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Effects of food supply on northern bay scallops *Argopecten irradians* reared under two pCO_2 conditions

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ABSTRACT: For calcifying organisms such as bivalves, short-term exposure to increased ocean acidification (OA; elevated pCO_2) may reduce growth rate, increase mortality, and disrupt shell formation. A growing body of research suggests that clearance rates and what particles bivalves select may change under high pCO_2 exposure; however, these experiments are acute, ranging from days to weeks. The effects of food supply on bivalves under long-term OA exposure remain incompletely understood. In this study, juvenile northern bay scallops *Argopecten irradians* (Lamarck) that had been reared since 4 h post-fertilization under one of 2 OA conditions (~500–600 or ~750–850 µatm pCO_2; ~1.37–1.5 or ~1.0–1.2 $\Omega_{aragonite}$), were subjected to 2 food levels for 42 d (low food: ~400, high food: ~1400 chlorophyll cells ml^{-1}). Standard metabolic rate (SMR) and clearance rate (CR) were measured on Day 0, and SMR, CR, growth, and survivorship were measured at 14 and 42 days of exposure to 2 food levels for each of the OA treatments. Juveniles under food scarcity had reduced survivorship and growth independent of OA treatment. We found no effect of OA treatment or an OA × food interaction for these metrics. There was only a food-level effect for SMR and no OA treatment effect; however, there was an interaction between food and OA for CR. Under elevated pCO_2 concentrations, scallops cleared *Chaetoceros neogracile* (strain Chaet-B) over *Tetraselmis chui* (strain PLY429) and natural seston. Altogether, these data suggest that tolerance to OA mediated by food may depend on food quality or other characteristics that influence particle selection under short-term experimental challenges.

KEY WORDS: Food availability · Ocean acidification · Physiology · Juvenile performance · Bay scallop

1. INTRODUCTION

The northeast coast of the USA has many important commercial bivalve fisheries (e.g. Atlantic sea scallop *Placopecten magellanicus*, Atlantic surfclam *Spisula solidissima*, ocean quahog *Arctica islandica*, eastern oyster *Crassostrea virginica*, and bay scallop *Argopecten irradians*) valued at US$ ~812 million (NOAA Fisheries Office of Science and Technology 2024). Both natural and farmed populations are dependent

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on planktonic food availability and seawater chemistry, among other factors (Philippart et al. 2014, Rheuban et al. 2018). The Mid-Atlantic Bight has undergone an average 14% decline in seasonal chlorophyll over recent decades (Schofield et al. 2008), and future projections anticipate a reduced duration (i.e. from 7.5 to 5 wk) and delayed onset of seasonal phytoplankton blooms (i.e. 33 d later; Friedland et al. 2023). Changes in the timing and magnitude of phytoplankton blooms in this region (González Taboada & Anadón 2014) are projected to continue (Friedland et al. 2018) and may affect bivalves that reproduce seasonally and depend upon seasonal food supply for offspring development and recruitment (Philippart et al. 2014). For example, winter mortality events (Cooley et al. 2015) and reduced scope for growth in bivalves are linked to seasonal food deficiency indicated by low chlorophyll concentrations (MacDonald & Thompson 1985a, Zang et al. 2022).

Contemporaneously, the northeast US continental shelf has observed an increase in elevated partial pressures of CO_2 (pCO_2) or ocean acidification (OA). For example, pCO_2 has increased by 2.5% from 2007 to 2015 (Wanninkhof et al. 2015), reaching highs comparable to global ocean OA projections for 2100 (~800 ppm pCO_2; Wright-Fairbanks et al. 2020). In addition to direct consequences for bivalves (Gazeau et al. 2013, Thomsen et al. 2015), OA may reduce the nutritional quality (e.g. total and long-chain polyunsaturated fatty acids; Rossoll et al. 2012, Bermúdez et al. 2015) and biomass of phytoplankton algae (e.g. iron-limited growth; McQuaid et al. 2018), decreasing the bioavailability of essential nutrients for bivalve consumers (Gao et al. 2012, Dörner et al. 2020, Jin et al. 2020). Thus, understanding the effects of OA on bivalve populations requires examining both food availability and OA.

The effects of elevated pCO_2 on marine life have attracted global attention, especially investigations of marine calcifiers (Gazeu et al. 2007, Fitzer et al. 2018, Vargas et al. 2022). OA can increase the energetic expense for shell formation (Waldbusser et al. 2015) and acid–base regulation (Pörtner et al. 2004) and decrease filtration rates (Meseck et al. 2020), thereby affecting performance, metabolism, and survivorship in bivalves (Doney et al. 2009, Melzner et al. 2020). Seston food availability — both quantity and quality — for suspension-feeding marine mollusks is highly variable on seasonal-to-daily timescales and fundamental in controlling energetic balance (Bayne et al. 1988, McCue et al. 2017). In previous studies, low food supply has elicited a greater response than OA, limiting growth and development (e.g. fish, coral, and bivalves; Holcomb et al. 2010, Towle et al. 2015, Hurst et al. 2017) and intensifying OA-induced responses (Hettinger et al. 2013, Brown et al. 2018, 2020). Furthermore, high food supply can reduce OA sensitivity (e.g. in oysters, scallops, and mussels; Hettinger et al. 2013, Thomsen et al. 2013, Ramajo et al. 2016a, Brown et al. 2018), partially ameliorating the energetic costs (Melzner et al. 2011, Kroeker et al. 2013, Ramajo et al. 2016b). Taken together, reduced food (Friedland et al. 2023) concurrent with rising OA (Wanninkhof et al. 2015, Wright-Fairbanks et al. 2020) along northeast US coasts may worsen OA effects on bivalves. Experiments that employ coupled pCO_2 enrichment and a food quality or quantity challenge are essential to understand impending environmental effects.

Understanding physiological responses and consequences of environmental change, including food supply, can provide insight into energetic requirements for suspension-feeding bivalves across environmental conditions. In bivalves, metabolic depression — reduced catabolic energy expenditure — can compensate for prolonged food scarcity (García-Esquivel et al. 2002, Haider et al. 2020) and extend survival under adverse conditions (Philipp & Abele 2010). Although the respiration rate of juvenile bivalves can remain largely unaffected by OA (Fernández-Reiriz et al. 2012, Sanders et al. 2013, Pousse et al. 2023), slowed metabolism under food scarcity may lead to increased susceptibility to environmental perturbations. Juvenile bivalves can also exhibit size-dependent resistance to shell dissolution under moderate OA (i.e. 1–3 mm *Mercenaria mercenaria* under ~1100 µatm pCO_2; Waldbusser et al. 2010), but if accompanied by a decrease in food supply (as predicted in the northeast coastal US; Friedland et al. 2023), a negative physiological response may be exacerbated by energy deficiencies (Melzner et al. 2011). By contrast, food supply provides the energetic means to overcome environmental challenges (Norkko et al. 2005, Fitzgerald-Dehoog et al. 2012, Aguirre-Velarde et al. 2018) and contributes to OA refugia (Kapsenberg & Cyronak 2019). A meta-analysis by Leung et al. (2022) found that under OA conditions, high food availability elicits compensatory feeding performance and growth, offsetting the negative effects of elevated pCO_2 — examples shown in the mussel *Mytilus edulis* (Thomsen et al. 2013), juvenile Chilean sea scallop *Argopecten purpuratus* (Ramajo et al. 2016b), and juvenile great scallop *Pecten maximus* (Sanders et al. 2013). Given the natural variability with which estuarine species are exposed to OA (Baumann et al. 2015) and food abundance (i.e. temporal variation in chlorophyll *a*; Cereja et al. 2021), measuring physiological catabolic

responses and clearance rates (CRs; removal of particles from the water) can provide important insights into the interactive effects of OA and food supply.

The northern bay scallop *Argopecten irradians* (Lamarck, 1819), is sensitive to elevated pCO_2 (i.e. decreased survivorship in juveniles; Talmage & Gobler 2011, Stevens & Gobler 2018); however, supplementary food renders the effects negligible in related species (*A. purpuratus*; Ramajo et al. 2016a), suggesting that food ration may affect tolerance of environmental challenge in the northern bay scallop. Furthermore, the timing of spawning in summer—early fall (Taylor & Capuzzo 1983) suggests that recruitment of pre-winter juvenile *A. irradians* may rely upon food abundance during autumn phytoplankton blooms (Bricelj et al. 1987, Epp et al. 1988) when OA is less severe (relative to mid-summer high; Wallace et al. 2014). A similar dependence upon seasonal food availability for growth and survival of the Atlantic sea scallop *Placopecten magellanicus* (MacDonald & Thompson 1985a,b, Cooley et al. 2015) highlights the energetic requirements for recruitment success in sea scallops. Given the evidence that food sufficiency may reduce sensitivity to elevated pCO_2 in other species of scallops, we tested the potential for low food supply to modulate the physiological effects of OA on bay scallops.

The northern bay scallop is an excellent species for experimental study because its short generation time (~20 d larval period, and <1 yr to reproduction) allows assessment of environment effects across lifetime exposures. Comparisons between this work and research on OA and food scarcity in the Atlantic sea scallop (Cameron et al. 2019, Pousse et al. 2023) will help determine whether bay scallops can serve as short-lived proxy for the Atlantic sea scallop. Bay scallops reared from embryos to the juvenile stage under continuous low and elevated pCO_2 (~500 and 800 µatm) were given a 4 wk food ration challenge to investigate how cohorts reared in low and elevated pCO_2 may differ physiologically. Standard metabolic rates (SMRs) and algal CRs were measured to investigate phenotypic differences in metabolism and resource acquisition, in addition to survivorship and growth.

2. MATERIALS AND METHODS

2.1. Experimental design

The experimental pCO_2 treatment levels selected for this experiment were based on the guidelines outlined in 'The guide to best practices for ocean acidification research and data reporting' (Riebesell et al. 2010), later updated following recommendations by McElhany & Busch (2013). These authors recommend that experimental OA treatments target observed values in the natural environment of the organism, including low, elevated, and future high OA scenarios. We initially used 3 treatments in our study: low pCO_2 (~560 µatm), elevated pCO_2 (~840 µatm), and high pCO_2 (~1680 µatm). Larval scallops did not survive to the juvenile phase under the high pCO_2 treatment. Therefore, only juvenile scallops from the low and elevated pCO_2 treatments were included in this study.

2.2. Animals

Adult bay scallops were collected in May 2021 from Ward Aquafarms (Megansett Harbor, Massachusetts, USA; 41° 39′ 18.7″ N, 70° 38′ 17.9″ W) and held at the Northeast Fisheries Science Center Milford Laboratory (Milford, Connecticut, USA; 41° 12′ 44.6″ N, 73° 03′ 10.6″ W) under flow-through seawater until they spawned in July 2021. In brief, gametes from 13 females and 16 males (scallops are hermaphrodites) were combined in 5 batches for fertilization to avoid self-fertilization and maximize genetic diversity among offspring. Larvae (from 4 h post-fertilization) were grown under 2 pCO_2 treatment conditions in a static system (15 l buckets with 5 replicates treatment^{-1}) as described in Meseck et al. (2021) until settlement and metamorphosis to the juvenile stage at 18 d post-fertilization (dpf). The 2 OA treatments used in this study approximated the seasonal variability that the organisms were exposed to during grow-out on Ward Aquafarm leases (means ± SD: pCO_2: 740 ± 266 µatm; aragonite and calcite saturation states Ω_{ar}: 1.19 ± 0.31 and Ω_{cal}: 1.87 ± 0.47; n = 4 sampling time points analyzed between April and December). In this static system, larvae were batch-fed a live mixed-algal diet consisting of *Tisochrysis lutea* and *Diacronema lutheri*, and, at Day 8 until the end of the larval stage, *Chaetoceros muelleri* ad libitum, using standard packed cell volume and adjusted for algal concentrations (measured with flow cytometry) to the equivalent of 4×10^4 cells ml^{-1} of *T. lutea*. Juvenile scallops (age 18 dpf) were then moved to downwellers in a flow-through OA seawater system described in Section 2.3.

2.3. OA system and seawater conditions

At 18 dpf, juvenile scallops were moved to a flow-through OA system and grown under the same OA treatment levels as the larvae. Two identical flow-

through systems were used for the pCO_2 × food ration challenge. Ambient seawater filtered through a 30 µm drum filter (Hydrotech) was delivered to 2 header tanks. Seawater flowed through PVC columns (11 cm × 215 cm; n = 4 pCO_2 per level) to obtain the same OA treatment levels as the larvae experienced (low pCO_2: ~530–600 µatm; elevated pCO_2: ~720–850 µatm) by bubbling a mixture of CO_2-stripped air and research-grade CO_2 mixed at different ratios using mass flow controllers (Aalborg Instruments and Controls). PVC column pCO_2 assignments were rotated weekly to avoid column bias. pCO_2-enriched seawater from each column continuously flowed at 1.5 ± 0.1 l min^{-1} into cylindrical downweller tanks (20 × 30 cm; total volume: 9.4 l) with 200 µm mesh to keep the animals off the bottom. Initially, cylindrical downweller tanks were stocked at 1500 juveniles per replicate tank. As the animals grew, densities were reduced in each replicate every 2–3 wk to a standardized biovolume and bottom mesh sizes were increased (500 µm at 37 dpf and 1 mm at 51 dpf). Each tank was continuously fed a live mixed-algal diet (detailed in Section 2.4) and bubbled with the appropriate CO_2-enriched air to maintain pCO_2 levels.

Seawater conditions and OA treatment conditions throughout the experiment are summarized in Table 1. Discrete chemistry was measured daily for dissolved oxygen (mg l^{-1}), salinity, and temperature (°C) in each replicate treatment tank (YSI Model 556). Seawater samples were collected weekly in dark polypropylene bottles (500 ml) from each replicate tank to measure pH, dissolved organic carbon (DIC; µmol kg^{-1}), and total alkalinity (TA, µmol kg^{-1}) by open-cell titration (method SOP 3b; Dickson et al. 2007). A UV-VIS spectrophotometer (Cary100, Agilent) was used to determine pH colorimetrically at 20°C with m-cresol purple indicator dye (Sigma-Aldrich) (Dickson & Goyet 1994), with Andrew Dickson TRIS 37 (n = 5) and 40 (n = 5) with a standard error of ±0.0014 (seawater scale). DIC was measured on an Apollo SciTech DIC analyzer (Apollo SciTech) with a precision of 0.5% of assigned values in an interlaboratory comparison (Bockmon & Dickson 2015). TA was measured using certified HCl titrant (~0.1 mol kg^{-1}, ~0.6 mol kg^{-1} NaCl; Dickson Lab, Batches 191 and 157) on a Metrohm alkalinity titrator (Mettler Toledo T5) with 0.17% standard error relative to certified reference materials (Dickson Lab CO_2 CRM Batch 191 and 157). Seawater DIC and pH were used in CO2SYS (Pierrot et al. 2006) for the calculation of partial pressure pCO_2 (µatm), carbon ion constituents (bicarbonate [HCO_3^-] and carbonate [CO_3^{-2}]; µmol kg^{-1}), and Ω_{ar} and Ω_{cal} using the following constants: K_1, K_2 from

Table 1. Discrete measurements (mean ± SE) of seawater (SW) chemistry during the pCO_2 × food ration challenge. Data records are shown from handheld probes (pH, temperature, salinity, and dissolved oxygen [DO]) and quantitative instrumentation of seawater samples for total inorganic carbon (total CO_2 [TCO_2] or dissolved inorganic carbon [DIC]) and total alkalinity (TA). DIC and pH were used to calculate pH (seawater scale), pCO_2, $\Omega_{aragonite}$, and $\Omega_{calcite}$ using CO2SYS (v2.1); additional carbonate chemistry constituents (i.e. CO_2, HCO_3^-, CO_3, etc.) are publicly archived (https://github.com/NEFSC/EAD-ASEB-Airradians_OA_foodsupply)

Treatment			Measured values					Calculated values (CO2SYS output)			
pCO_2	food	n	Temperature (°C)	Salinity	DO (mg^{-1})	pH (chosen scale)	TCO_2 (DIC) (µmol kg^{-1}SW)	TA (µmol kg^{-1}SW)	pH (seawater scale)	pCO_2 (µatm)	$\Omega_{aragonite}$	$\Omega_{calcite}$
Elevated	High	16	21 ± 0.22	26 ± 0.19	9.38 ± 0.031	7.72 ± 0.013	1750 ± 7.36	1820 ± 8.69	7.71 ± 0.013	840 ± 28.7	1.04 ± 0.033	1.63 ± 0.051
Low	High	17	21 ± 0.21	26 ± 0.20	9.41 ± 0.029	7.86 ± 0.008	1710 ± 7.38	1810 ± 8.52	7.84 ± 0.010	591 ± 15.3	1.37 ± 0.032	2.16 ± 0.050
Elevated	Low	25	21 ± 0.22	26 ± 0.14	9.06 ± 0.070	7.79 ± 0.010	1740 ± 5.46	1830 ± 7.63	7.77 ± 0.011	724 ± 20.0	1.19 ± 0.028	1.88 ± 0.044
Low	Low	25	21 ± 0.22	26 ± 0.15	9.11 ± 0.058	7.90 ± 0006	1710 ± 4.91	1830 ± 7.77	7.88 ± 0.007	535 ± 8.36	1.51 ± 0.030	2.38 ± 0.045

Lueker et al. (2000), potassium sulfate from Dickson (1990), and boron from Lee et al. (2010).

2.4. pCO_2 × food ration challenge

At age 52 dpf, juvenile bay scallops from each pCO_2 treatment were not different in size (detailed in Section 3.1) and had a mean ± SE shell height (maximum distance from the hinge to the margin of the shell) of 2.39 ± 0.13 mm under low pCO_2 (n = 4) and 2.32 ± 0.06 mm under elevated pCO_2 (n = 4). Scallops in each replicate for each OA treatment were redistributed to 2 tanks based on total biovolume, resulting in 8 total replicate tanks. Four replicates were exposed to high food availability, with supplemented algae, and 4 to low food availability, without supplemented algae (n = 4 pCO_2 × food ration tanks treatment^{-1}; Fig. 1). Cylindrical downweller tanks were stocked at 625 scallops tank^{-1} (2.5 × 10^3 scallops m^{-2}), below the recommended stocking rates for bay scallops under 10 mm shell height for aquaculture grow-out (Leavitt & Karney 2005). All treatments received 30 µm drum-filtered seawater that removed 30–60% of background natural algae, but the high food ration was supplemented with continuous delivery of 1:1 (volumetrically) mixed-algal diet of live cultured *Chaetoceros neogracile* (strain Chaet-B) and *Tetraselmis chui* (strain PLY429) cells (22:1 based upon cell density, 1.5:1 based on cell biovolume). These 2 species were chosen because of differences in size and nutritional quality (*C. neogracile* is small with high levels of docosahexaenoic acid (DHA); *T. chui* is larger, with no DHA but with high eicosapentaenoic acid levels and metabolizable phytosterols; Brown et al. 1997, Giner et al. 2016). Supplemental cultured algae were delivered at 2 ml min^{-1} with a variable peristaltic pump (Goldander BT-100F-1, DG10-12) and averaged 3.4 × 10^8 high-chlorophyll cells d^{-1} (determined by flow cytometry) to each high-food replicate tank. Cell counts were determined periodically for both high-food and low-food replicate tanks (n = 19 total days) using flow cytometry (BD Accuri™ C6 Plus Flow Cytometer) with custom gating thresholds to quantify all phytoplankton and seston. Two phytoplankton gates were used to isolate high-chlorophyll (>2 µm, cultured algal particles) and low-chlorophyll particles (<2 µm, seston). The low-food treatment for both OA treatments received equal seston relative to the high-food treatment (mean ± SE, n = 8: low food: 7.59 × 10^4 ± 4.1 × 10^3 seston ml^{-1}; high food: 8.72 × 10^4 ± 5.4 × 10^3 seston ml^{-1}), but were significantly reduced in high-chlorophyll algal particles (Scheirer-Ray-Hare, food ration: $H_{1,12}$ = 11.29, p < 0.001) at approximately one-third of the ration received by the supplemented treatment for both OA treatments (mean ± SE, n = 8: low food: 423 ± 23 high-chlorophyll cells ml^{-1}; high food: 1418 ± 89 high-chlorophyll cells ml^{-1}). Achieving food treatments within a flow-through system separates the effects of intended nutritional levels from confounding chemical artifacts associated with waste product accumulation, thus providing confidence in our measures of OA effects upon scallop physiology relative to long-term food limitation. An appreciable difference in experimental food ration was used, as bay scallops are typically unaffected by subtle differences in food quantity or quality when the food availability is above 5 µg l^{-1} chlorophyll, the maximal ration assimilatable (Shriver et al. 2002). Juvenile bay scallops were held under the target pCO_2 × food conditions for 42 d (Fig. 1); the experiment ceased at 42 d as mortality reached >50% under low food supply.

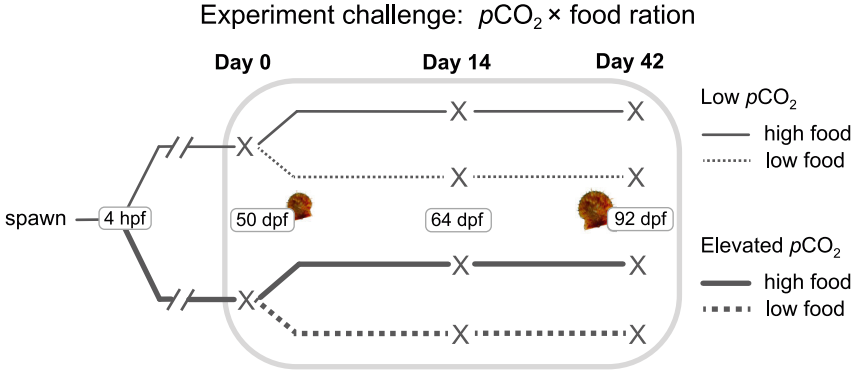

Fig. 1. Schematic of the experimental design and sampling timeline; gray box: specific timeline of this study. Line thickness represents pCO_2 conditions and line type represents the dietary treatment. Sampling time points of juvenile bay scallops are marked as 'X' with the experiment day and age in hours and days post-fertilization (hpf and dpf)

2.5. Physiological assessments

Physiological measurements were conducted on Day 0 (50 dpf) and after 14 d (66 dpf) and 42 d (92 dpf) of exposure to the pCO_2 × food ration treatments (Fig. 1). All scallops in each replicate were counted to estimate survivorship, and a subset from each replicate was measured (haphazardly and non-destructively) for shell height (n = 40–50 replicates tank^{-1}) to calcu-

late growth rate (µm shell height d^{-1}). Shell heights were measured to the nearest 0.01 mm with an image analysis system (ImageJ v.1.53m). Bay scallops were sampled from both high-food pCO_2 treatments on Day 42 (n = 4–11 replicates $tank^{-1}$, 88 total measured) to determine dry shell weights (60°C for 48 h), dry tissue weights (DTW; 60°C for 48 h), and ash-free dry weights (as loss at ignition at 450°C for 4 h). Values were used to calculate height-corrected dry shell weight ([mg dry shell weight / mm shell height] × 100), DTW ([mg DTW / mm shell height] × 100), and condition index (CI = [mg ash-free dry weight / mm shell height] × 100). Tissues of scallops from the low-food pCO_2 treatments and previous time points could not be dissected because of shell fragility and small size.

Bay scallops from all replicates of each treatment were chosen haphazardly to measure oxygen consumption (Day 0: n = 2–3 $tank^{-1}$; Day 14: n = 3–5 $tank^{-1}$; Day 42: n = 2 $tank^{-1}$) and CR (Day 0: n = 3 $tank^{-1}$; Day 14: n = 4–5 $tank^{-1}$; Day 42: n = 2–3 $tank^{-1}$). First, scallops were depurated for 24 h in 0.35 µm-filtered seawater conditioned to corresponding pCO_2 treatments. Depuration was necessary to reduce the effects of ingestion and digestion on measured SMR and CR (Bayne 2017). Following depuration, oxygen consumption was measured with an 8-channel (Loligo® Systems; Wiltrox 4) or 24-channel SensorDish® reader (Loligo® Systems; resolution: ±2% air saturation) depending upon the size of the scallops; oxygen concentrations never reached <80% saturation to avoid oxygen-related stress. Raw oxygen consumption rates (mg O_2 min^{-1}) were estimated using the 'LoLinR' package in R with the authors' recommended parameters for weighting and minimum window size to fit local regressions (Olito et al. 2017). SMRs were corrected for vessel volume (V, l) and blank rates from chambers filled only with 0.35 µm-filtered pCO_2-conditioned seawater and converted to moles of O_2 min^{-1}. This corrected SMR value (SMR_{cor}, µmol l^{-1} O_2 h^{-1}) was normalized (SMR_{norm} or VO_2, µmol l^{-1} O_2 mm^{-1} h^{-1}) using an allometric scaling exponent (b) to account for the allometric relationship of metabolism with size (Bayne 2017; see 'Allometric scaling' in Text A1 in the Appendix) as shell height of the individual (SH_{indiv}, mm) standardized to the mean shell height of all scallops measured (SH_{mean}: 4.2 mm) according to the following equation:

$$SMR_{norm} = V_{O_2} \times (SH_{mean} / SH_{indiv})^b \quad (1)$$

The scaling factor was estimated from logarithm-transformed SMR_{cor} and SH_{indiv} data fit to a simple ordinary least squares linear regression as:

$$\ln(SMR_{cor}) = \ln(a) + b\ln(SH_{indiv}) \quad (2)$$

A scaling exponent of 2.0 was calculated from the data in this study, and details are included in Text A1 in the Appendix.

CRs were conducted in 25 ml vessels following respiration measurements and after scallops were re-exposed to 0.35 µm-filtered seawater conditioned to pCO_2 treatments corresponding to pCO_2 seawater that was at 100% oxygen saturation for ~20 min. CR measurements began by dosing each vessel, including blanks and those with a scallop, with live algal cells (*Chaetoceros* and *Tetraselmis*) to a target concentration of ~4.0×10^4 cells ml^{-1}. Average live algal cell concentrations were $4.2 \times 10^4 \pm 430$ cells ml^{-1} at a ratio of 14:1 *Chaetoceros* to *Tetraselmis*. Samples of 300 µl were taken immediately after adding algae and every 10–20 min over a 1 h period. Cells were counted using fluorescence flow cytometry to quantify high-chlorophyll algal cells within 2 distinct peaks for *Chaetoceros* and *Tetraselmis* (2–10 µm) and low-chlorophyll seston (FL1 fluorescence and <2 µm). CRs were estimated over the elapsed time during which the highest and lowest recorded cell counts were measured, using the following equations (Coughlan 1969, Riisgård 1988, McFarland et al. 2013):

$$CR = \left(\frac{V}{t} \times \left[\ln\left(\frac{C_0}{C_t} \right) - \Delta A \right] \right) \quad (3)$$

$$CR_{norm} = CR \times (SH_{mean} / SH_{indiv})^b \quad (4)$$

Parameters include V, the elapsed time interval (t), cell loss over the elapsed interval t (C_0 and C_t, cells ml^{-1}), and average cell loss (due to sinking) in blank vessels over the elapsed interval (ΔA, cells ml^{-1}). Rates lower than ΔA were omitted from the analysis. CR was normalized (CR_{norm}, cells ml^{-1} mm^{-1} h^{-1}) by using an allometric scaling exponent (b) to describe the change in clearance with shell height. A theoretical scaling exponent of 1.78 was chosen based on reported shell height-standardization of CRs in bivalves (Cranford et al. 2011, Bayne et al. 2017). A detailed explanation is provided in Text A1 in the Appendix, including the rationale for choosing a theoretical over the measured CR scaling exponent in this study.

2.6. Data analysis

Survival, mean shell height, and mean physiological rate data (per replicate tank) were analyzed using 1-way and 2-way ANOVAs to test the fixed-effects of

pCO_2 level (Day 0), food availability, and their interaction (Days 14 and 42). In all cases, the normality of model residuals was examined with Shapiro-Wilk's test (Razali & Wah 2011), and homogeneity of variance was tested using Levene's test (Brown & Forsythe 1974). Non-parametric models for 1-way (Kruskal-Wallis test) and 2-way ANOVAs (Scheirer-Ray-Hare test) were used when assumptions of normality or variance homogeneity were violated. A significant interaction term was assessed using Tukey's HSD tests ('lsmeans' in R; Lenth 2016). Tables of results of statistical tests are provided in Tables S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m740p061_supp.pdf. Data analysis was completed in R (R Core Team 2023, Posit team 2024) and all code is available (https://www.ncei.noaa.gov/data/oceans/ncei/ocads/metadata/0289954.html).

3. RESULTS

3.1. Day 0

Prior to the food ration challenge, mean shell height was not different (1-way ANOVA; $F_{1,6}$ = 0.23, p = 0.65; Table S1) for juveniles reared under low (mean ± SE: 2.39 ± 0.13 mm; n = 4) and elevated pCO_2 (2.32 ± 0.06 mm; n = 4; see Fig. 3). Mean SMRs were also not different (1-way ANOVA; $F_{1,6}$ = 0.07, p = 0.90; Table S1) under low (0.16 ± 0.03 µmol l^{-1} O_2 mm^{-1} h^{-1}; n = 4) and elevated pCO_2 (0.14 ± 0.02 µmol l^{-1} O_2 mm^{-1} h^{-1}; n = 4; see Fig. 3). Total CRs of high-chlorophyll cells were significantly affected by pCO_2 (1-way ANOVA high-chlorophyll; $F_{1,6}$ = 10.58, p = 0.02) with higher CRs under elevated pCO_2 (11.0 ± 1.66 cells ml^{-1} mm^{-1} h^{-1}; n = 4) than low pCO_2 (5.29 ± 0.60 cells ml^{-1} mm^{-1} h^{-1}; n = 4). CRs of *Chaetoceros neogracile* cells were significantly affected by pCO_2 (1-way ANOVA *C. neogracile*; $F_{1,6}$ = 7.49, p = 0.03), with higher CRs under elevated pCO_2 (11.5 ± 1.64 cells ml^{-1} mm^{-1} h^{-1}; n = 4) than low pCO_2 (6.57 ± 0.76 cells ml^{-1} mm^{-1} h^{-1}; n = 4; Fig. 2). There was no effect of pCO_2 level on CRs of *Tetraselmis chui* and seston (Table S2).

3.2. Day 14

By Day 14, survival was significantly affected by food ration (Scheirer-Ray-Hare: $H_{1,12}$ = 4.38, p = 0.04; Table S1), with 10% greater mean survival (±SE) under high food (98.6 ± 0.6%) than low food ration (88.8 ± 5.5%; Fig. 3). There was no significant main effect of pCO_2 level and no significant pCO_2 level × food ration interaction on survival (Table S1).

Shell height was significantly affected by food (2-way ANOVA: $F_{1,12}$ = 108.94, p < 0.001; Table S1) with scallops being ~1.33 mm larger under high food (3.64 ± 0.11 mm; n = 8) than low food ration (2.31 ± 0.05 mm; n = 8; Fig. 2). Shell growth rate was also affected by food (Scheirer-Ray-Hare: $H_{1,12}$ = 11.29, p < 0.001), with high mean growth rates under high food (98.9 ± 5.8 µm d^{-1}; n = 8) and absent shell growth under low food (−3.7 ± 3.1 µm d^{-1}; n = 8; negative value an artefact of high mortality). There was no significant main effect of pCO_2 level or pCO_2 level × food ration interaction on shell height and growth rate (Table S1).

Lastly, total CRs of high-chlorophyll cells were significantly affected by food supply (2-way ANOVA: $F_{1,12}$ =5.95, p = 0.03; Table S2), with rates reduced under low food (32.1 ± 3.61 cells ml^{-1} mm^{-1} h^{-1}; n = 8) relative to high food (93.8 ± 1.2 cells ml^{-1} mm^{-1} h^{-1}; n = 8). There was no effect of pCO_2, food ration, or pCO_2 level × food ration interaction on CRs of *T. chui*, *C. neogracile*, or seston, or on SMR (Table S2).

3.3. Day 42

Survival was significantly affected by food ration (2-way ANOVA: $F_{1,12}$ = 230.8, p < 0.001; Table S1), with 32.1% mean survival (±3.6; n = 8) over the 42 d period under low food relative to 94% mean survival (±1.2; n = 8) in bay scallops under high food (Fig. 3). There was no effect of pCO_2 or pCO_2 level × food ration interaction on survival (Table S1). Shell height was significantly affected by food ration (2-way ANOVA: $F_{1,12}$ = 358.67, p < 0.001) with scallops being ~5.7 mm larger under high food (8.84 ± 0.24 mm; n = 8) relative to low food (3.16 ± 0.14 mm; n = 8). Similarly, shell growth rate was also affected by food (2-way ANOVA: $F_{1,12}$ = 439.8, p < 0.001), with higher mean growth rates under high food (158.2 ± 5.7 µm d^{-1}; n = 8) than low food (19.7 ± 2.5 µm d^{-1}; n = 8). There was no effect of pCO_2 or pCO_2 level × food ration interaction on shell height and growth rate (Table S1). DSWs, measured only in scallops under high food, were significantly affected by pCO_2 (Kruskal-Wallis; H = 5.33, p = 0.02; Table S1), with greater mean shell mass under high-food—low-pCO_2 (0.68 ± 0.11; n = 4) than high-food—elevated-pCO_2 (0.39 ± 0.02; n = 4; Fig. 4). There was no effect of pCO_2 on CI (Table S1).

Physiological rates differed in response to food availability after 42 d of the pCO_2 × food ration challenge. SMRs were significantly affected by food

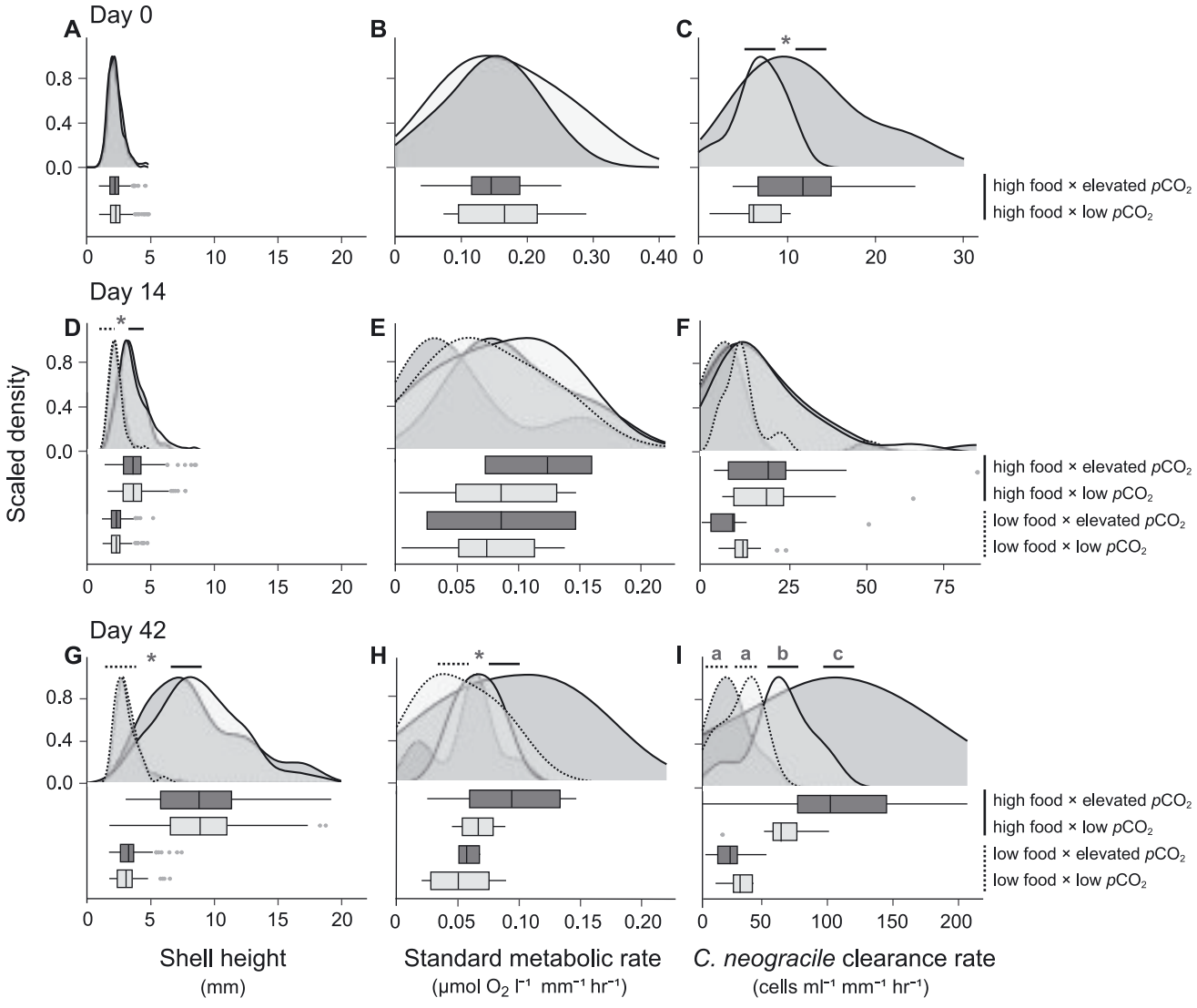

Fig. 2. Shell height, standard metabolic rates, and clearance rates of bay scallops on (A–C) Day 0, (D–F) Day 14, and (G–I) Day 42 of the pCO_2 × food ration challenge. Physiological rates were standardized allometrically. Scaled density plots display the frequency of physiological data grouped by treatment and scaled to 1. Boxplots display the 25th and 75th percentiles (boxes), 1.5 × interquartile range (whiskers), mean (vertical line), and points outside this range (gray points). Shading of density and boxplots represent pCO_2 treatment (light grey: low pCO_2; dark grey: elevated pCO_2) and line type in density plots represents food ration (solid: high food; dashed: low food). Asterisks represent significant main-treatment effects ($p < 0.05$) and lowercase letters as pairwise significant differences ($p < 0.05$)

ration (Scheirer-Ray-Hare: $H_{1,12}$ = 3.98, p = 0.05), with greater mean SMRs under high food (0.078 ± 0.013 µmol O_2 l^{-1} mm^{-1} h^{-1}; n = 8) than low food (0.053 ± 0.040 µmol O_2 l^{-1} mm^{-1} h^{-1}; n = 8; Fig. 2). There was no significant main effect of pCO_2 level or pCO_2 level × food ration interaction on SMR (Table S1). Total clearance rates of high-chlorophyll cells and CRs parsed by *T. chui* and *C. neogracile* cells were significantly affected by food ration (2-way ANOVA: p < 0.001; review Table S2). Scallops under high food ration had ~3-fold greater mean CRs (e.g. 84.2 ± 8.52 *C. neogracile* cells m^{-1} mm^{-1} h^{-1} [n = 8] and 200.0 ± 20.3 *T. chui* cells ml^{-1} mm^{-1} h^{-1} [n = 8]) than those under low food (e.g. 27.2 ± 4.22 *C. neogracile* cells ml^{-1} mm^{-1} h^{-1} [n = 6] and 80.1 ± 19.6 *T. chui* cells ml^{-1} mm^{-1} h^{-1} [n = 5]; Table S4). There was also a significant pCO_2 level × food ration interaction on the CR of *C. neogracile* cells (2-way ANOVA: $F_{1,10}$ = 8.62, p = 0.01; Table S2). Pairwise differences (Tukey's HSD, p < 0.05) document greater mean clearance of *C. neogracile* cells under high-food–elevated-pCO_2 (79.4 ± 23.3 *C. neogracile* ml^{-1} mm^{-1}

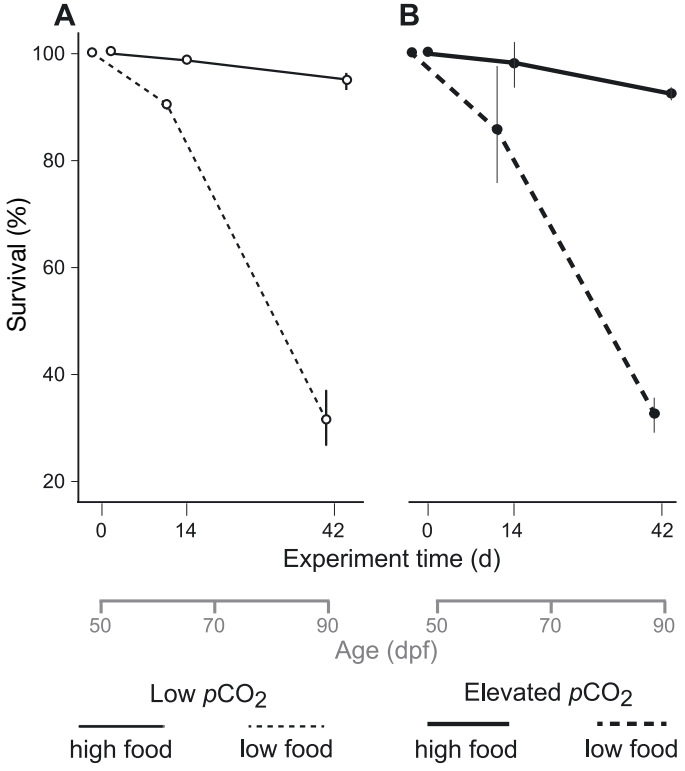

Fig. 3. Percent survival (mean ± SE; n = 4) of bay scallops over the duration of the pCO_2 × food ration challenge under (A) low and (B) elevated pCO_2 treatment. dpf: days post-fertilization

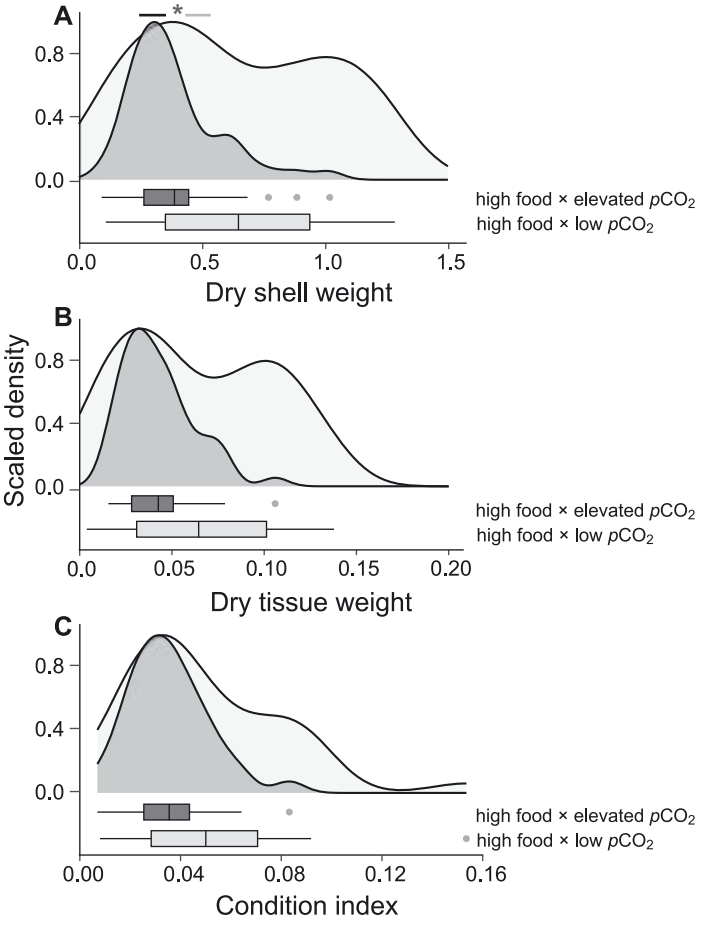

Fig. 4. Shell height-corrected (A) dry shell weights, (B) dry tissue weights, and (C) condition index of bay scallops on Day 42 under the high-food treatment (90 days post-fertilization); all data as (mg tissue weight mm shell height^{-1}) × 100. Scaled density plots display the frequency of data grouped by treatment and scaled to 1. Boxplots display the 25th and 75th percentiles (boxes), 1.5 × interquartile range (whiskers), mean (vertical line), and outliers (grey points). Shading of density and box plots represent pCO_2 treatment (light grey: low pCO_2; dark grey: elevated pCO_2). A significant main treatment effect is shown as an asterisk ($p < 0.05$)

h^{-1}; n = 4) than high-food–low-pCO_2 (64.7 ± 5.1 *C. neogracile* cells ml^{-1} mm^{-1} h^{-1}; n = 4; Fig. 2). There were no significant main effects pCO_2 level and food ration, or pCO_2 level × food ration interaction on clearance of seston particles by Day 42 (Table S2).

4. DISCUSSION

We investigated the effects of food availability on juvenile bay scallops *Argopecten irradians* reared from embryonic to juvenile stage under low (~530–600 µatm) and elevated pCO_2 (~720–850 µatm). Exposure to low food, independent of pCO_2 treatment, severely reduced growth, survival, and removal of high-chlorophyll cells after 14 d. We observed similar shell height and survival for scallops fed supplemented algae under both OA conditions; however, we found greater *Chaetoceros neogracile* particle CRs and reduced dry shell weights under elevated pCO_2 for scallops fed supplemented microalgae (42 dpf). Our results suggest that assessments of bivalve performance in laboratory experiments need to include nutritional quantity and quality (e.g. live mixed-algal diets) and highlight a gap in our understanding of interactive effects of OA and food limitation on bivalves and the algal particles they consume.

A question remains as to why there was a prevailing absence of pCO_2-induced responses observed in our experiments. First, we speculate that OA-induced effects were largely absent because the elevated pCO_2 condition was within a tolerable intensity (i.e. $\Omega_{ar} > 1$) for bay scallops. For example, reduced biomass accumulation and growth rate of the Peruvian scallop *A. purpuratus* under an OA condition similar to this study (891 µatm pCO_2; Lagos et al. 2016) suggests that juvenile *A. irradians* are less sensitive to ~800–

900 µatm pCO_2 (Ω_{ar} ~1.0–1.2). A higher severity of OA challenge (>1000 µatm pCO_2 and <1 Ω_{ar}) causes significant reductions in the survival of larvae (Talmage & Gobler 2010) and juvenile *A. irradians* (~2–18 mm shell height; Talmage & Gobler 2011, Stevens & Gobler 2018). Indeed, in our experiments, larvae exposed to more severe OA (~1680 µatm) did not survive to the juvenile stage. Lastly, the observed physiological similarities between low- and elevated-pCO_2-reared scallops (e.g. survival, shell height, SMR, and tissue biomass; Figs. 3 & 4) support the possibility of selection and/or acclimation to the levels of OA in our experiment. Seawater pCO_2 during parental gonad development (mean ± SD pCO_2: 740 ± 266 µatm) and chronic lifetime exposure from embryo to juvenile stage could have resulted in juveniles with genetic or non-genetic traits (Foo & Byrne 2016), imparting resilience in the performance metrics we tested. Environmental changes during early 'windows' of development can also drive phenotypic trajectory (Fawcett & Frankenhuis 2015). In our study, scallop embryos and larvae were exposed to the 2 OA treatments 4 h post-fertilization, and could either have acclimated to the pCO_2 levels or suffered selective mortality, removing individuals sensitive to the elevated pCO_2 treatment and creating a genetic bottleneck at the juvenile stage. These speculations could explain the findings of White et al. (2014) that document high mortality of *A. irradians* during embryonic exposure to high OA (~2600 µatm pCO_2 and 0.6 Ω_{ar}) yet no growth difference in larvae that survived. To date, one cross-generational study in *A. irradians* found a low capacity for acclimation, although OA conditions were far more severe than this study (pCO_2 ~2500 µatm, Ω_{ar} < 1; Griffith & Gobler 2017). Follow-up experiments are underway to investigate the effects of chronic exposure to elevated pCO_2 across multiple generations in bay scallops.

We further speculate that the low-food treatment (unfiltered natural seston from Milford Harbor, Connecticut, USA) was below a maintenance ration for bay scallops. Bivalves are known to undergo metabolic rate depression under food limitation (e.g. *Crassostrea virginica*, *Mya arenaria*; Haider et al. 2020, McFarland et al. 2020), but it remains unclear how changes in pCO_2 affect metabolic rates (reviewed by Lefevre 2016). There were no insights gained in this study regarding the directionality of pCO_2-induced metabolic adjustments; however, slowed metabolic rate under food scarcity was evident. Low resource availability generally decreases the capacity to mitigate the energetic costs of environmental challenges (Norkko et al. 2005, Fitzgerald-Dehoog et al. 2012), and metabolic rate depression is described as a strategy to conserve energy (Pörtner et al. 2004) and enable time-limited survival under energetically limiting conditions (Hochachka et al. 1996). Metabolism was unaffected and mortalities remained low after the initial 2 wk of food scarcity (~80% survival), but this preceded a dramatic increase in mortality and metabolic decline thereafter (~20–25% survival by Day 42), suggesting a temporal threshold for metabolically sustained survival on the order of weeks. Lastly, an emergence of positive shell growth after food-limited scallops reached >50% mortality highlights that bay scallops were below maintenance ration. Altogether, the influence of food scarcity on organismal performance is well established (e.g. reduced metabolic rate, decreased reproductive status, mobilization of reserves, etc.; Bayne 1973, Liu et al. 2010, Haider et al. 2020), and our findings reinforce its importance for a primary consumer.

Our results also confirm a few general concepts that have emerged in scallop ecology: the dependence on resource surplus for scallop habitat suitability and successful juvenile scallop overwintering (i.e. autumn algal blooms; Bricelj et al. 1987, Epp et al. 1988) and the low-chlorophyll threshold to reach maximum growth and maintenance ration in *A. irradians* (relative to *C. virginica* and *Mercenaria mercenaria*; Shriver et al. 2002, Carmichael et al. 2012).

Coincidentally, our contrasts in total food ration (low food: natural seston; high food: natural seston + algal culture supplement) resulted in a 14% reduction in total particle availability between fed and food-limited conditions. Although low scallop survival suggests that food contrasts were extreme, the Northeast USA has undergone a 14% decline in seasonal chlorophyll in past decades (Schofield et al. 2008), and food scarcity is projected to intensify (e.g. delayed bloom onset; Friedland et al. 2023). Thus, sole exposure to natural seston relative to supplemented ration conveys putative physiological consequences of a continued 14% decline in food supply for this region — an impending challenge for fisheries.

Even though some common metrics used to assess OA effects (survival, growth, and SMR) were independent of OA at different food treatments, the CR data were more complex. The use of flow cytometry to discriminate types of particles revealed that low food exposure impeded the removal of high-chlorophyll cells (*C. neogracile* and *Tetraselmis chui*) when high-food availability was restored instantaneously during CR measurements. Importantly, food-limited scallops were efficient in the removal of smaller low-chlorophyll or non-algal particles (seston) during CR measurements. Failure to capture *C. neogracile* and *T. chui*

suggests that lectin-sugar particle recognition of algal cells as food (Pales Espinosa et al. 2009, 2010) may be affected by the absence of sugar moieties present on *C. neogracile* and *T. chui* during prolonged food limitation. The plasticity of particle processing mechanisms or those traits constitutive in the bay scallop remain topics for further study.

A few differences between low- and elevated-pCO_2-reared juveniles were found under high food supply. First, tissue weights were unaffected by elevated pCO_2 (CI and DTW) but dry shell weight was reduced, suggesting that less energy was allocated toward calcification under elevated pCO_2. Similarly, the king scallop *Pecten maximus* under summer temperature diverts excess energy toward tissue growth at the expense of shell calcification when exposed to OA (454–2750 µatm pCO_2 and Ω_{cal} 6.8–1.5; Cameron et al. 2019). Reduced shell weights are common in juvenile bivalves exposed to OA (Gazeau et al. 2013); however, these results are in contrast to a lack of calcification effects under food surplus for some species (Brown et al. 2018). Second, the CR of *C. neogracile* was greater under elevated pCO_2 than the low pCO_2 treatment prior to the low food challenge (50 dpf) and at the end of the experiment (90 dpf). By contrast, other studies have found a decrease in filtration rate (juvenile *A. purpuratus*; Vargas et al. 2015) and gill cilia beat rate under OA (adult *Mytilus edulis*; Meseck et al. 2020). This finding emphasizes the importance of parsing apart the OA effects on particle discrimination (the consumer) from algae (the resource). Although pre-ingestive sorting can enable the uptake of high-nutritional algae (Ward & Shumway 2004), physicochemical properties of algal cells are altered by OA (Rost et al. 2008, Gao et al. 2018) and are fundamental to particle discrimination and selection rates in bivalves (Rosa et al. 2017, 2018). OA effects on algal cells in this study were unlikely because of the short duration under flow-through conditions (on the order of minutes; less than one cell division). Further research is required to disentangle consumer demands under OA from the possible electrochemical interactions of OA on algal surface characteristics that ultimately dictate particle collection. Present-day coastal conditions along the coastal USA are already experiencing seasonal pCO_2 fluctuations in excess of 800–900 µatm in summer months (Rosenau et al. 2021), and results herein show susceptibility to OA in *A. irradians* whether or not elevated pCO_2 levels co-occur with low or high food supply.

In general, improved feeding performance may stimulate compensatory mechanisms to satisfy energetic demands and offset reduced growth under elevated pCO_2 for marine calcifiers (e.g. mussels, pheasant snail, Peruvian scallop, staghorn coral; Melzner et al. 2011, Hettinger et al. 2013, Thomsen et al. 2013, Towle et al. 2015, Leung et al. 2018, 2022), such as ameliorating the effects of elevated pCO_2 and hypoxia in Chilean scallops *A. purpuratus* (Ramajo et al. 2016b). Maintained feeding and CRs under elevated pCO_2 in juvenile *Placopecten magellanicus* (Pousse et al. 2023), however, did not offset costs of shell production (presumed from dry shell weights), similar to our findings for juvenile bay scallops here (Fig. 4). Conversely, scallops can maintain soft tissues at the cost of reduced shell weight during OA exposure (Córdova-Rodríguez et al. 2022), as we found no change in tissue biomass yet reduced dry shell weights under high-food and elevated pCO_2 (Fig. 4). This suggests that somatic growth and energy storage is prioritized in *A. irradians* to satisfy energetic requirements under environmental change (Sokolova et al. 2012). Our results for bay scallops are consistent with published literature findings and offer insight into the dependence on food supply during post-larval development in this species, which can be a proxy for related scallop models.

OA is a growing concern for fisheries in the Northwest Atlantic (Cooley et al. 2015, Hare et al. 2016), where scallops represent a multi-million dollar resource. Historically, bay scallop populations have suffered collapse under eutrophication-driven change (e.g. habitat loss and monospecific algal blooms; Stewart et al. 1981, Bricelj & Kuenstner 1989, Shumway 1990, Summerson & Peterson 1990) and more recently by pathogen introduction (Pales Espinosa et al. 2023) and co-occurring abiotic factors (Tomasetti et al. 2023). A 2-fold change in pCO_2 from 400 to 800 µatm pCO_2 over the next century is projected to risk a 50% population decline for bay scallops (Grear et al. 2020) and Atlantic sea scallops (Rheuban et al. 2018).

The Atlantic sea scallop *P. magellanicus* is one of the most valuable and vulnerable taxa (Rheuban et al. 2018, Zang et al. 2022). Predictive models for *P. magellanicus* populations are limited to generalizations inferred from experimental findings in related species (Rheuban et al. 2018) because their long larval period (40–60 d), slow growth rates (Shumway & Parsons 2006), low optimal thermal range (10–15°C; Culliney 1974, Desrosiers et al. 1996, Coleman et al. 2021), and early development asynchronies (Galley et al. 2017) together make them difficult to culture (Morse et al. 2020). Although few, recent experimental findings with wild-caught juvenile and adult *P. magellanicus* report that moderate pCO_2 enrichment (~800–900 µatm pCO_2, Ω_{ar} ~1.0, and Ω_{cal} ~1.5) reduces shell

biomass independent of life stage. By contrast, metabolic rates are depressed in adults (Cameron et al. 2022) yet are unaffected in juveniles under OA (Pousse et al. 2023); however, the Cameron et al. (2022) study used lower food rations than the study with juveniles. Similar to Pousse et al. (2023), we also found no effect on metabolism yet reduced shell weight in juvenile *A. irradians* exposed to elevated pCO_2. A discrepancy between OA effects on metabolic rates in the 2 *P. magellanicus* studies could be a result of inherent contrast between different developmental stages (juvenile vs. adult) and the use of continuous as opposed to non-continuous algal diets. OA-induced metabolic depression when resources were limited (Cameron et al. 2022) supports the plausibility of a mitigating effect from food surplus (Ramajo et al. 2016a,b) and the potential importance of nutritional quality and quantity to accurately predict *P. magellanicus* fisheries.

5. CONCLUSIONS

Bay scallops are a historical economic resource, but persistent environmental perturbations can affect fisheries. This study highlights the importance of food ration, especially food limitation on survivorship and performance under 2 pCO_2 conditions tested. Thus, the effects of OA on phytoplankton communities, and therefore food, may lead to added indirect effects on bivalves. Collectively, these findings shed light on the ability of bay scallops to tolerate moderate OA, and provide important future considerations regarding food-mediated tolerance and particle fate under short-term experimental challenges. Our results also highlight the importance of ecosystem-level nutrient quantity and quality data for modeling scallop fisheries, especially as the employed contrasts for food ration in this study (14% change in total particles) approximate reported food scarcity in the northeastern USA (Schofield et al. 2008).

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Appendix. Text A1: Allometric scaling

The relationship between organismal rates (metabolism and clearance) and body mass requires allometric standardization (Schmidt-Nielsen 1984), especially when size variance is high in a population of samples. Shell size varied greatly across the duration of this study (minimum shell height: 1.7 mm; maximum shell height: 14.3 mm), deeming it necessary to employ allometric scaling for metabolic and clearance rates. A well-established method uses a *b* factor, or scaling exponent, estimated as the slope of logarithm-transformed rate versus allometric size data. Though dry tissue mass is commonly used to standardize mollusk rates (Bayne 2017), shell height was used as an accurate allometric trait alternative to inaccuracies from extracting tissues from small or young scallops (~45% of data on scallops of <3 mm). Regressions for logarithm-transformed metabolic and clearance rates were completed for all data and parsed by food ration and pCO_2 treatments (Figs. A1 & A2). Either the calculated scaling exponent (from study data) or the theoretical exponent (from literature consensus of related taxa) was chosen to normalize rates based on the following criteria: (1) use the calculated scaling exponent if the full data set and treatment-parsed data shows consistent linearity and directionality, (2) else use theoretical scaling exponent. Following this criteria, SMR abided criterion 1, and a scaling exponent of 2.0 was used to standardize SMR for this study (Fig. A1); similar values are reported for shell size standardization of respiration rates in marine bivalves (e.g. 2.20–2.23 in geoduck clam *Panopea zelandica* and mussel *Mytilus galloprovincialis*; Arranz et al. 2016, Le et al. 2017). As with SMR, allometric scaling was estimated from logarithm-transformed clearance rates (CR_{cor}; corrected for blank) and individual shell height data (SH_{indiv}) fit to a simple linear regression as the following: $[\ln(CR_{ccor}) = \ln(a) + b\ln(SH_{indiv})]$. A theoretical scaling exponent of 1.78 (Cranford et al. 2011, Bayne 2017) was used to standardize clearance rates due to inconsistent directionality of linear regressions suggesting strong associations between supplementary-fed and food-limited scallops (Fig. A2).

Although scaling is preferred, the authors recognize that numerous studies standardize solely for the individual (rate per unit size or number of individuals). Physiological rate data are reported with allometric standardization in the main text [rate per (mean / observed size)^b] and individual-corrected data as rate per mm shell height provided in the Supplement (Tables S3–S5, Fig. S1).

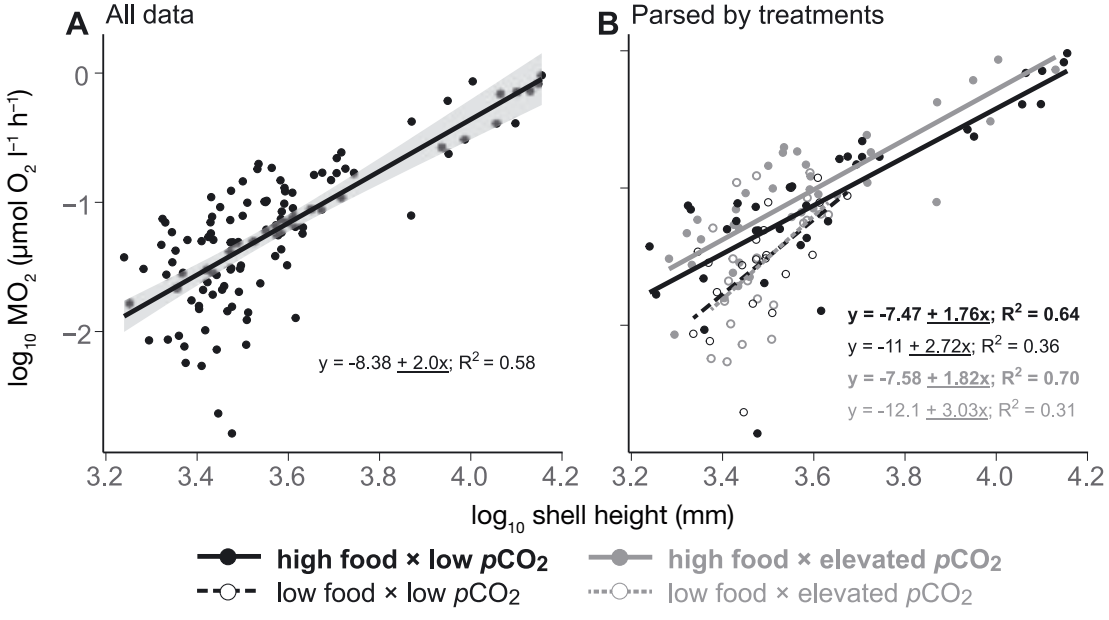

Fig. A1. Fitted ordinary least squares (OLS) regressions for the allometric scaling (shell height) of standard metabolic rate. Scaling exponents were estimated by linear regression of $\log(MO_2)$ (µmol O_2 l^{-1} h^{-1}) versus log(shell height) (mm) using (A) all data and (B) data parsed by pCO_2 × food supply treatments, scaling exponent as underlined text. Plots are additionally supplemented with OLS regression coefficients and a 95% confidence interval for all data (A; gray shading)

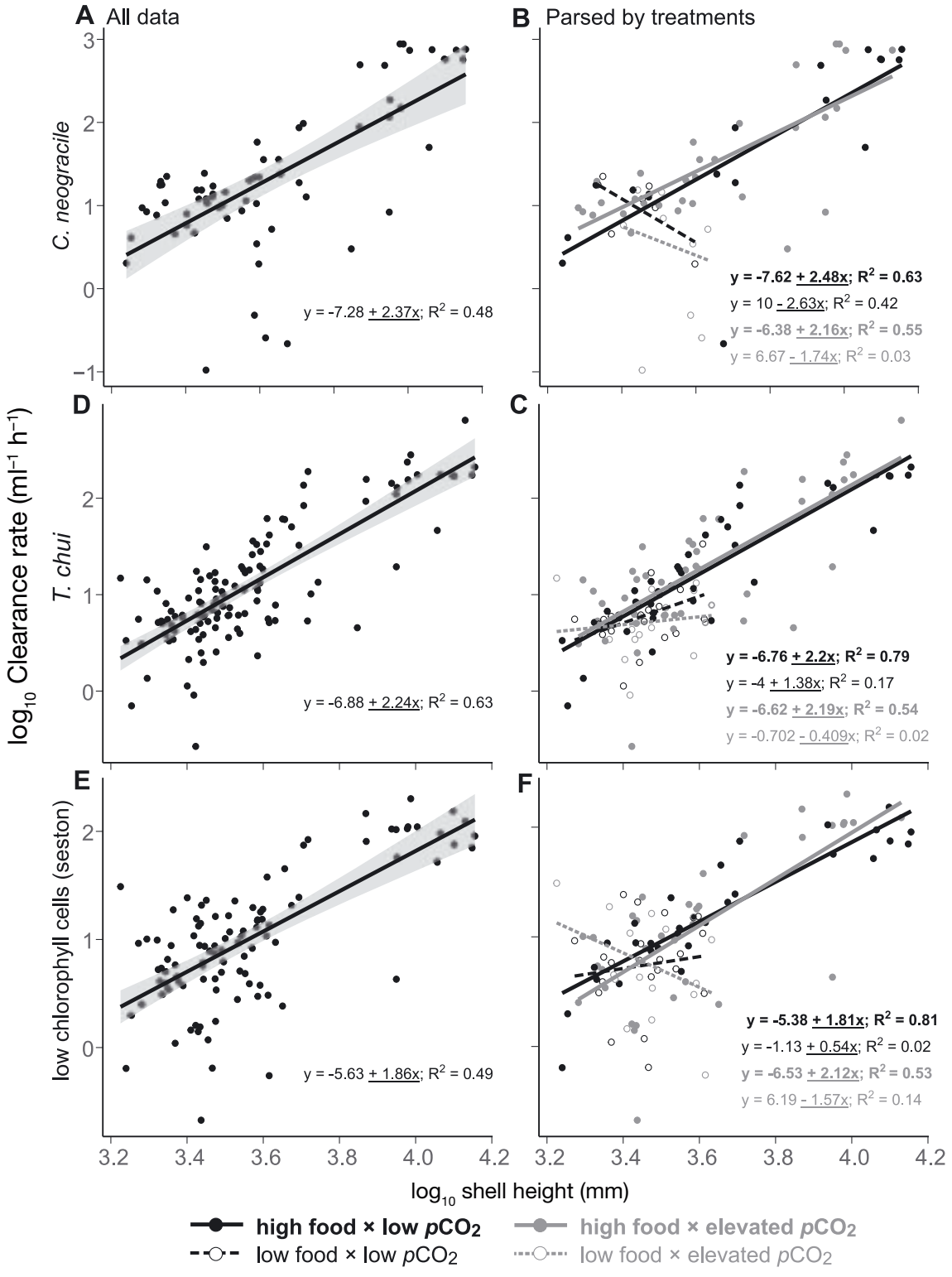

Fig. A2. Fitted ordinary least squares (OLS) regressions for the allometric scaling (shell height) of clearance rates parsed by high-chlorophyll cells (*Chaetoceros neogracile* and *Tetraselmis chui*) and low-chlorophyll cells (seston). Scaling exponents are represented from the slope of log(clearance) versus log(shell height) using (A,C,E) all data and (B,D,F) data parsed by pCO_2 × food supply treatments, scaling exponent as underlined text. Plots are additionally supplemented with ordinary least squares regression coefficients and a 95% confidence interval for all data (A,D,E; gray shading)

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