation in food availability impacts bivalve larvae growth, PLD and survival, further suggesting that food may be limiting for bivalve larvae in MAB shelf waters.

Together, larval growth and PLD results suggest that climate change OW and decreased food availability may slow larval development, increasing time spent in the planktonic larval stage before settlement (Siegel et al., 2003; Pineda et al., 2007). From a spatial perspective, as a larva is transported through patchy habitat (e.g., fronts or eddies that produce temperatures and food availability ranges different than other water masses), development rates may significantly change based on said habitat patchiness (Yoder et al., 1981; Simoes-Sousa et al., 2022). For example, if larvae are transported near the Hudson River plume, an area of high primary production, growth rates may increase due to increased food availability (Schofield et al., 2013). Furthermore, surfclam larvae undergo vertical migration (Garland et al., 2002; Ma and Grassle, 2004). Therefore, development rates may be significantly faster when larvae are in the surface mixed layer and experiencing moderate temperatures and low food availability compared to conditions below the surface mixed layer (Pearce et al., 2004; Ouellet et al., 2007).

Results presented here suggest that the range of temperatures and food availability that surfclam larvae encounter in the coastal ocean have high explanatory power for PLD. There is growing interest in explaining PLD in marine larvae, particularly for commercially and economically important species (Sanvicente-Añorve et al., 2018; Bashevkin et al., 2020). No studies have investigated whether food availability may impact bivalve larvae PLD and only one study (to our knowledge) has investigated whether food availability may impact marine invertebrate (sea star) PLD (Pratchett et al., 2017). Considering that food availability combined with temperature explained  $\sim 80\%$  of the variance in PLD, these results may provide substantial insight in a developing field with many knowledge gaps. Biophysical models attempt to simulate larval dispersal patterns and often emphasize PLD variability (Metaxas and Saunders, 2009; Lett et al., 2010). While such models typically include temperature-dependent PLD functions (Nicolle et al., 2013; Figueiredo et al., 2021), they rarely include food

availability-dependent PLD functions, but likely should, given results from the larval experiment, since increased temperature and decreased food availability increase PLD. Increased PLD likely yields longer dispersal distances and potentially different dispersal paths, thereby affecting recruitment patterns and population connectivity (Robins et al., 2013; Ospina-Alvarez et al., 2018). Furthermore, increased PLD may increase planktonic predation risk, as more time is spent in the water column before settlement (Sponaugle and Grorud-Colvert, 2006). While lower temperatures yielded higher larval survival, they also increased PLD, which may result in decreased survival in the field. Follow-up in situ larval dispersal studies are needed to further investigate these connections.

#### 4.3. Habitat suitability implications and geographical trends

It is well documented that OW is occurring in the MAB (Friedland et al., 2020a, 2022). While climate change impacts on primary production in the MAB comes with more uncertainty, evidence suggests that climate change has and will continue to decrease primary production in that region (Friedland et al., 2020b; Henson et al., 2021). Therefore, the interactive effects of climate change associated with OW and decreased food availability may decrease larval survival and growth throughout much of the range of the Atlantic surfclam. In southern and middle northwest Atlantic latitudes within the distribution of the surfclams, mean summer SSTs already eclipse 23 °C (Hammerschlag et al., 2022; Czaja et al., 2023), suggesting larvae may be presently exhibiting negative responses to environmental change. That is, in these regions, should temperature increase to 26 °C by the end the century, aligning with projected 3.0 °C increases in SST (Pörtner et al., 2019, 2022), larval growth may decrease and survival may further decrease by 50%. However, spawning phenology should be considered, as bivalves may spawn earlier due to OW, allowing larvae to experience similar temperatures in previous years or decades (Philippart et al., 2014). Although, environmental factors, including temperature, have been linked to decreased bivalve larval growth at interannual time scales (Poitevin et al., 2023). Additional field monitoring and modeling analyses are needed to estimate the consequences of changing environmental conditions at interannual scales in the MAB to infer fate of larval surfclams. Nevertheless, results from the larval experiment suggest that natural variability in food availability and temperature may decrease survival by 50%.

Seawater temperatures from 21 to 23 °C and food availability levels >5000 cells/ml led to optimal larval development (growth and PLD), with lower temperatures leading to optimal survival. This suggests that high chlorophyll areas including Georges Bank, Nantucket Shoals and most coastal areas in New England may yield optimal larval development (Yoder et al., 2002; Pan et al., 2010). In addition, these results suggest that cooler, more northern areas (i.e., Georges Bank and Gulf of Maine) may yield optimal survival but warmer, middle latitude areas (New York Bight) may yield optimal growth and PLD, and therefore provide context for habitat suitability and surfclam fishery production. For example, while surfclam fishery production in New York State (NYS) waters (within three nautical miles of the coast) has fallen significantly in recent years (O'Dwyer and Hornstein, 2013; Czaja et al., 2023), surfclam production farther off the south shore of Long Island (i.e., in deeper NYB waters) has increased in recent decades, but modeled maximum length has decreased (Díaz, 2022). Surfclam production in inshore NYS waters is declining likely due to negative impacts of OW on adult physiology and/or recruitment, as temperatures above 20 °C lead to decreased adult growth (Munroe et al., 2016; Hornstein et al., 2018) and positive SST anomalies lead to poor recruitment years (Czaja et al., 2023). Present results demonstrated that larval survival decreased with increasing temperature. Impacts due to OW on larval survival may explain the link between OW and declining surfclam recruitment in NYS waters; however, OW may positively affect larval growth. That is, there appears to be a habitat suitability mismatch in inshore NYS waters

where conditions may be ideal for larval growth but are simultaneously leading to decreased larval survival, adult growth and fisheries production. However, the relative impact of decreased larval survival (due to OW) in driving NYS surfclam recruitment declines may be small, as predation can play a large role in surfclam recruitment patterns in the NYB (Weissberger and Grassle, 2003; Quijon et al., 2007). Larval responses may also be linked to increased predation on recruits via latent effects (see Pechenik, 2006 and references therein). Decreases in feeding or metabolic activity of larvae, as a result of environmental stress, can lead to decreased recruit growth, potentially via irregular gill function, energy stores at metamorphosis or molecular links (see Pechenik et al., 1998 and references therein; Pechenik et al., 2002; Pechenik, 2006). Reduced recruit growth may then limit size refuge from predators (Paine, 1976; Eggleston, 1990). In other words, latent effects may increase predation mortality on recruits by decreasing growth of recruits. Indeed, previous studies have found that environmental stress at the larval stage, including poor food quality or quantity, can lead to latent effects in bivalves where juvenile growth rates are negatively impacted (Phillips, 2002; Wacker et al., 2002). This mechanism may also explain the link between OW, declining surfclam recruitment in NYB waters and larval processes. Near Georges Bank however, an area that experiences high surfclam production unlike NYB/NYS waters (NEFSC, 2014; Díaz, 2022), larval development and survival may be relatively high. While success of the surfclam fishery on Georges Bank may be due to ideal conditions for adults, results from the larval experiment suggest that conditions in Georges Bank may also be optimal for planktonic growth and survival.

#### 4.4. Experimental design considerations

While authors of the present study assert that employed approaches minimize lab-based confounding artifacts (e.g., simulating natural planktonic grazing pressure in the lab via lower larval and algal densities), caution should be taken in firmly concluding food limitation due to inherent experimental limitations. For example, natural processes in the plankton such as interspecific competition, interspecific variability in nutritional properties of phytoplankton taxa, increased patchiness in food availability and hydrodynamic impacts all likely play a role in larvae-phytoplankton interactions and are difficult to account for in a lab experiment (Harris, 1988; Rothschild and Osborn, 1988; Seuront, 2005). Mesocosm experiments in the field may provide further insight on food limitation for bivalve larvae. Nevertheless, it should be pointed out that the observed algae cell concentrations equate to a range of chlorophyll concentrations (based on the quantified linear relationships between cell and chlorophyll concentrations) of ~0.8–6.8 µg/L. Mann (1985) documented abundances of larval surfclams on Georges Bank within a chlorophyll concentration range of 0.1–3.0 µg/l. Additionally, Tremblay and Sinclair (1990) documented abundances of larval sea scallop (which overlap in distribution with surfclams) in the Gulf of Maine with a chlorophyll concentration range of 0.1–6.0 µg/l. These studies therefore highlight the potential ecological relevance of the food availabilities (and therefore their impacts on surfclam development) used in the present experiments.

Substantial variability was unexplained, particularly for larval survival. Therefore, inferring survival results to the natural environment should be done with caution. While it is not uncommon for larval bivalve survival to be highly variable, sources of such survival variation should be considered. Observed food availability levels were highly variable. Variable food availability, although a characteristic of phytoplankton supplies in continental shelf waters in the northwest Atlantic, may have contributed to remaining response variability (Flagg et al., 1994; Zhang et al., 2023). Nevertheless, there should be more confidence in extrapolating growth and PLD results to the natural environmental, relative to survival results. Therefore, these authors recommend that the employed experimental design may be appropriate for future studies concerned with growth and/or PLD, but alternative designs (e.g., those including



true replicates) may be necessary for more reliable survival results.

While experimental target temperatures were met, target food availability levels were not. More specifically, observed algae concentrations for the low food availability levels (100, 200 and 500 cells/ml) were substantially higher than target levels. This is not entirely surprising as clearance rate trials, which helped determine specific volumes for algal additions to meet target algal concentrations, did not account for the effect of food availability on clearance (loss) rates. Therefore, loss rates in the low food availability experimental units were likely over estimated, as decreased food availability is known to decrease invertebrate larval clearance rates (Almeda et al., 2010; Fileman et al., 2014). Therefore, this outcome may limit the robustness in making accurate predictions for locations that experience food availability levels lower than those observed in this experiment. Additionally, observed algae concentrations were more variable than observed temperatures. However, it may be that the high variability observed in algae cell concentrations should not limit habitat quality implications and predictions for the field, as surfclam larval habitat also experiences large variability in food availability levels. For example, Xu et al. (2013) found that in summer, MAB surface waters (i.e., surfclam larvae habitat), chlorophyll concentrations may quadruple on time scales less than one month (i.e., surfclam larvae PLD). Furthermore, diurnal cycling may allow for such variation on time scales less than 24 h. For example, Lucas et al. (2014) found that in continental shelf waters off South Africa, chlorophyll concentrations may also quadruple in less than 24 h.

Relative to the traditional feeding regime approach of batch feeding (also known as pulse feeding) every 24 h, the semi-continuous feeding regime approach used in the present experiments may better capture invertebrate larvae-phytoplankton interactions and encounter rates (Martínez et al., 1995; Ramirez et al., 1999). This speculation is based on the idea that a batch feeding regime would create strict cycles including steady declines in food availability, followed by sharp increases in food availability, a presumably uncommon phenomena in the plankton. Temporal trends and variation in natural invertebrate larvae-phytoplankton interactions and encounter rates remain unknown, but it is likely that such encounter rates do not include well-defined cycles with dramatic increases, as represented by a 24-h batch feeding regime approach. Future studies may consider Lagrangian models coupled with field work that track marine invertebrate larvae through time to unravel how food availability and prey encounter rates change temporally throughout the PLD. Such work has been done for fish larvae and related models have provided insight on copepod-prey encounter rates (Caparroy, 2003; Torri et al., 2023). This information could then be used to design experiments and feeding regimes that simulate natural phytoplankton-larvae interactions and encounter rates more accurately.

Local adaptation must also be considered when extrapolating results throughout the distribution of the surfclam and when comparing results to other studies (Sanford and Kelly, 2011). Specifically, since broodstock were collected from the Gulf of Maine, extrapolating results to the MAB may be interpreted with caution due to potential local adaptation (Sorte et al., 2011). Although it should be noted that the present study found that 22–23 °C yielded optimal larval growth and previous studies using broodstock from the MAB, also found that 22–23 °C yielded optimal growth (Loosanoff and Davis, 1963). Local adaptation may however explain the surprising results regarding recruit survival continuously increasing with temperature, as Acquafredda et al. (2019) found that in aquaculture settings using broodstock from New Jersey, post-settlement surfclam survival decreased above 18 °C. Nevertheless, in addition to local adaptation or geographic-based trait differences, experimental design may explain these seemingly contradicting results. For example, in the present study, recruits were held at experimental conditions for only three weeks. It is possible that had the experiment been extended beyond that time, higher temperatures may have negatively impacted recruit survival similar to those observed for larvae. Additionally, prior to the experiment, recruits were held at 23 °C, per standard hatchery

protocols, and may have been acclimated to, or unintentionally selected for higher temperatures (Morley et al., 2012). It should be noted however that in the recruit experiment, surfclam growth peaked at 20–21 °C, aligning with Acquafredda et al. (2019), who also found that surfclam recruit growth was highest at 20.2 °C. Although intended to mimic natural/field conditions (e.g., via natural organism densities), recruit experiment results should be interpreted with caution when extrapolating to field conditions due to potential experimental design artifacts. While these results may contradict previous studies, there is coherence within the present study. Specifically, recruit clearance rate increased with increasing temperatures, suggesting that higher temperatures may be ideal and increase recruit metabolic activity.

#### 4.5. Conclusions

Analyzing how commercially and ecologically important species respond to temperature variability is common. However, less common is predicting how a species may respond to the full breadth of temperature and food availability levels it may encounter throughout its distribution. Furthermore, in a laboratory setting, the interaction between natural variation in food availability and temperature is relatively understudied for marine invertebrate larvae due to difficulty in simulating planktonic trophic interactions. The present study found that development at two life stages of the commercially important bivalve, *Spisula solidissima*, the Atlantic surfclam, will vary substantially based on natural variability in temperature and food (phytoplankton) availability found throughout its range. More specifically, larval development in coastal areas may benefit from increased food availability, and larval growth in middle latitude areas (e.g., New York Bight and Georges Bank) may benefit from moderate temperatures, but temperature increases will likely negatively impact larval survival. These results also suggest that larval processes, such as larval dispersal, may be impacted by changes in temperature and food availability that alter PLD. Furthermore, climate change induced decreases in food availability and OW may have negative consequences for Atlantic surfclams throughout most of its distribution. Results of this study should contribute to improved biophysical models that simulate larval dispersal, and in creating habitat suitability models that assess variability in larval growth and survival in habitat through space and time. While this study used the Atlantic surfclam as a model species, food availability results may suggest potential food limitation for larvae of other marine invertebrates and bivalves. Furthermore, the unique experimental design used in this study may not only be considered for assessing how other marine taxa may respond to variability of habitat characteristics that may be manipulated in a laboratory setting, but can also be considered for future studies interested in habitat suitability modeling.

#### CRediT authorship contribution statement

**Raymond Czaja:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Brian Beal:** Resources, Project administration, Investigation, Funding acquisition, Conceptualization. **Kyle Pepperman:** Methodology, Investigation, Conceptualization. **Emmanuelle Pales Espinosa:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition. **Daphne Munroe:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Robert Cerrato:** Formal analysis, Conceptualization. **Evan Busch:** Resources, Methodology, Investigation. **Bassem Allam:** Writing – review & editing, Supervision, Investigation, Funding acquisition, Conceptualization.

#### Declaration of competing interest

The authors declare no competing interests.

## Data availability

Data will be made available on request.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2023.108515>.

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