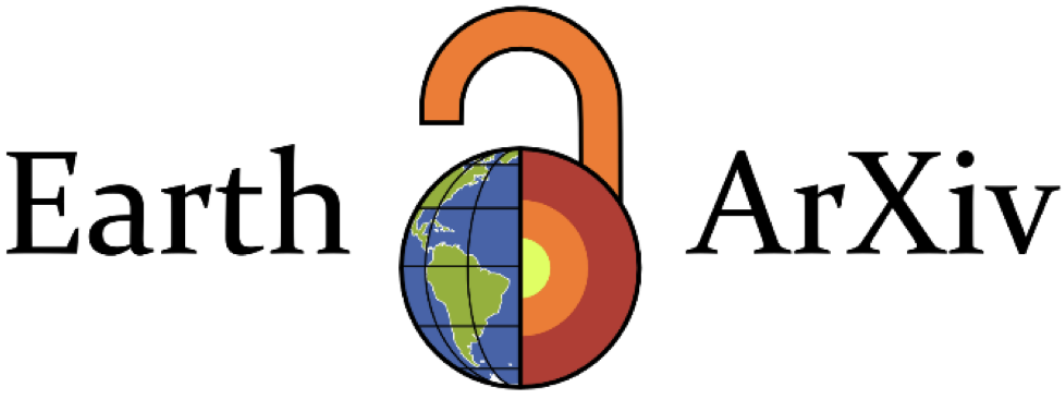

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Ocean warming and acidification alter larval development and swimming behavior in the Atlantic sea scallop, *Placopecten magellanicus*

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Abstract

Ocean warming (OW) and ocean acidification (OA) are expected to have wide-ranging consequences for populations in marine systems caused by organism-level responses at a range of life history stages, including early larval stages. The Atlantic sea scallop, *Placopecten magellanicus*, is an economically important bivalve species that may be vulnerable to ocean change, but larval responses remain unclear. While the effects of OW and OA are known to impact adult sea scallops, little is known about the interactive effects of these two factors on early life stages. Larval dispersal is key to population-level patterns (e.g. abundance and distribution), but is contingent on growth rates and vertical swimming behaviors, which are both influenced by environmental conditions. Here, we evaluate the combined effects of OW and OA on larval development and behavior in a factorial lab experiment. We maintained larval sea scallop cultures up to metamorphosis under a range of physico-chemical conditions (17°C and 14°C, and pH 7.3, 7.6, 7.9). Sea scallop larval development time was temperature dependent (1 vs. 1.5 months). There was an interactive effect of OW and OA on growth, where OA limited gains in growth experienced in warmer conditions. OA limited a decline in distribution late in development, while OW dominated individual vertical swimming behavior in intermediate development. Finally, Ω_{Ar} growth sensitivity was intermediate compared to that of other bivalve taxa. These results contribute to an improved understanding of developmental and behavioral responses to OW and OA, and provide information necessary for improved larval dispersal models under ocean change.

KEYWORDS: Atlantic sea scallop; *Placopecten magellanicus*; larvae; ocean acidification; ocean warming; laboratory experiment; survival; growth; pelagic larval duration; swimming

Introduction

Shifts in the distribution and abundance of populations caused by ocean change (Ross et al. 2023) threaten ocean-based livelihoods and food security (SDG 14)(UN DESA 2025). For many marine species, dispersal, or the exchange of individuals across space and time, happens primarily during the pelagic larval stage (Cowen & Sponaugle 2009). This phase in early life history is often sensitive to multiple environmental conditions (Espinel-Velasco et al. 2018), and resulting physiological and behavioral responses underlie consequences for connectivity and population distribution (Raimondi & Keough 1990). Ocean warming and ocean acidification have been recognized to affect a range of biological processes in marine species (Kroeker et al. 2010, Parker et al. 2013, Ekstrom et al. 2015, Alter et al. 2024). Early life history stages are especially sensitive to the surrounding environment (Byrne & Przeslawski 2013, Przeslawski et al. 2015), and altered development and movement at this stage may drive changes in population connectivity and distributions (Pineda et al. 2007).

Most marine invertebrate larvae rely on swimming behavior, propelling themselves within the water column using a combination of cilia and/or muscles. Development and swimming are inextricably linked, since as larval develop and progress towards settlement and metamorphosis, their density increases, and their tendency to sink exceeds the ability to swim (Chia et al. 1984). Given that there can be advantages of the free-swimming dispersal (e.g. avoidance of competition, inbreeding, and abiotic and biotic issues at the benthos), and disadvantages (e.g. movement away from suitable habitat, cost of delayed metamorphosis), the duration and extent of dispersal is a mechanism that can constrain marine invertebrate populations (Pechenik 1999). While horizontal advection is well known to have wide ranging impacts on larval spatial distribution and thus dispersal in the ocean, swimming behavior may regulate the position of larvae in the water column and alter transport and dispersal (Metaxas 2001). Given the large-scale population-level consequences that may result from altered dispersal, successfully understanding and managing risk to fished species requires characterizing species-specific developmental and behavioral

responses to ocean change (Cooley et al. 2015, Shotwell et al. 2023, Northeast Fisheries Science Center (U.S.) 2025). Individual-based models (IBMs) of larval transport offer a framework with which to assess how multiple components, or traits, of larval swimming and size-based changes in movement alter vertical distribution of larvae and how future ocean conditions may affect these traits (Zhang et al. 2015, 2016a, Munroe et al. 2018a, Wright-Fairbanks et al. 2025). The inferences derived from these models, however, can be limited by a lack of lab-based larval behavior data, particularly considering how multiple factors affect behavior of understudied species such as the Atlantic sea scallop (Wright-Fairbanks et al. 2025).

The Atlantic sea scallop (*Placopecten magellanicus*, hereafter called 'sea scallop') has the fourth highest value of the U.S. fisheries at 660 million USD (National Marine Fisheries Service 2024). Sea scallops are considered vulnerable to ocean change throughout their life history (Rheuban et al. 2018, Wright-Fairbanks et al. 2025, Berger et al. 2026), as environmental conditions drive patterns in population distribution and abundance (Shumway et al. 1987, Zang et al. 2022). Throughout their life history, sea scallops are exposed to a range of seawater temperature and carbonate chemistry conditions (Hart & Chute 2004, Xu et al. 2017) that can affect their physiology and growth at the juvenile (Pilditch & Grant 1999, Pousse et al. 2023) and adult stages (Grant & Cranford 1991, Cameron et al. 2022). Sea scallops also experience a range of seawater temperature and carbonate chemistry conditions as they disperse during their larval stages (Munroe et al. 2018a, Chen et al. 2021a, Wright-Fairbanks et al. 2025). During development, sea scallop larvae can be transported by ocean currents hundreds of kilometers over a period of up to 45 days (Figure 1) (Culliney 1974a, Tremblay & Sinclair 1990, Tremblay et al. 1994, Munroe et al. 2018a, Chen et al. 2021a, Wright-Fairbanks et al. 2025). Sea temperature experienced during this pelagic stage is known to affect growth, development, and behavior of sea scallop larvae, resulting in predicted shifts in dispersal (Munroe et al. 2018a), but the sensitivity of these traits to elevated pCO_2 is not well understood (Wright-Fairbanks et al. 2025).

For most bivalve species, early larval life stages are extremely sensitive to temperature and elevated pCO_2 (Kroeker et al. 2010, Parker et al. 2012, 2013, Byrne & Przeslawski 2013, Przeslawski et al. 2015, Waldbusser et al. 2015, Alter et al. 2024) because of the dependence of larval shell development and growth on calcium carbonate saturation state (Waldbusser & Salisbury 2014a). Although OA has been shown to affect the growth and survival of larvae of other species of scallops (Parker et al. 2012, 2017, Andersen et al. 2013, Scanes et al. 2014, Griffith & Gobler 2017), lab culture of sea scallop larvae remains an active area of research because these larvae are notoriously hard to grow in a laboratory setting (Avena et al. 2026). Despite these challenges, previous work has demonstrated effects of temperature (Culliney 1974a, Hart & Chute 2004), salinity and temperature stratification (Manuel et al. 2000, Gouda et al. 2006), and food composition (Avena et al. 2026) on the development and behavior of sea scallop larvae. Characterizing responses of sea scallop larvae to seawater carbonate chemistry, and the interaction of OA with temperature, has been however largely unaddressed. This work is crucial, however, to improve our understanding of behavioral mechanisms underlying transport and dispersal (Pineda et al. 2007), better identify and predict shifts in response to ocean change (Fuchs et al. 2020, Wright-Fairbanks et al. 2025) , as well as improve hatchery larval culture efforts (Avena et al. 2026).

Larval dispersal is influenced by developmental speed and the duration that larvae are suspended near the ocean surface, as well as the vertical distribution and vertical swimming behavior of larvae (Pechenik 1999, Pineda et al. 2007). Vertical swimming can depend on environmental conditions including temperature (Munroe et al. 2018a, Chen et al. 2021a) and ocean acidification (Chan et al. 2015). This behavior may be size-dependent (Mann et al. 1991, Manuel et al. 2023), or larvae may alter their swimming to have net movement that is invariant to larval size (Chan et al. 2015). Seawater carbonate chemistry can influence multiple larval traits, including growth, feeding rates, shell calcification rates, and energy balance of bivalves (Stumpp et al. 2013, Waldbusser et al. 2015, Alter et al. 2024) and scallops species (Parker et al. 2012, 2017, Andersen et al. 2013, Scanes et al. 2014, Griffith & Gobler 2017). Such shifts in growth, density, and behavior (Czaja et al. 2023), might affect sea scallop vertical

movement and dispersal (Wright-Fairbanks et al. 2025). Lab experiments on the growth, development, and behavior of sea scallop larvae are thus needed to improve the realism and application of such larval dispersal models.

Here, we cultivate sea scallop larvae across a factorial set of seawater temperature and OA conditions and evaluate development and behavior by focusing on the specific traits used to parameterize IBM-coupled larval dispersal models, including survival, growth, distribution, and individual behavior. We hypothesize that (1) warming from 14°C to 17°C will accelerate growth and development, while OA (pH 7.9, 7.6, 7.3) will counteract these gains; (2) faster development in warmer water will cause earlier downward movement characteristic of later-stage larvae, while OA will counteract this response; and (3) faster development in warmer and ambient pH conditions will cause a decline in upwards vertical swimming late in development. Finally, we quantify larval growth as a function of aragonite saturation state (Ω_{Ar}) to evaluate OA growth sensitivity, a parameter necessary for improving sea scallop dispersal models. By evaluating how temperature and OA affect developmental and behavioral responses, our results provide lab-based data needed to improve dispersal projections under ocean change.

Methods

Animal Husbandry

The experiment was conducted at the Downeast Institute (DEI) Ocean and Coastal Acidification Laboratory (Beals, Maine, USA). This experimental system consisted of 30 independent tanks, which were 6L flat-bottomed polypropylene aquaria independently controlled to ± 0.01 pH units and ± 0.1 to 0.3°C (Apex, Neptune Systems, Morgan Hill, CA USA) (Czaja et al. 2023). Custom heat jackets heated a water bath surrounding each experimental aquaria. The pH probes used to control the system (Neptune Systems double junction pH probes) were first calibrated with NBS buffers. Then a pH offset was calculated for each pH probe using a fast-response pH probe (Oakton glass double junction, 35805-67,

Charleston, SC USA) calibrated to synthetic seawater buffers prepared at DEI (Paulsen & Dickson 2020, Czaja et al. 2023). These offsets were calculated every other day throughout the experiment to control CO_2 addition based on measured pH on the total hydrogen ion scale (pH_T).

A fully factorial design was used to test two temperatures and three OA treatments. The six experimental treatments were randomly assigned to each of the 30 tanks using a random number generator (n = 5). Temperature treatments (14°C and 17°C) represent current and future SST conditions (Alexander et al. 2020) and are within a range of temperatures likely experienced by larvae, depending on the season and latitude (Munroe et al. 2018a). Carbonate chemistry treatments (7.9, 7.6, 7.3 pH) were selected to represent current (>7.9 pH, >2.5 aragonite saturation state, Ω_{Ar}) and future (7.6 pH, ~1.5 Ω_{Ar}) scenarios for surface waters in the Northeast Atlantic and New York Bight (Cooley et al. 2015, Gruenburg et al. 2021, 2023). Very high pCO_2 conditions (pH 7.3, ~0.7 Ω_{Ar}) are not expected in sea surface waters as a result of OA alone (Cooley et al. 2015), but were used here to investigate the effect of extreme conditions, which might occur when OA is combined with coastal acidification (Salisbury et al. 2008, Waldbusser & Salisbury 2014b), or under mixing and respiration processes involving deeper CO_2 enriched water (>30m) (Feely et al. 2010, Gruenburg et al. 2021).

Broodstock were collected from Cobscook Bay and Jonesport, ME, and maintained in flow-through chambers at DEI for 2-3 years prior to spawning. These animals were conditioned at temperatures ranging from 7-11°C and in pH ~7.8. A total of 2 males and 3 females were spawned for this experiment because of the difficulty of spawning this species. Spawning and fertilization were conducted according to standard hatchery procedures. Briefly, animals were removed from the conditioning tank, rinsed with fresh water, and kept out of water at room temperature for 45 minutes. A single male was strip spawned, and 3-5mL of live sperm added to a floating tray holding the females where they were agitated using an airstone for 30 minutes at 16°C to induce egg release. Females were also cold shocked at 9C for 30 minutes after 2 cycles of the warm water. After females spawned, an additional male was strip spawned,

and eggs harvested then combined with the remainder of the sperm for fertilization. Following fertilization (visible polar bodies), embryos were rinsed on a 25µm sieve, and transferred to a 400L conical at 15°C where initial growth and survival was monitored for 3 days.

Developing veliger larvae were stocked in 30 experimental tanks (n = 5 replicates per treatment) at a density of 4 individuals mL^{-1} in filtered seawater (FSW, 0.5 µm filter) at ambient conditions (15°C, pH 7.8). Experimental conditions were then achieved by adjusting temperature 1°C and pH 0.1 units no faster than every 3 hours in each tank until target treatment settings were met over a three day period (Czaja et al. 2023). FSW was bubbled with air for 2-4 hours and then pH was adjusted by adding CO_2 (as described above), prior to filling the experimental chambers. All tanks received continuous low flow aeration producing relatively still conditions in the tanks (≤1 bubble s^{-1}) and were maintained at a constant temperature and pH, as described above. Larvae were fed 30,000 cells mL^{-1} of 80% *Tisochyrsis lutea* (Tiso) and 20% *Diacronema lutheri* (Mono) until they were >63µm, at which time they were fed 40% Tiso, 20% Mono, and 40% *Chaetoceros muelleri* (Tremblay et al. 2020, Avena 2025). Tanks were cleaned, water replaced, and larvae were sieved and fed on a two-day cycle. The concentration of food (cells mL^{-1}) was measured on the day after feeding with hemocytometer counts, and food was not added on these days because counts remained high (>20,000 cells per mL). Experiments were terminated at 33 days (17°C treatment) and 44 days (14°C treatment), as larval density in the 17°C treatment declined earlier than in the 14°C treatment.

Seawater pH on the total hydrogen ion scale (pH_T, Oakton glass double junction, 35805-67, Charleston, SC USA, ± 0.01 pH unit) and temperature (Oakton, ± 0.01°C) were measured in each of the experimental chambers every other day. Seawater samples (500mL) were collected in borosilicate bottles and preserved using mercuric chloride for later total alkalinity (TA) and dissolved inorganic carbon (DIC) analysis. Salinity was measured at the time of sample collection (YSI ProSolo, ProDSS ODO+CT, Yellow Springs, OH USA), and pH_T was measured for each bottle sample (Oakton, 35805-67). TA and DIC were analyzed

using a VINDTA 3C automated analyzer (Marianda, Kiel, Germany). TA was analyzed through Gran titration and DIC was coulometrically measured (Dickson et al. 2007). TA and DIC were verified using certified reference material (CRM, batches 221 & 224, Scripps Institution of Oceanography, UC San Diego USA). The TA and DIC analyses were used to correct a pH-dependent offset in pH_T measurements (n = 15, 0.04 root mean square). TA and pH_T were chosen for carbonate chemistry calculations because pH_T was measured frequently throughout the experiment, and was thus considered to provide a more representative estimate. CO2sys (v2.1) (Environmental Sciences Division 2012) was used to calculate the remaining parameters (pCO_2, aragonite saturation state, or Ω_{Ar}) from average TA and pH_T for each treatment (K_1 and K_2 from Leuker et al. (2000); $KHSO_4$ from Dickson (1990); B_T from Uppström (1974)). Standard error of pCO_2 and Ω_{Ar} was then estimated in CO2sys based on the full range of the standard errors for TA and pH_T.

Developmental responses

Survival was quantified on days 5, 9, 17, 25, 31, 36, 40, and 44 by estimating the total number of remaining live larvae (using ciliary movement, and shell contents) relative to the initial number of live larvae in each tank at the end of the acclimation period (day 5). The number of larvae was estimated from three, 1-3mL samples of ~9X concentrated larvae (6L tanks concentrated in 700mL) as part of the tank cleaning and transfer process. Larvae were preserved with 0.05% glutaraldehyde on days 5, 9, 17, 23, 25, and 31 for size measurements and stored at 4°C for growth rate analyses. After day 31, only larvae from the 14°C treatment remained. To avoid uneven sampling across time, the growth and swimming analyses focused on the first 31 day period in which individuals from all treatments were present. Growth rate was measured by the increase in larval shell length through time (15 larvae per tank per sampling) using image analysis in ImageJ (Schneider et al. 2012) on photos captured on an inverted compound microscope (100X, Nikon Eclipse TE2000-S Melville, NY USA). Features of larval development

assessed included shell shape (straight-hinge, umbo veliger), the appearance of a foot, and bottom seeking behavior (Culliney 1974b).

The proportion of larvae suspended was used to evaluate pelagic larval duration (PLD) over the course of the experiment. To capture the vertical profile of the larvae and evaluate the proportion suspended at the top of the water column, seawater was sampled directly from each tank and the larval concentration in these samples was compared to the overall larval concentration measured in each tank (Figure S1). 50mL of seawater was sampled from the tank at the top (5 cm from the surface) and middle (15cm from the surface) of the experimental chamber, and the larvae from each sample were carefully concentrated on a 3.5cm diameter 45µm sieve, poured into individual wells (1 well per tank) on 6-well plates, and counted on an inverted microscope (Nikon Eclipse Ts2). At the end of the experiment, the sample volume collected from each tank was increased to 100mL to increase our ability to make counts at a low larval density. The proportion of larvae suspended was evaluated as the ratio of the average concentration of the middle and top samples divided by the overall concentration of larvae in the tank. Gompertz fit curves were used to evaluate suspension over time, and a separate analysis during days 33 – 44 were used to evaluate pH differences at the end of the larval stage (see statistical analysis section below for details). A qualitative estimate of PLD was also reported as the duration of time before the proportion of suspended larvae fell below 1%.

Behavioral responses

Larval swimming behavior was recorded as described by Caracappa and Munroe (2019) and Manuel et al. (2023). Videos were recorded at 2.5 and 4 weeks post fertilization of larvae from each of the 30 tanks (18-22 and 28-32 days post fertilization, DPF, respectively). Larvae were illuminated with an overhead light and an 18-minute video was recorded using a waterproof digital camera (macro mode, Olympus Tough TG-7, Bethlehem, PA USA), as illustrated in Figure 2. Chambers were located within a 1.5L water bath filled with FSW at the appropriate experimental temperature. The camera was submerged in the

water bath and elevated ~1.5cm above the base of the chamber. The focal area was approximately 1cm high by 1.7cm wide with a focal distance of 7cm, and was centered approximately 4cm above the base of the chamber. Larvae were added to 1.3L of FSW at the experimental pH and temperature to obtain a density of about 0.7 larvae mL^{-1}. Seawater pH and temperature were measured at the start and end of each video to evaluate stability in the swimming chambers. Approximately 1/3 of the opening of the top of the 30cm high chamber was covered with a plexiglass sheet, stabilizing the ruler and light source. The light source was a flashlight (COAST Polysteel 600, 17800cd, 6850K) (Caracappa & Munroe 2019), which was fitted with a neutral density filter (0.9ND, Renian, polyester film) that transmitted just 11.7% of light (over the range 300-1000nm), to ensure low light conditions. Additional trials compared larval swimming in low (0.9ND) and high light (0.3ND filter, which transmitted 48.2% of light), but since light is known to alter swimming behavior in sea scallop larvae, as reviewed in Chen et al. (2021a), low light was used for all further analyses. After larvae were transferred to the recording chambers they were briefly acclimated to the chambers (Manuel et al. 2023), over 5-10 minutes to allow acclimation while avoiding drift in pH and temperature. Then, after starting the video, the latter 15 minutes of the 18 minute video were used in subsequent analyses.

The videos were analyzed with a machine-learning based particle tracking software, Idtracker.ai (v. 6.0.7)(Romero-Ferrero et al. 2019), with Python (v. 3.12.0), NumPy (v. 2.0.1)(Harris et al. 2020), and OpenCV (4.12.0.88, Figure S2) (Bradski 2000). For each video, 30 10s clips were randomly subsampled using an automated Bash script from the latter 15 minutes of each 18 minute video (FFmpeg Developers 2025). Size was calibrated by the ruler in the video frame (ImageJ(Schneider et al. 2012)). To enable tracking of particles in low light conditions, we tracked particles that were frequently visible and filtered out transient bright spots visible in the videos. This was achieved by automating python (Shapelyv.2.1.1) (Gillies et al. 2025) and idtracker.ai to identify for each 10 sec clip, individual arenas (>100 by 100 pixels) that frequently included a bright particle, and select a minimum threshold brightness value that produced no more than 4 tracks per 10s clip. This pipeline was also validated for videos taken at a higher

light level (described above) to ensure tracking accuracy. Idtracker.ai was used to generate position and time data for the larval tracks . Automated post-processing was then used to remove artifacts in the position data (Caracappa & Munroe 2019, Manuel et al. 2023). This included removing large jumps at each 1/60th second time increment, as well as removing short track segments that were <3s duration (Caracappa & Munroe 2019, Manuel et al. 2023). The tracks were then down-sampled from a $60s^{-1}$ framerate to 60 × 170ms increments by averaging each 10 frames, and these tracks were used for subsequent calculations of behavioral components. This method avoided errors associated with smoothing functions.

Video clips typically contained 1-3 high quality larval tracks. To avoid clips with many tracks (i.e. >3) dominating the analysis, all swimming behavior metrics (w, P, P_{up}, s. w_{up}, w_{down}) were summarized at the video clip level, as described below. Vertical velocity (w) was calculated as the median vertical velocity for each individual larval track, and then aggregated by averaging for each clip. Swimming speed (s) and swimming angle (Θ) were calculated for each trajectory before aggregating by estimating one median value for each video clip. Swimming angle was calculated as follows ($\Theta = arctan(median(\triangle y)/median(\triangle x))$), where $\triangle x$ and $\triangle y$ are the incremental changes in x and y over time within each trajectory (Caracappa & Munroe 2019).

The fractional components (fraction of time swimming - P, fraction of time swimming up - P_{up}) were calculated as follows. The fraction of time swimming was first calculated as the percentage of non-zero speed increments for each trajectory (speed > 2.5% quartile, or 18μm s^{-1}). The fraction of time swimming up was calculated from non-zero speed increments as the percentage of positive velocity increments for each trajectory. To classify the fractional data (Manuel et al. 2023), individual larval tracks were first determined to be either swimming or non-swimming (>80% of intervals), and then further classified as upward swimming when 50% of the intervals had a positive vertical velocity. Each video clip was then

297 assigned a binary value, where clips in which the majority of tracks were oriented upward were assigned
298 as 1 and those dominated by downward tracks were assigned as 0.
299
300 The vertical velocity model components (vertical velocity up - w_{up}, vertical velocity down - w_{down}) were
301 estimated as the median upwards or downwards velocity for each individual trajectory. These were then
302 aggregated by calculating the median w_{up} or w_{down} for each clip. For two tanks in the pH 7.9 and 17°C
303 treatment at 2.5 weeks there were no downward trajectories, so an estimation of downwards velocity is
304 limited to videos from 3 tanks.

305 ## Data analysis

306 Statistical analyses were performed using the R programming language (R v. 4.5.2, Rstudio v.
307 2025.09.2+418) and the packages nlme, ggplot2, lme4, glmTMB, and MuMIn (Pinheiro et al. 1999, Bates
308 et al. 2003, Wickham et al. 2007, Bartoń 2010, Brooks et al. 2017a, R Core Team 2020). Survival rate
309 was modeled directly from change in concentration relative to day 0 ($Survival_{day} = C_{day,Tank} - C_{0,Tank}$) to
310 avoid introducing sampling error in the discretization of concentration to a time-event data structure
311 (Kotani et al. 2011), and because <10% were removed by destructive sampling throughout the 44 day
312 experiment. A Gompertz model was chosen (Survival rate = exp(-(b / a) * (exp(a * day) - 1))) to describe
313 the relationship between time and survival where mortality risk exponentially increases with age (Hazard
314 = b exp(a * day)) (Wilson 1994). An AIC grouped model comparison suggested temperature and not pH
315 be included as a factor in the model (Table S1, NLS, minpack.ls package). A subsequent non-linear mixed
316 effects analysis (nlme package) was used to predict survival rate for each temperature treatment as a
317 function of time with tank as a random factor, where pH treatment was pooled.
318
319 To evaluate growth, AIC comparison was used to compare alternative exponential growth model
320 structures. The selected exponential model was ($L = a\, e^{b\, day}$), where L is length, and day is the number of
321 days post fertilization, where the coefficient for growth (a, size at 0 days post fertilization) was held

constant across treatments. This model was fit using a two-step process. First, the coefficient (a) was determined for all data. Then, a nonlinear mixed-effects model was used to evaluate the effect of temperature, pH, and time, on the exponential growth rate (b) with the tank as the random factor (Pinheiro et al. 1999, Pinheiro & Bates 2000) and evaluated with likelihood ratio tests of the grouped model comparison.

The proportion of larvae suspended over time was modeled using a modified Gompertz model, where a coefficient was added (c) to scale to the initial value rather than assume an initial value of 1. One outlier was removed in which the proportion suspended was twice the value of all other samples. This model was $R_S = c * \exp(-(b / a) * (\exp(a * day) - 1$ with R_S as proportion suspended. An AIC grouped model comparison was used to evaluate model fits, and modified Gompertz model fit separately at each temperature was selected as the best model among the non-linear models tested (Table S4). Given that treatment differences were qualitatively observed for ~ 1 day at 17C and ~ 10 days 14°C, a separate Kruskal Wallis rank order test of the effect of pH on suspension was performed on the pooled average of tank samples from day 33 – 44 at 14°C. A low sample size (n = 2 for two out of three treatments) precluded statistical analysis of the 17°C treatment when differences were visually apparent.

Generalized linear mixed-effects models (GLMMs) were used to evaluate the effect of pH, temperature and time on all swimming parameters, with distributions chosen specifically for each metric. In all cases, AIC comparisons of models were performed to eliminate interactive effects that increased the AIC score (Bartoń 2010). In all cases, simulated residuals were used to assess the residuals and confirm appropriateness of hierarchical model choices (Hartig 2016).

Vertical velocity had a distribution with a large tail, so a GLMM with a Student's t distribution (Caracappa & Munroe 2019) was used to evaluate the effect of pH, temperature and time on vertical velocity (w) of larval swimming with the tank as a random factor (glmmTMB package). The Student's t

distribution does not work with Restricted Maximum Likelihood (REML) so the corresponding models were fit with Maximum Likelihood.

The fractional and velocity individual swimming behavioral components were analyzed differently. First, binomial GLMMs were used to evaluate the effect of pH, temperature and time on fraction swimming and fraction swimming upwards (P, P_{up}), with the tank as a random factor (glmer function) (Bates et al. 2003). This model predicts the probability that a randomly sampled clip will have a majority of swimmers or upwards swimmers.

Swimming speed (s), was heavily skewed with a long tail at higher velocities, so a gamma distribution with a log-link was used for this analysis, and a GLMM was used to evaluate the effect of pH, temperature and time on s with the tank as a random factor (glmmTMB package). For both w and s, dispersion differed by treatment, the effect of temperature, pH, and time was evaluated using AIC comparison and included in the analysis (dredge function) (Bartoń 2010). A gamma distribution with a log-link was also used for analyses of upwards and downwards vertical velocities (w_{up}, w_{down}). Specifically, Gamma log-link GLMMs were used to evaluate the effect of pH, temperature and time on w_{up} and w_{down} with the tank as a random factor (glmmTMB) (Brooks et al. 2017b). A summary of the effect sizes of temperature and pH on net vertical velocity and individual swimming behavioral components at both 2.5 and 4 weeks is also reported in the supplement, though reported effect sizes scale differently for each group (net vertical velocity, proportions, and kinetic responses) depending on data transformation and GLM distribution family.

Results

Water chemistry

The experimental manipulation produced a range of pH and Ω_{Ar} values (Table 1). TA was relatively among the treatments, such that average total alkalinity (TA) ranged 2200 to 2207 umol kg^{-1}. (Table 1). The lowest Ω_{Ar} occurred in the 14°C & 7.3 pH treatment, while the highest Ω_{Ar} occurred in the 17°C & 7.9 pH treatment (Table 1, range ~0.67-2.9 Ω_{Ar}).

Developmental responses

Larvae experienced earlier mortality at 17°C as compared with 14°C, but there was no effect of OA on mortality (Figure 3, Figure S3, Table S1, S2). There was a significant interaction between OA and temperature on growth rate per day (likelihood ratio test: $\chi^2 = 6.51$, df = 2, P = 0.039, Figure 4, Table S3, Figure S4). OA (7.3 and 7.6 pH) limited otherwise faster growth at 17°C observed at ambient pH (7.9; Figure 4, Table S3, Figure S4).

The animals were in the veliger stage for all behavioral and growth measurements. No discernable eye spots were observed during the experiment, and no probing feet were observed until after the conclusion of the experiment (1 animal on >day 46). At the end of the 31 days, 100% of the veligers at 14°C remained in the straight-hinged stage or an intermediate stage. In contrast, >15% of the veligers had grown into the umbo veliger stage by this date in the 7.9 & 17°C treatment (Figure S5).

The proportion of larvae suspended in the experimental chambers ranged from values above 1, indicating larvae had a higher concentration in upper water column samples, to very low values (<0.01) indicating concentrations in samples collected from the top and middle of each tank were much less than the average overall concentration in the tank. Overall, the decline in larval suspension differed by temperature, where

394 the proportion of larvae suspended declined more gradually at 14°C compared to those at 17°C (Figure 5,
395 Table S4). This decline in overall suspension over time was also mirrored in comparisons of the count of
396 animals in the top, mid, and base of the chambers (Figure S6). While the proportion of larvae suspended
397 dropped dramatically at the end of each trial in the 7.9 treatment group in both experimental temperatures,
398 the more gradual decline at 14°C allowed for improved sampling at this crucial time, and larval
399 suspension was significantly reduced at ambient pH (Dunn $p = 0.033$, Figure 5).
400
401 A pattern was observed visually in tank cultures as well, where animals in the intermediate OA group
402 (7.6) remained suspended as tank cultures concentrations of live larvae dropped off (17°C, DPF 31, 14°C
403 DPF 44). Small sample sizes on this final day limit statistical analysis of this phenomenon at 17°C, where
404 the proportion of larvae suspended declined dramatically in both the 7.3 and 7.9 treatments ($n = 2$ tanks
405 remaining), but not the 7.6 treatment. Similarly, on the final day in which survival dropped below 5% for
406 larvae grown at 14°C (DPF 31), the proportion of larvae in the 7.9 group declined dramatically, but ~20%
407 of larvae in the 7.3 or 7.6 group remained suspended.

408 ## Behavioral responses

409 A total of 926 larval tracks (500 10-sec clips) from 36-140 larvae per treatment were used in the analysis.
410 Larvae swam at a vertical velocity ranging from 510 μm s^{-1} downwards to 252 μm s^{-1} upwards (0.01%
411 and 99% quantiles), which was movement up to 3-5 times their body length s^{-1}, depending on their size.
412 No swimming metrics were normally distributed (Shapiro-Wilk, $p < 0.05$). Median vertical velocity (w),
413 speed (s), velocity upwards (w_{up}), and downwards (w_{down}) had a distribution with long tails, and (w) was
414 skewed at the low end. The fraction of time swimming (P) and the fraction of time swimming upwards
415 (P_{up}) was often skewed towards 1.
416
417 There was a significant effect of temperature, but only a marginal effect of OA on the median vertical
418 velocity (Table 2, Figure 6). The vertical velocity tended to be negative at 14°C, and positive at 17°C.

Binomial models showed there was no significant effect of OA on the fraction of time swimming or fraction of time swimming upwards (Table 2, Figure 7). Warming was also associated with a positive swimming angle, in contrast with 14°C conditions (θ, Figure S7). Warming increased the fraction swimming and the fraction swimming upwards, and for the fraction swimming upward, this difference increased with time (Table 2, Figure 7). There was also an interaction between the time, temperature, and the OA condition, consistent with increased frequency of upwards swimming in the intermediate OA treatment (pH 7.6).

There was considerable tank-level variability in swimming speed (s), and while there was an interaction between time, temperature, and pH, indicating the interaction between temperature and pH may depend on time, no individual treatment differences were observed for this metric (Table 2, Figure 6). Temperature increased mean upwards velocity, apparent only at week 4 (Table 2, Figure 8). There were interactions between pH and time, and temperature and time on the downwards velocity, with Sidek post hoc tests indicating that downwards velocities were highest in combined warming and OA conditions (pH 7.3 and pH 7.6, Table 2, Figure 8).

Discussion

Overview

Larval dispersal underlies population connectivity and recruitment in marine species, and ocean change could significantly reshape these processes by altering developmental and behavioral mechanisms underlying transport (Zhang et al. 2016b, Munroe et al. 2018a, Chen et al. 2021a, Zang et al. 2022, Wright-Fairbanks et al. 2025). Empirical data linking ocean change with developmental and behavioral traits that might alter transport and dispersal, however, is limited and necessary for the improvement of these models (Cooley et al. 2015, Munroe et al. 2018b). In this study, warming had wide-ranging effects on development and behavior, while the effects of OA were largely constrained to slower growth and a

delayed downward shift in distribution. We found that OA conditions counteracted gains in growth and development caused by warmer temperature (H1), consistent with OA experiments with other species of scallops (Parker et al. 2012, 2017, Andersen et al. 2013, Scanes et al. 2014, Griffith & Gobler 2017). We also found that both OA and warming altered the timing of a shift in vertical distribution, with intermediate OA counteracting a shorter duration of suspension in the water column (H2). Finally, (H3) warming had a wide-spread effect on all individual swimming traits, while OA caused an increase frequency of upward swimming late in development consistent with (H2), OA also caused an increase in downwards swimming speeds at warmer temperatures (H3). These results suggests that warming is a more widespread driver of behavior, but that both OA and warming play a role in sea scallop growth and suspension. Examining these developmental and behavioral responses of larval performance is integral to improving larval dispersal models (Munroe et al. 2018a, Chen et al. 2021b, Wright-Fairbanks et al. 2025), and our findings suggest that both OA and warming may affect the transport and dispersal of this commercially valuable species.

Developmental responses

OA conditions counteracted the positive effect of temperature on growth. Elevated temperature (17°C) increased growth, which is consistent with previous work on sea scallop larvae (Culliney 1974a). However, this positive effect of warming was counteracted by OA. A negative effect of OA on growth is well documented in other species of bivalves (Talmage & Gobler 2011, Waldbusser et al. 2015). By 31 days, the combination of warming and ambient pH produced larvae that were 20% larger than those in the other treatments (shell height, Figure 4, Figure S3). Elevated temperature also caused earlier mortality (Figure 3, Table S1, S2), but there was no effect of OA on survival despite slower growth during this period. This study focused on the first 31 days of larval development, during which larvae grew to an average of 140 µm in the warmer (17°C) and ambient pH treatment, which is smaller than typically reported for animals approaching settlement (230 µm) (Culliney 1974a). Although morphometric analyses after day 31 were limited, we observed that a small number of larvae sampled at day 40 had reached the

typical settlement size (230-250 μm), but lacked defining features of pediveliger larvae, such as an eye spot and distinct pedal foot. Sea scallops are known to have the ability to delay metamorphosis depending on environmental conditions (Culliney 1974a), and delays often have adverse outcomes for mollusc larvae (Pechenik 1990, Scanes et al. 2014). Underlying energetic mechanism of developmental delays from cooler conditions differ substantially from that reported under OA. OA can increase metabolic costs and reduce energy available for growth and development, whereas cooler temperatures are typically associated with a similar or reduced metabolic rate (Padilla-Gamiño et al. 2013, Czaja et al. 2023, Gurr et al. 2025). Future work integrating physiological and energetic measurements is needed to determine how these OA and warming influence developmental timing, survival, and metamorphosis.

Vertical distribution is a key component of larval transport and dispersal (Munroe et al. 2018a), and can shift over developmental time (Manuel et al. 1996, Gallager et al. 1996, Munroe et al. 2018b). Since larvae did not develop indicators that they were ready to metamorphose and settle (eye spots, etc.), conclusions about the full pelagic larval duration (PLD) are limited (Culliney 1974a, Munroe et al. 2018a, Wright-Fairbanks et al. 2025), but the duration that larvae remained suspended in the water column differed by treatment. Warming caused a 30% decrease in the duration that larvae were suspended, and larval suspension was lower at ambient pH at the end of the experiment (33 – 44 DPF). These findings suggest that both factors might affect the duration that larvae spend in the surface waters during the pelagic phase. The late veliger D-stage is a known bottleneck for sea scallop hatchery cultivation (Avena et al. 2026), and thus understanding the timing of shifts in vertical distribution is warranted for culture of this species. Certain culture methods may be better suited to increased downwards movement, especially in the late veliger stages (Avena et al. 2026), including a reduced food supply (Culliney 1974b), and thermally stratified tank culture (Pearce et al. 1998, Manuel et al. 2000). The relationship between development and vertical distribution is key for larval settlement success, yet is rarely quantified and warrants further attention for understanding both natural and cultured larval populations.

Behavioral responses

Vertical swimming behavior is a major mechanism controlling larval dispersal because it determines exposure to differing hydrography, temperature, and carbonate chemistry across the water column (Munroe et al. 2018a, Chen et al. 2021a, Zang et al. 2022). Vertical velocities and average speeds (-0.5 to 0.2 mm s^{-1}; ~ 0.15 mm s^{-1} for a 140 um larva at 17°C) were comparable to speeds reported previously (~0.2 mm s^{-1} for a 200 um larva) (Gallager et al. 1996, Munroe et al. 2018a). Warming increased net upwards vertical movement (Figure 6, Table 2), and mean net vertical movement was often positive at 17°C and negative at 14°C (Figure 8, Table 2). This positive effect of temperature on swimming is consistent with studies on other bivalve species, including increased climbing and decreased drifting with warming (Wang & Xu 1997), and changes in viscosity (Larsen & Riisgård 2009), and shifts in ciliary development and action (Yoshihiro et al. 1992). Enhanced upwards movement, however, contradicts the proposed mechanism that thermal response alone causes thermocline-seeking behavior (Munroe et al. 2018a). In thermally stratified lab settings, sea scallop larvae can be 100X more concentrated within the top cm of the water during the night, and then move downwards toward the thermocline in the day (Gallager et al. 1996). This work, in which larvae were cultured in constant temperature and carbonate chemistry conditions over the course of their development, differs from that experienced in a thermocline where larvae experience a thermal gradient as they move, and suggests that acclimation to a single temperature alone does not explain the phenomena of thermocline-seeking behavior.

Capturing the influence of temperature and OA on individual state-dependent components of swimming is necessary to understand and simulate mechanisms underlying net vertical movement (Munroe et al. 2018a). These components included the proportion of time swimming, the proportion of time swimming upwards, and the mean vertical velocity upwards and downwards (Munroe et al. 2018a). Warming, and not OA, increased the proportion swimming, and the proportion swimming upwards (Figure 7, Table 2), corresponding with an altered swimming angle (Figure 6). There was no effect of warming or OA on

519 swimming speed upward or downwards early in development, but by late development there was a
520 significant interaction between OA and warming on downward swimming (Figure 6, Table 2), suggesting
521 a synergistic response (e.g. up/down velocity) for this metric. This finding suggests that the frequency of
522 upwards and downwards movement, while potentially modified by swimming speed, may largely drive
523 the direction of movement.
524
525 Overall, temperature was the main driver of net vertical velocity and frequency metrics, but there was an
526 interaction between OA and warming on velocity downwards. Vertical movement is often dependent on
527 larval size (Mann et al. 1991), but while size differed among treatments, net vertical movement was
528 mostly invariant to OA, consistent with compensatory response observed in another invertebrate larval
529 species (Chan et al. 2015). Consistent with increased upwards distribution in this treatment described
530 above, there was also a trend of increased net upwards movement in the intermediate OA condition. OA
531 can slow shell calcification rates (Stumpp et al. 2013, Waldbusser et al. 2015, Alter et al. 2024), and
532 might prolong or increase upwards swimming by counteracting reduced larval buoyancy as larvae grow
533 larger (Czaja et al. 2023). Finally, increased time swimming may also increase feeding (Qiu et al. 2015),
534 and there may be a greater energetic cost of swimming in these conditions (Czaja et al. 2023). Previous
535 work has focused on the OA sensitivity of larval transport in terms of their size-dependent behavior
536 (Wright-Fairbanks et al. 2025). These results suggest that the combined effects of OA and warming
537 conditions on variability in vertical swimming could be an additional mechanism by which OA could
538 affect larval transport.
539

540 ## Implications for larval transport

541 Accurately evaluating regional transport requires updating models with lab-based data, and understanding
542 the strengths and weaknesses of applying lab results to predictive region-wide models of these complex
543 systems. We found that warming and OA had effects on growth, vertical distribution, and swimming

544 behavior, which each may translate to shifts in larval transport. Recent sea scallop larval transport
545 simulations used a range of OA growth rate sensitivities to evaluate potential effects of altered size-based
546 differences in behavior on transport and settlement. In comparison with model assumptions, we found
547 growth at 17°C over the first four weeks was 90% less sensitive to Ω_{Ar} compared to the growth of bivalve
548 larvae identified as sensitive to OA (OA-sensitive, Table 3) (Wright-Fairbanks et al. 2025). A more
549 moderate response of shell growth to OA has been previously documented in another species of scallop,
550 relative to the response of oysters and mussels (Scanes et al. 2014). In the cooler 14°C, larval growth did
551 not show sensitivity to OA in this same period of time, as growth was already slow at this temperature
552 (Table 3). The environmental conditions in this study were within a range of temperature and OA
553 conditions experienced by sea scallop larvae simulated in hydrographic models (Munroe et al. 2018a,
554 Wright-Fairbanks et al. 2025), allowing comparisons to be made. Simulations with this extreme OA
555 sensitivity suggested a lack of settlement in many regions (Wright-Fairbanks et al. 2025), so our findings
556 of a less sensitive growth curve at cooler temperatures, might be more realistic and result in non-zero
557 settlement percentages in affected regions. In model simulations, OA sensitivity shifted success from the
558 summer to the fall, a time where Ω_{Ar} and pH are high in surface waters (Wright-Fairbanks et al. 2025),
559 despite opposing seasonal shifts in the carbonate chemistry of deeper waters (Zang et al. 2022) that might
560 also be a risk for settling larvae (Green et al. 2013). The vertical distribution, and swimming behavior,
561 may further modify and/or counteract changes in settlement success or larger scale larval connectivity
562 (Wright-Fairbanks et al. 2025). Several aspects of our experimental design constrain the extent to which
563 these lab-based findings can be applied to natural populations across the North Atlantic Shelf. First, there
564 were a limited number of spawning adults used for this study, limiting the generality (Frieder et al. 2017).
565 Atlantic sea scallops are notoriously difficult to spawn in hatchery settings, and the responses of a limited
566 number of broodstock (>0.7 million larvae from five adults, 2 males and 3 females) may not be suited to
567 extrapolating to populations across the North Atlantic Shelf. Second, while the spawning adults were wild
568 broodstock from a single population (Maine, USA), and may represent a wider genetic diversity than
569 hatchery bred animals, we did not evaluate differences across populations. Sea scallop vertical migration

570 can differ by population, which may be explained by strong selective pressure on the return to suitable
571 habitat (Manuel et al. 1996). Third, the study design was of only the larval stage of a single generation,
572 and did not evaluate adaptation, or responses across generations (Ross et al. 2023). For scallop *spp*., adult
573 exposure to coastal acidification or future OA conditions can reduce larval growth, development, and
574 survival in response to OA (Parker et al. 2012, 2025) and increase vulnerability to additional stressors,
575 suggesting a lack of transgenerational acclimation (Griffith & Gobler 2017). However, adaptive responses
576 to OA of bivalves across generations of bivalves, including the bay scallop (*Argopecten sp*.) (Foo &
577 Byrne 2016), suggest that adaptation might limit negative response to OA for scallop species (Gurr et al.
578 2025) over evolutionary timescales.
579
580 The extent to which these lab-based findings can be applied to pelagic systems is also constrained because
581 controlled laboratory conditions differ from the complex environmental variability experienced by larvae
582 in ocean environments. Larvae were exposed to relatively constant temperature and carbonate chemistry
583 conditions within tanks over time (Table 1), while in the ocean they can modulate their vertical position
584 across heterogeneous environmental conditions. Larval growth and movement may be influenced by
585 vertical gradients in temperature, salinity, and density, observed in stratified water. Their movement may
586 also shift in response to other environmental factors. In ocean environments larvae are exposed to a wide
587 range of macro- and micro-scale turbulence, which can influence swimming behavior (Wheeler et al.
588 2015, 2017), and differ from controlled laboratory conditions where agitation is minimized. Sea scallop
589 larvae are also phototactic, and response to light may produce patterns in vertical migration that result in
590 different outcomes for regional transport (Chen et al. 2021). Larvae experience a range of light intensities
591 and spectral compositions, that vary with depth, diel and seasonal cycles (Kirk 2003), and depend on the
592 optical properties of seawater (Kirk 2003) and the focusing of light from wind-generated surface waves
593 (Darecki et al. 2011, Hieronymi & Macke 2012), which may differ in surface water from low light
594 intensities used in controlled laboratory conditions (Caracappa & Munroe 2019, Manuel et al. 2023).

Future work expanding on larval responses to multiple dynamic and heterogeneous conditions may further improve our understanding of larval behavior in field conditions.

Effective climate risk assessment and management for fished species require integration of species-specific biological responses (Shotwell et al. 2023). For many sessile invertebrates, the exchange across regional scales that shapes long-term population dynamics is determined during the brief free-swimming portion of the life cycle (<1.5 mo) despite the much longer adult phase (e.g. 30+ yr) (Raimondi & Keough 1990, Hart & Chute 2004). Our results demonstrate that ocean warming and ocean acidification alter larval vertical distribution and swimming behavior, revealing a behavioral mechanism that contributes to vulnerability of this species to climate change. Existing sea scallop larval transport models incorporate hypothesized larval behaviors into ocean transport projections (Munroe et al. 2018a, Chen et al. 2021a, Wright-Fairbanks et al. 2025). However, improved empirical observations of climate-sensitivity of development and behavior are essential to refine projections and improve management strategies under climate change.

Acknowledgments

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Figures and Tables

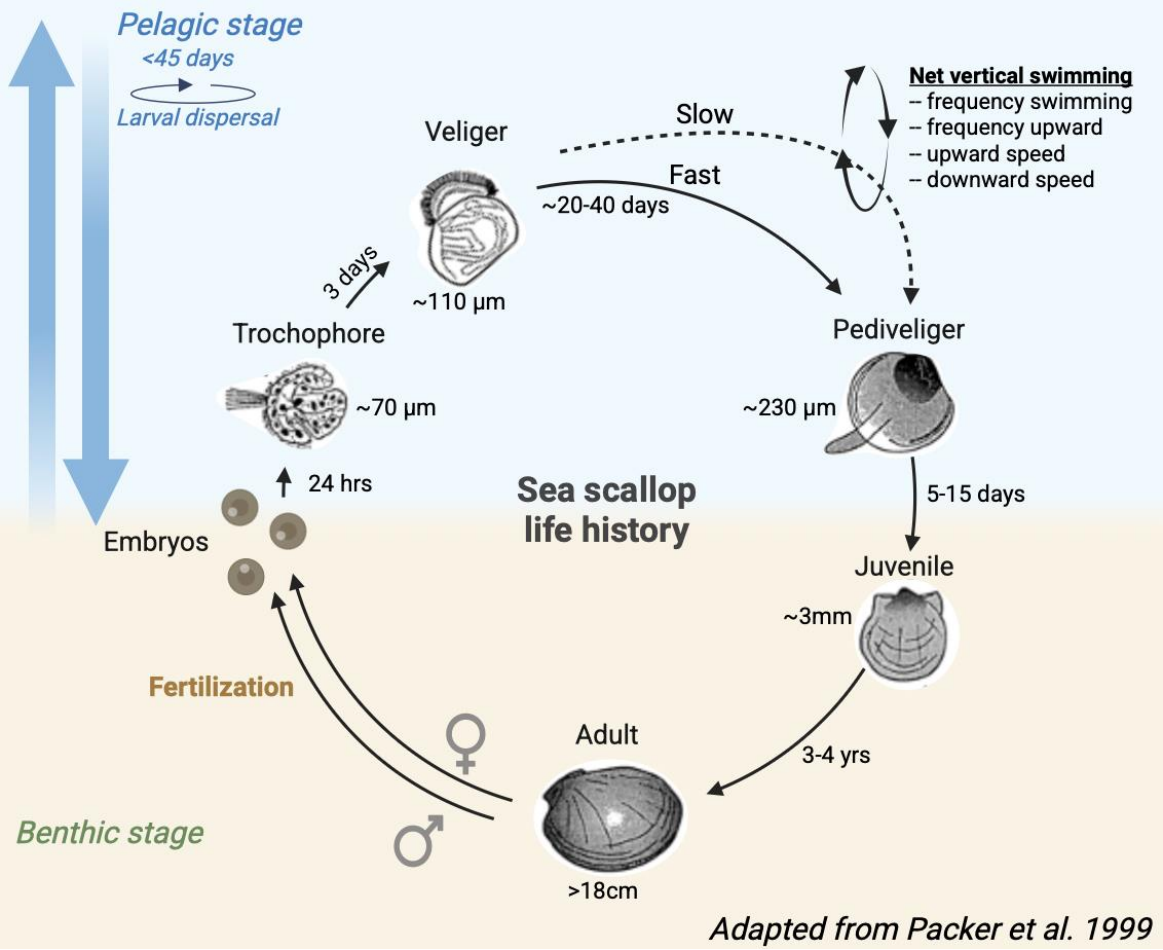

Figure 1. Diagram of sea scallop (*Placopecten magellanicus*) life history. While the embryo and trochophore stage typically remain near the benthos, veliger stage larvae swim upwards in the water column where their swimming behavior can alter movement by ocean currents. Environmental conditions can cause a wide range of developmental speeds (~20 – 40 days) and a range of vertical swimming behavior, which is a function of swimming frequency and velocity. Finally, pediveliger stage larvae are typically bottom-seeking, but still able to swim, as they search for a place to settle and metamorphose into a non-swimming juvenile. Illustrations of life history stages are from Packer et al. (1999). Diagram created using Biorender.com.

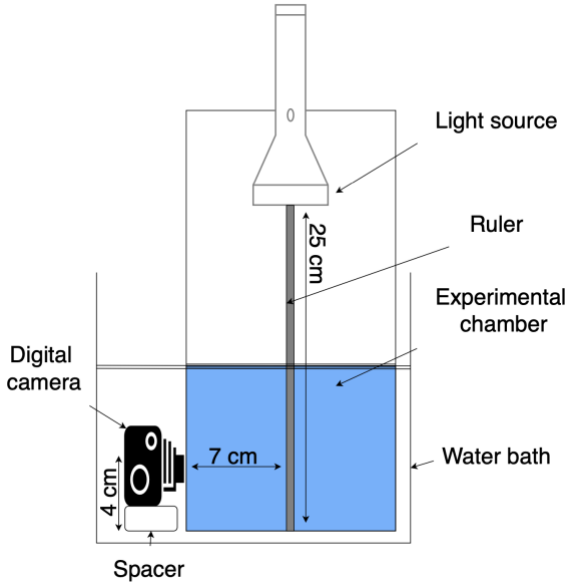

Figure 2. Diagram of the recording chamber, lighting, and camera setup adapted from Caracappa and Munroe (Caracappa & Munroe 2019) and Manuel et al. (Manuel et al. 2023).

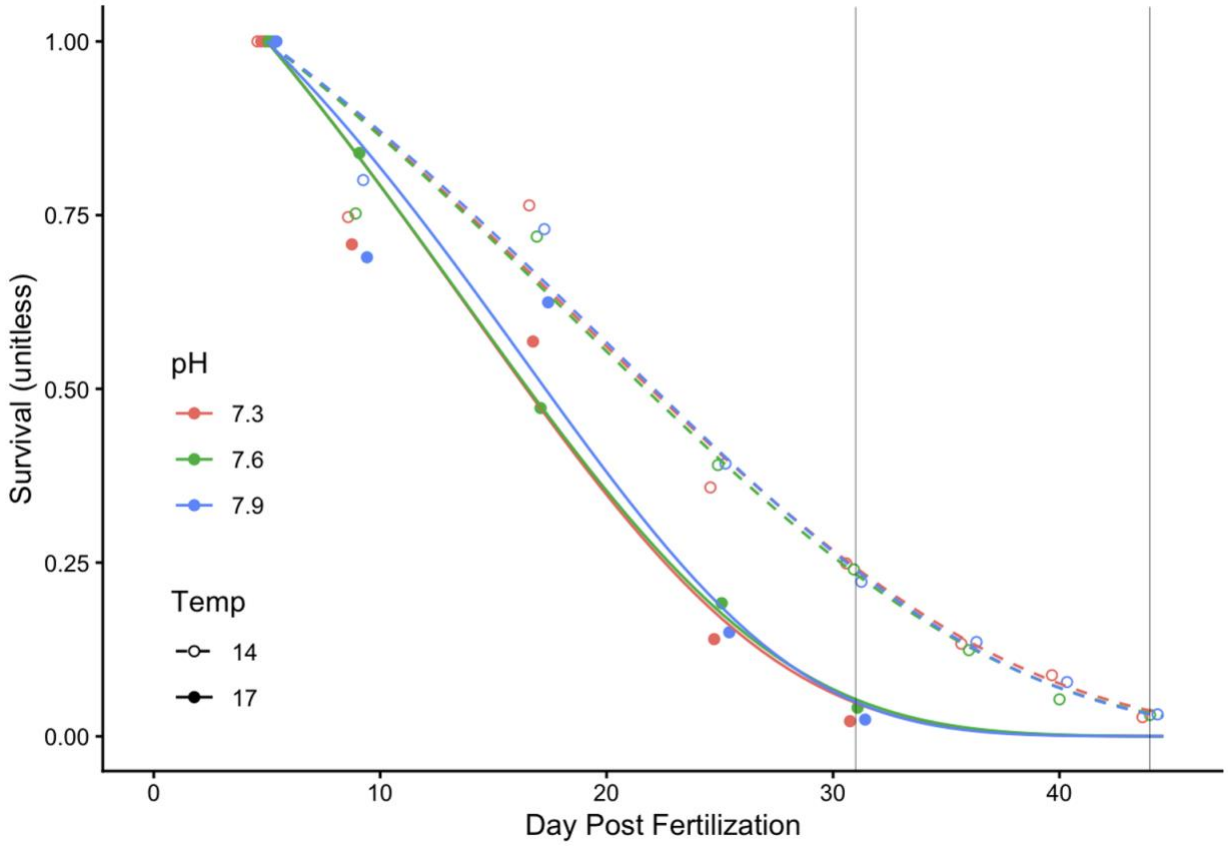

Figure 3. Survival as a function of time for each pH and temperature treatment. Survival is represented with a Gompertz function based on larval survival rate (Survival = exp(-(b / a) * (exp(a * day) - 1))) where the tank is a random factor. Points represent treatment means. The vertical lines mark the experiment end date in the 17°C (31 days) and 14°C (44 days) treatments. The model that predicted survival based on each temperature treatment (17°C and 14°C) had the lowest AIC score (AIC grouped model comparison, Table S1).

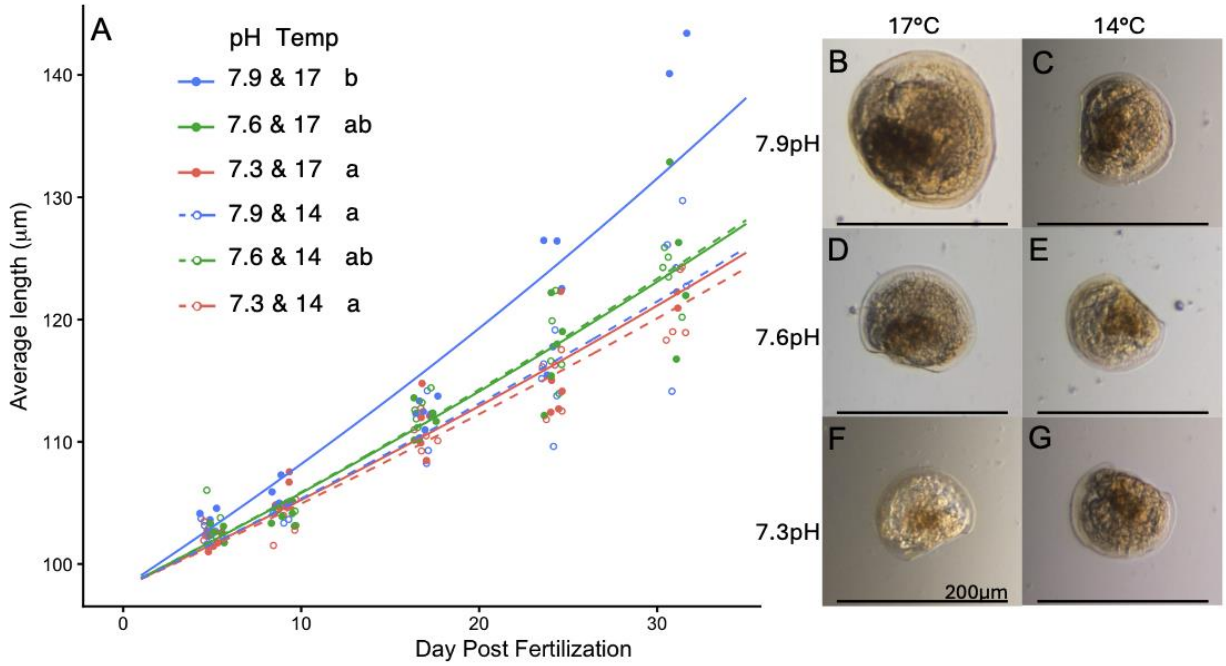

Figure 4. OA (pH 7.3, 7.6) counteracted a positive effect of warming on growth. (A) Shell length as a function of the number of days post fertilization for the low and high temperature treatments (14°C - dashed line, open circles, and 17°C - solid line, closed circles) and three pH treatments (7.9 - blue, 7.6 - green, 7.3 - red). Growth rate is represented as an exponential function of shell length over time (Length = $a\, e^{b\ day}$). Lower case letters indicate Tukey post hoc groups for growth rate (b, Table S3). Points represent mean shell length in each tank, and lengths from adjacent days are pooled (e.g., lengths from day 23 and 25 are combined). (B-G) Representative images of larvae from each treatment group on day 31.

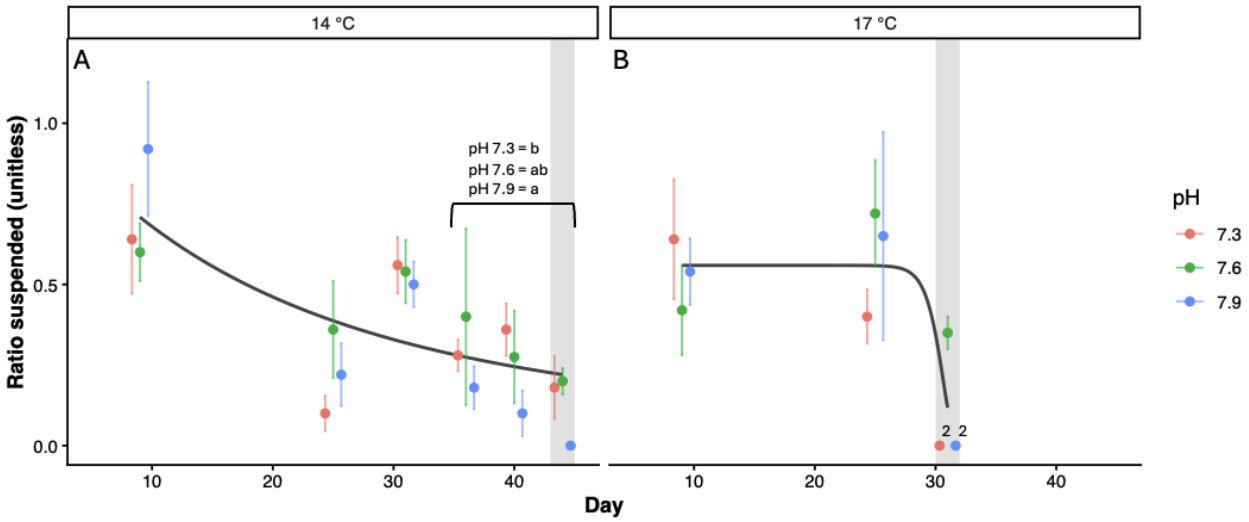

Figure 5. The proportion of larvae suspended as a function of day in each pH and temperature treatment. The proportion of the larval concentration in the suspended sample relative to the known concentration of larvae in the tank as a function of time (days post fertilization, DPF). Points and error bars indicate the means ± SE (4-5 tanks, except for n = 2 where marked in panel B). Curves are fitted modified Gompertz functions estimated separately for each temperature (Table S4). A) Letters indicate differences among pH treatments in the final 10 days of the 14°C experiment (values are pooled across tank, Kruskal Wallis rank sum test, $\chi^2 = 6.59$, df = 2, p-value = 0.034). B) Very few larvae were counted in the final few days of the 17°C, precluding further statistical analysis.

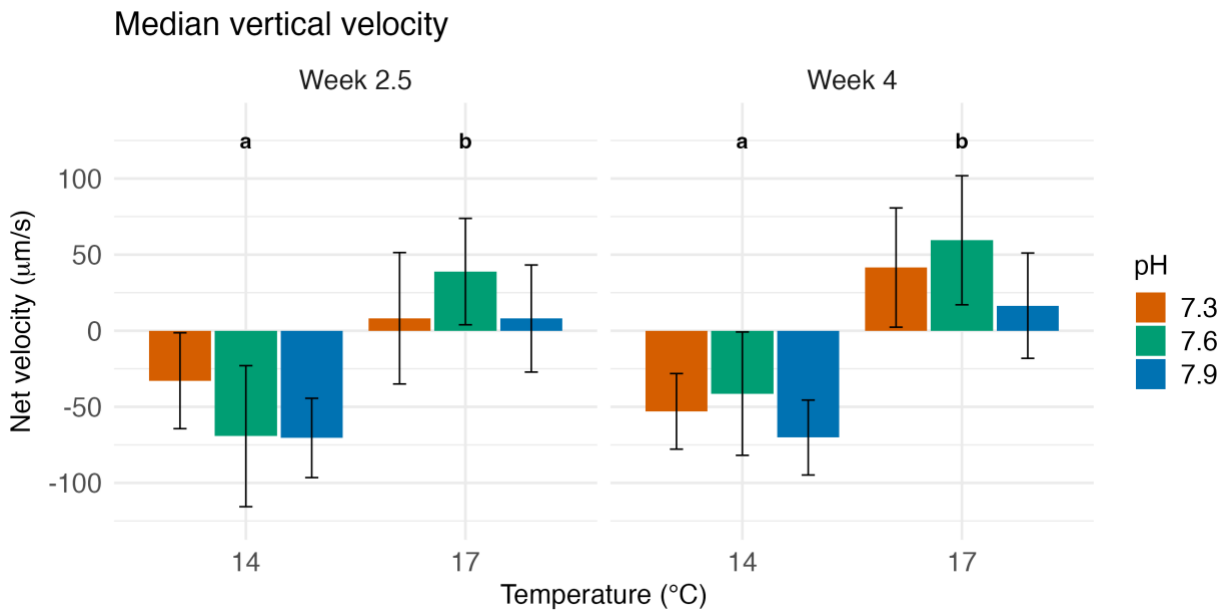

Figure 6. Median vertical velocity (w, A) as a function of temperature and pH treatment at both 2.5 and 4 weeks. Estimated marginal means and CI are calculated for each response variable based on the GLM mixed effects model (Table 2). Letters indicate Sidek posthoc tests among each temperature and pH treatment for each timepoint separately (week 2.5, week 4).

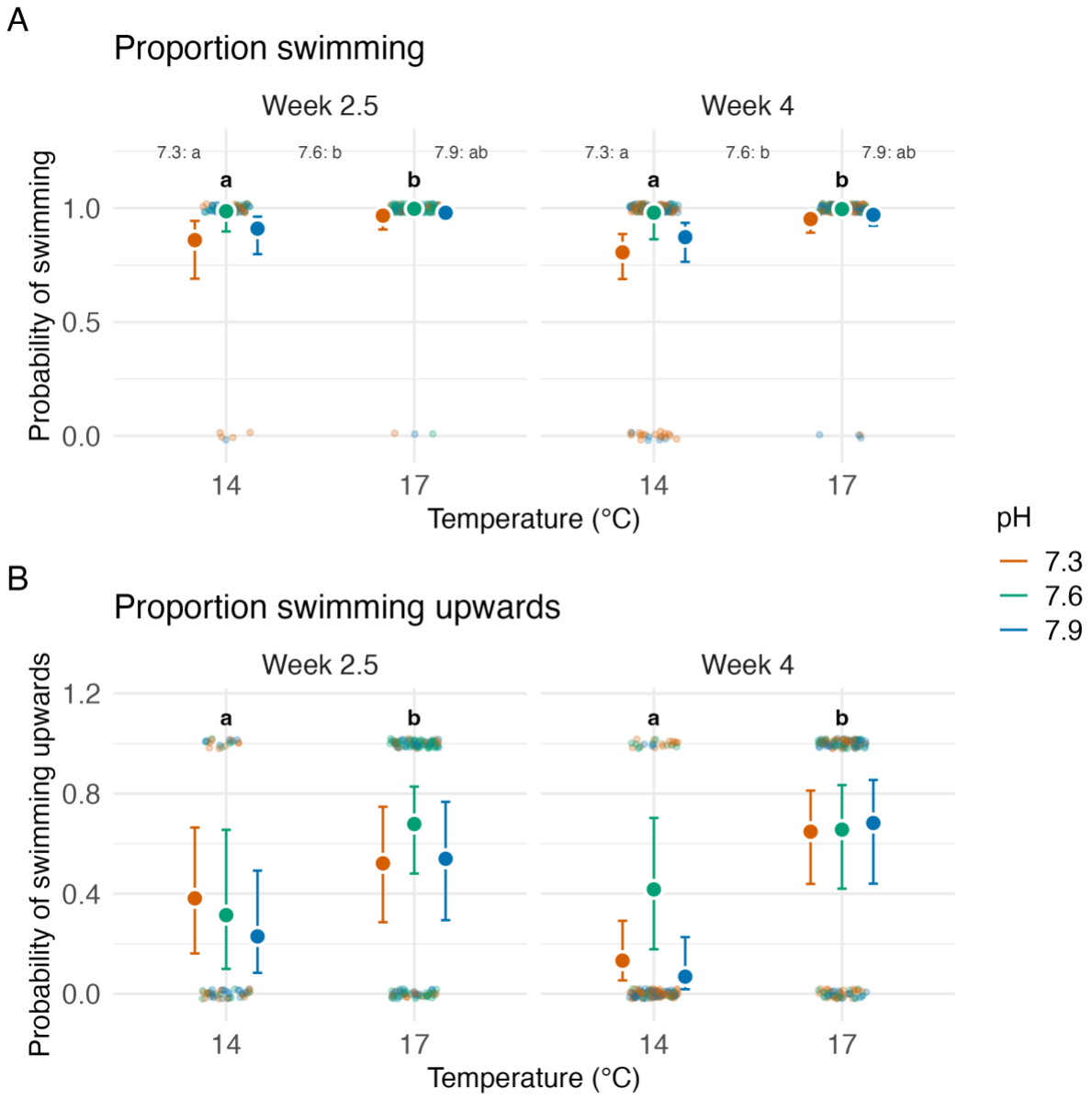

Figure 7. Binomial probabilities of the percent swimming (A, B) and percent swimming upwards (C, D) over time (week 2.5, week 4) and for each combination of temperature (14°C, 17°C), and pH (7.3 - red, 7.6 - green, 7.9 - blue). Individual binomial clip data are represented with individual points (at 0 or 1). Probabilities are calculated as estimated marginal means (± CI) and account for replication at the level of the tank (Table 2).

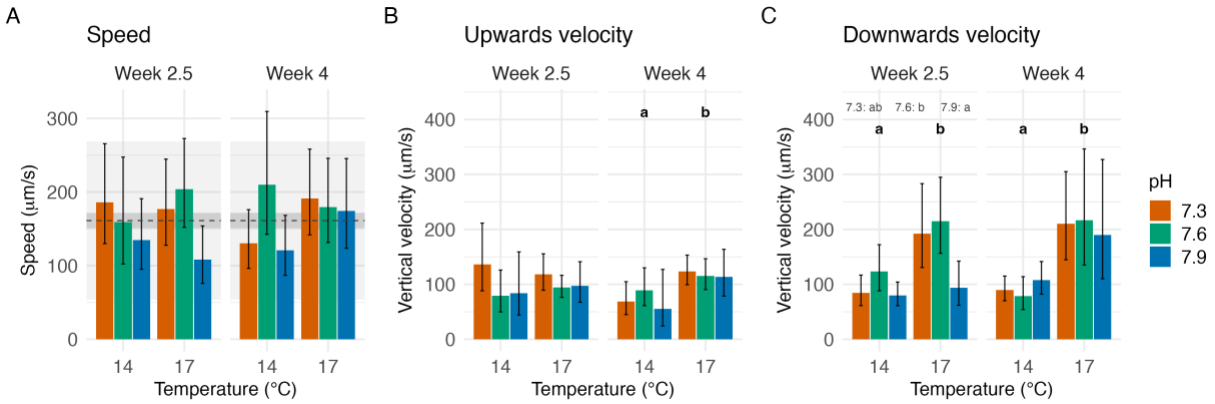

Figure 8. Kinematics of swimming. Median speed (A), upwards velocity (w_{up}, B), and downwards velocity (w_{down}, C), as a function of temperature and pH treatment at both 2.5 and 4 weeks. Upwards and downwards velocities are the vertical velocity component from upwards and downwards trajectories. Estimated marginal means and CI are calculated for each response variable based on the GLM mixed effects model (Table 2). Letters indicate Sidek posthoc tests among each temperature and pH treatment for each timepoint separately (week 2.5, week 4). (A) Median speed was variable and gray ribbons indicate marginal means SE and SD. An interaction between temperature, pH and time on median speed suggests that the combined effects of pH and temperature differed over time, but within each week there were no effects of pH and/or Temperature, or of their interactions. (B & C) Warming increased upwards velocity in Week 4, and (C) Warming increased downwards velocity, and OA increased downwards velocity in Week 2.5.

721 Table 1. Carbonate chemistry parameters for each treatment. Reported are means ± SE. Measured
722 temperature, pH, salinity, TA, DIC, pCO2, and aragonite saturation state (Ω_{Ar}). Asterisks mark means and
723 SE calculated from both the 5 replicate tanks and multiple timepoints (17°C - 15, 14°C - 19
724 measurements).
725

Group	Temp* (°C)	pH*	Salinity (PSU) n = 3	DO (% sat) n = 3	TA (µmol kg^{-1}) n = 4	DIC (µmol kg^{-1}) n = 4	pCO_2* (µatm)	Ω_{Ar}* (unitless)
14 & 7.9	14.1 ± 0.1	7.89 ± 0.01	32.3 ± 0.2	99 ± 1	2202 ± 8	2086 ± 4	587 ± 15	2.47 ± 0.06
14 & 7.6	14.2 ± 0.1	7.57 ± 0.01	32.1 ± 0.2	101 ± 1	2200 ± 5	2166 ± 8	1305 ± 33	1.26 ± 0.03
14 & 7.3	14.2 ± 0.1	7.28 ± 0.01	32.6 ± 0.2	100 ± 1	2203 ± 5	2241 ± 11	2618 ± 65	0.67 ± 0.02
17 & 7.9	17.2 ± 0.1	7.92 ± 0.01	32.4 ± 0.2	100 ± 1	2207 ± 9	2087 ± 12	548 ± 14	2.93 ± 0.07
17 & 7.6	17.0 ± 0.2	7.59 ± 0.01	32.6 ± 0.2	100 ± 1	2201 ± 7	2161 ± 10	1256 ± 31	1.47 ± 0.04
17 & 7.3	17.2 ± 0.2	7.26 ± 0.01	32.2 ± 0.2	100 ± 1	2204 ± 9	2241 ± 9	2799 ± 64	0.71 ± 0.02

726

Table 2. Type III Wald-Chi square tests of GLM mixed-effects models of vertical velocity (scaled w, μm / s), proportion of time swimming, proportion of time swimming upwards, swimming speed (s, μm / s), and median upwards velocity, and median downwards velocity as a function of temperature (14°C, 17°C) and pH (7.3, 7.6, 7.9 pH) treatment, and time (Week 2.5, Week 4). Each metric was first aggregated by clip prior to the analysis, and tank (n = 5) was included as a random factor. Dispersion was evaluated for each factor, pH, temperature, and date, and dispersion factors were included based on model AIC comparisons. A Benjamini-Hochberg ranked adjustment of p-values (p B-H adjust) was used to control for false discovery rate on multiple metrics derived from the same dataset. Bold numbers indicate a significant effect. The GLM Distribution family (Student's t, Binomial, and Gamma) and the number of clips per analysis (Num) are indicated below. Since most individuals were actively swimming, the proportion swimming (1B) analysis did not converge when all interactions were included, so interactions are not included.

1. Overall movement					2. Kinematics			
1A. Vertical velocity (scaled)			Student's t; Num = 496		2A. Speed			Gamma; Num = 496
Term	χ^2	Df	p value	p B-H adj.	χ^2	Df	p value	p B-H adj.
(Intercept)	1.75	1	0.186	0.373	6079.67	1	**<0.001**	**<0.001**
pH	3.46	2	0.177	0.373	4.82	2	0.09	0.180
Temp	43.36	1	**<0.001**	**<0.001**	0.53	1	0.467	0.557
date	2.11	1	0.146	0.373	0.48	1	0.488	0.557
pH:Temp	1.26	2	0.534	0.596	0.17	2	0.920	0.920
pH:date	1.04	2	0.596	0.596	6.02	2	**0.049**	0.123
Temp:date	1.25	1	0.264	0.389	3.01	1	0.083	0.180
pH:Temp:date	2.46	2	0.292	0.389	11.98	2	**0.003**	**0.012**
1B. Proportion swimming			Binomial; Num = 500		2B. Upwards velocity			Gamma; Num = 168
(Intercept)	73.31	1	**<0.001**	**<0.001**	3720.92	1	**<0.001**	**<0.001**
pH	6.10	2	**0.047**	0.114	1.65	2	0.439	0.554
Temp	11.81	1	**<0.001**	**0.002**	3.80	1	0.051	0.123
date	0.75	1	0.388	0.467	0.82	1	0.364	0.485
pH:Temp					0.35	2	0.838	0.875
pH:date					6.54	2	**0.038**	0.114
Temp:date					4.81	1	**0.028**	0.097
pH:Temp:date					3.27	2	0.195	0.319
1C. Proportion swimming up			Binomial; Num = 496		2C. Downwards velocity			Gamma; Num = 215
(Intercept)	3.52	1	0.061	0.118	6152.13	1	**<0.001**	**<0.001**
pH	2.80	2	0.247	0.371	3.10	2	0.213	0.319
Temp	20.30	1	**<0.001**	**<0.001**	30.05	1	**<0.001**	**<0.001**
date	0.74	1	0.390	0.467	1.57	1	0.210	0.319
pH:Temp	1.49	2	0.474	0.517	2.95	2	0.229	0.323
pH:date	1.21	2	0.547	0.547	9.10	2	**0.011**	**0.042**
Temp:date	4.80	1	**0.028**	0.085	2.44	1	0.118	0.218
pH:Temp:date	5.35	2	0.069	0.118	1.13	2	0.568	0.619

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Table 3. Comparison of slope and intercept values relating change in growth as a linear function of Ω_{Ar} of OA-sensitive and non-OA sensitive species compiled in Wright-Fairbanks et al. 2025. The slope and intercept are calculated from the change in mean length in each tank at days 9 and 31. Tanks with fewer than 5 length measurements were not included in this analysis. Sensitivity is estimated as a linear function of Ω_A (Δ length = a * Ω_A + b, units $\mu m\ d^{-1}$).

Group	Slope (a)	Intercept (b)	Reference
OA-sensitive species	3.71	-3.78	Wright-Fairbanks et al. 2025
Non-OA sensitive species	-0.0024	+0.19	Wright-Fairbanks et al. 2025
Sea scallops at 17°C	0.36 ± 0.10	0.31 ± 0.18	This paper
Sea scallops at 14°C	0.03 ± 0.05	0.67 ± 0.08	This paper

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