Environ Biol Fish
https://doi.org/10.1007/s10641-024-01561-y

Resiliency of black sea bass, *Centropristis striata*, early life stages to future high CO_2 conditions

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Received: 19 December 2023 / Accepted: 26 May 2024

Abstract Ocean acidification is a symptom of marine climate change resulting from the uptake of anthropogenic carbon dioxide (CO_2) into the world's ocean, thereby potentially affecting survival, growth, and numerous other traits in fish early life stages. But some fish species are clearly more CO_2-resilient than others, perhaps because they reside in more CO_2-variable, inshore habitats as opposed to more CO_2-stable offshore waters. Here we studied the early life CO_2 sensitivity of an ecologically and economically important fish species (Black Sea Bass, *Centropristis striata*) that seasonally migrates between offshore overwintering and inshore feeding and nursery grounds. We produced embryos from wild spawners and reared them until 10 days post-hatch (dph) at three contrasting pCO_2 levels (~400, ~2200, ~3000 µatm), finding no statistical effects of pCO_2 on hatching success (~28%) or survival to 10 dph (~23%). At the extreme pCO_2 level, surviving larvae were 1.2× larger and grew 55% faster compared to control pCO_2 conditions. These results extend pioneering work by Meseck et al. (2022; https://doi.org/10.1002/mcf2.10200) to confirm a surprising CO_2 tolerance of *C. striata* early life stages. This suggests existing adaptation to high CO_2 conditions either because of seasonal exposures at productive inshore environments or at offshore depths during overwintering.

Keywords Ocean acidification · Climate change · Northwest Atlantic · Growth

Introduction

Anthropogenic carbon dioxide (CO_2) levels continue to increase in the atmosphere and thus in the surface ocean, where CO_2 dissociation produces H^+ ions to reduce both pH and total alkalinity — a symptom of marine climate change called ocean acidification (Jansen et al. 2002; Caldeira and Wickett 2005; Doney et al. 2008). Presently, the average partial pressure of CO_2 (pCO_2) in the average surface ocean is ~400 µatm, which under business-as-usual scenarios could increase to 1200 µatm or even 2200 µatm by the years 2100 and 2300, respectively (Caldeira and Wickett 2005). This rapid global change has motivated an entire field of experimental research dedicated to the question of how marine organisms will respond to it (Lotterhos et al. 2021). For marine fishes, experimental work has shown that future pCO_2 conditions can reduce survival in some but not most species, with lethal effects almost always constrained

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to the earliest life stages (Baumann et al. 2012; Murray et al. 2019; Dahlke et al. 2020). More commonly, high CO_2 levels are observed to induce non-lethal changes to a wide suite of traits, including growth (Murray and Baumann 2020), behavior (Ashur et al. 2017), reproduction (Concannon et al. 2021), metabolism (Schwemmer et al. 2020; Siegfried and Johnson 2023a), and genetic variation (e.g., Tasoff and Johnson 2019). In future oceans, CO_2-resilient species may thus gradually gain fitness advantages over less CO_2-resilient species that could translate into diverging population dynamics.

Similar to what has already been demonstrated for invertebrates (Kelly et al. 2013; Vargas et al. 2017), fish early life CO_2 sensitivities, too, likely depend on the level of short-term CO_2 variability that species already experience in their environment (Baumann 2019). This may explain why nearshore, coastal fishes tend to be less CO_2-sensitive than species from more CO_2-stable offshore environments (Baumann et al. 2022). Fast development rates, as typically found in tropical to subtropical fishes, may also be conducive to CO_2 tolerance, if such species acquire acid–base competency too fast for detectable adverse survival effects to accrue (Baumann 2019). However, these hypotheses still need further empirical support, particularly from candidate species inhabiting offshore habitats or which seasonally alternate between inshore and offshore environments.

One such candidate species is black sea bass (*Centropristis striata*), a subtropical to temperate grouper (Serranidae) of commercial importance in the Northwest Atlantic (Moser and Shepherd 2009; Watanabe et al. 2021). In recent decades, the northern stock component of *C. striata* has rapidly increased in abundance within Southern New England (Bell et al. 2015; Zavell et al. 2023) and the Gulf of Maine (McBride et al. 2018; McMahon et al. 2020; Bandara et al. 2023), thus motivating new ecological research. Unlike other fishes that could be characterized as primarily inshore (e.g., sticklebacks, *Gasterosteus aculeatus* and sheepshead minnows, *Cyprinodon variegatus*) or offshore residents (e.g., northern sandlance, *Ammodytes dubius*), northern stock *C. striata* overwinter offshore but migrate to coastal regions to spawn and feed (Moser and Shephard 2009; Miller et al. 2016). Hence, unlike other previously tested species, *C. striata* inhabit CO_2-stable offshore environments while maturing, which might confer high early-life CO_2 sensitivity. On the other hand, *C. striata* eggs are released into highly CO_2-variable coastal waters during late spring and early summer, and they develop relatively fast (hatching occurs 32–74 h post-fertilization; Berlinsky et al. 2004), which should confer CO_2 tolerance. The latter was suggested by the only previous study to date (Meseck et al. 2022), which, however, was restricted to 48-h-old embryos produced from laboratory-kept adults. Fish brood stocks generally experience artificial food, temperature, and light conditions in addition to pCO_2 levels that far exceed future ICPP projections and are less variable than in the wild — all of which may alter offspring sensitivities to high pCO_2 via epigenetic effects or maternal provision (Ellis et al. 2016; Kwan et al. 2021). To avoid potential laboratory artifacts, CO_2 sensitivity experiments therefore ideally begin with offspring produced from wild-captured spawners.

The goal of our study was thus to obtain independent empirical evidence on the CO_2 sensitivity of *C. striata* in early life stages. We caught wild, spawning ripe adults in spring 2022 in Long Island Sound and then reared their embryos at three contrasting pCO_2 conditions until 10 days post-hatch (dph), while measuring early life survival, growth, and morphological traits. We generally expected to find small to neutral CO_2 effects on these traits but hypothesized that the wild-derived offspring would be less resilient to extreme pCO_2 conditions compared to the brood stock-derived offspring used in Meseck et al. (2022).

Materials and methods

Spawning and fertilization

Spawning ripe *C. striata* were collected on May 20th, 2022, off Stonington Borough in Eastern Long Island Sound (LIS; 41.3359°N, 71.9059°W) via hook and line angling. Adults were transported in 150-l coolers to the Rankin Seawater Laboratory at the University of Connecticut, Avery Point Campus. Upon arrival, adults were distributed into two 600-l flow-through tanks supplied with seawater from Eastern LIS (15–16 °C, 8.15 pH, 30 psu) and held there for three days before strip-spawning. On May 23rd, spawners were separated by sex and individually anesthetized with clove oil (50 mg l^{-1}). Eggs and milt ($N_{female} = 4$;

N_{male} = 3) were pooled across two 2 l spawning trays containing 1 l of filtered (1 µm) and UV-sterilized seawater and mixed until eggs had water hardened (i.e., hardening of the chorion). A 5 ml sample of eggs was randomly allocated to each replicate within 90 min of fertilization. Nine additional 5 ml samples were randomly collected, fixed immediately in 5% buffered formalin and then used to quantify the total number of embryos per 5 ml replicate.

Experimental design

We used three $p\text{CO}_2$ treatments (Table 1) referred to hereafter as control (400 µatm, ~8.15 pH), elevated (2200 µatm, ~7.45 pH), and extreme (3000 µatm, ~7.20 pH). The elevated treatment corresponded to the maximum open-ocean $p\text{CO}_2$ prediction by 2300 (Caldeira and Wickett 2003; Salisbury and Jönsson 2018) that is a common benchmark in OA studies (Baumann et al. 2022). The extreme $p\text{CO}_2$ level is currently reached only rarely in productive, nearshore environments during summer (Baumann et al. 2015), but such extremes may become more common under future climate and eutrophication scenarios (Wallace et al. 2014). For this initial study, we chose a single, static rearing temperature of 22 °C for all $p\text{CO}_2$ treatments, because northern stock *C. striata* initiate spawning when bottom temperatures reach ~15 °C continuing throughout the summer (Mercer 1978, 1989; Slesinger et al. 2021) and because aquaculture studies report optimal development between 19 and 22 °C (Watanabe et al. 2021).

Experiments were conducted in the Automated Larval Fish Rearing System (ALFiRiS), which consists of nine recirculating units that can each hold eight 19 l rearing containers (Murray and Baumann 2015, 2018; Baumann et al. 2022). ALFiRiS sequentially pumps water from each unit once per hour across a central pH electrode (Hach pHD digital electrode calibrated weekly using NIST 2-point pH references), and a custom-designed LabView routine compares read pH with set points, adjusting treatment level accordingly by bubbling 100% bone dry CO_2 or CO_2-stripped air into each units sump tank. LabView also measures temperature via thermistors and then controls submersible heaters (Finnex Deluxe Titanium, 800 W) or in-line chillers (DeltaStar 1/3 horsepower). For this experiment, three ALFiRiS units were assigned to each $p\text{CO}_2$ treatment, with each unit receiving eight individual replicates. Replicate containers consisted of 750 ml plastic cups with 100 µm mesh bottoms, which were floated in larger 19 l containers (fitted with 150 µm mesh screens to allow for water transfer), and each 750 ml rearing container received a gravity-fed flow (4 l h^{-1}) of treatment water. We measured total alkalinity via endpoint titration from filtered water samples (300 ml) taken every 9 days from each tank (Murray and Baumann 2018). Tank temperature, pH, and total alkalinity values were then used to calculate actual $p\text{CO}_2$ levels using CO2SYS (V2.3, Lewis and Wallace 1998; available at https://www.ncei.noaa.gov/access/ocean-carbon-acidification-data-system/oceans/CO2SYS/co2rprt.html). Ammonia (ppm) was measured once a week while

Table 1 Mean (± SD) seawater chemistry parameters over the course of the experiment

Tank	Target pCO_2(µatm)	Actual pCO_2(µatm)	pH	Temperature (°C)	Salinity (psu)	Ammonia (ppm)
1	400	375 ± 28.18	8.11 ± 0.01	21.84 ± 0.2	31 ± 0	0
2	3000	3731 ± 453.03	7.14 ± 0.14	21.92 ± 0.14	30.5 ± 0.58	0
3	2200	2256.1 ± 214.1	7.49 ± 0.06	21.83 ± 0.21	30.5 ± 0.58	0
4	2200	2260.2 ± 191.0	7.49 ± 0.03	21.75 ± 0.23	31 ± 0	0
5	3000	3030.1 ± 31.2	7.16 ± 0.11	21.85 ± 0.2	30.5 ± 0.58	0
6	2200	1956.2 ± 223.4	7.44 ± 0.07	21.86 ± 0.15	31 ± 0	0
7	3000	3562.8 ± 207.7	7.22 ± 0.04	21.67 ± 0.32	30.5 ± 0.58	0
8	400	398.8 ± 34.7	8.09 ± 0.01	21.75 ± 0.22	30.5 ± 0.58	0
9	400	389.4 ± 34.3	8.09 ± 0.01	21.51 ± 0.35	30.5 ± 0.58	0

salinity was measured every nine days (psu). All water quality values can be found in Table 1.

At hatch, half of the replicates were euthanized with an overdose of MS-222 and immediately preserved in cold (2–4 °C) paraformaldehyde (PFA) in phosphate-buffered saline (PBS). The remaining replicates were reared until 10 dph and then preserved identically. For the first two dph, larvae were fed greenwater (RGComplete, Reed Mariculture, Campbell CA, USA) ad libitum 3× a day. Starting on 1 dph, larvae were fed live L-type rotifers (Reed Mariculture, Campbell CA, USA) ad libitum 3× a day.

Response traits

On the day of hatch (~48 h post-fertilization), we counted all hatched larvae, unhatched embryos, and non-fertilized eggs in the four replicates sacrificed per ALFiRiS unit in order to calculate percent fertilization and percent hatch. To determine percent survival at 10 dph (in the remaining 4 replicates per unit), we first calculated the number of embryos by multiplying the average number of eggs per 5 ml replicate by the average replicate fertilization success (%) within each unit. Second, we estimated the number of hatched larvae per replicate by multiplying the estimated embryo count per replicate with the average replicate hatching success. Third, the number of larvae surviving to 10 dph was divided by the estimated number of hatched larvae (0 dph) to calculate survival (%) to 10 dph for each replicate.

Both 0-dph and 10-dph larvae were individually photographed using calibrated images (Nikon SMZ1000, Image-Pro Premier V.9.3.3, Media Cybernetics, Rockville MD). The 0-dph individuals were measured for total length (TL; mm) and body depth (BD; mm). The 10-dph individuals were measured for TL, standard length (SL; mm), BD, eye diameter (ED), and mandible length (ML; mm). Two data points were removed as outliers: a BD at 0 dph (BD > 1.15 mm) and an ED at 10 dph (ED > 1.11 mm). In a small number of larvae, some morphological traits were not measurable due to fixation damage. Length growth rates (GR, mm day^{-1}) were calculated by dividing the difference between replicate TL means at 0 and 10 dph by 10. We also derived theoretical, treatment-specific GR distributions by constructing a matrix of all 0 dph × 10 dph TL to then calculate every possible GR of 10 dph survivors (values of GR < 0 were excluded). As a proxy for larval condition, we calculated the BD to TL ratio as described by Ferron and Legget (1994).

Statistical analysis

All data were inspected for normality (Shapiro-Wilks test; $P < 0.05$) and homogeneity of variance (Levene's test; $P < 0.05$) with residual plots from each model inspected visually. Proportional data were arcsine transformed prior to analysis (Sokal and Rohlf 1995; Zar 1998; Gotelli and Ellison 2012). Univariate general linear models (GLM) were used to examine the effects of $p\mathrm{CO}_2$ on hatching success, TL (0 and 10 dph), BD (0 and 10 dph), and GR. All GLMs were type III to account for the unbalanced design. Significant differences among $p\mathrm{CO}_2$ treatments were then examined using Tukey's posthoc test ($\alpha = 0.05$; SPSS). DPH was included in the GLM testing for $p\mathrm{CO}_2$ and DPH effects on the BD to TL ratio. Across all $p\mathrm{CO}_2$ treatments, 10-dph survival was highly variable between replicates; therefore, replicates were first scored as either a "100% mortality" (0) or "survival" (1), which was then compared using a Pearson's chi-squared test. In addition, a GLM was used to test for the effect of $p\mathrm{CO}_2$ on survival when replicates with 100% mortality were excluded.

In addition, linear regressions were used to quantify relationships between TL and each morphological parameter (SL, BD, ML, ED). The residuals of these relationships were then examined using univariate GLMs to test for potential $p\mathrm{CO}_2$ effects. Statistical analyses and calculations were conducted in SPSS (v 28.0.11(15); linear regressions between TL and each morphological parameter and their respective GLMs, BD to TL GLM) or in R (v4.02, R Core Team; all remaining analyses).

Results

Fertilization success ranged from 6 to 39% with an average of 17% (SD, 8.2%) across all $p\mathrm{CO}_2$ treatments. Experimental $p\mathrm{CO}_2$ treatment had no effect on hatching success (GLM, $P = 0.414$, Fig. 1A; Table 2). Hatching occurred in every replicate container, and the mean (SD) hatching success at control, elevated, and extreme $p\mathrm{CO}_2$ conditions was 23.5% (14.5%), 31.6% (20.0%), and 29.3% (12.9%), respectively. In

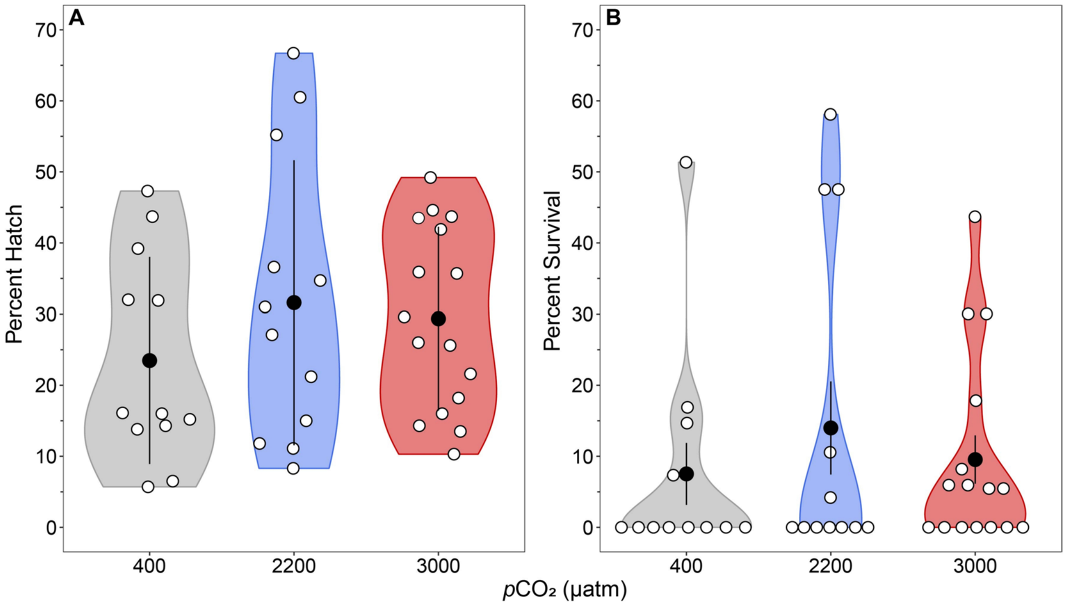

Fig. 1 Jittered violin plots depicting (**A**) percent hatch at 48 hpf and (**B**) estimated percent survival from 0 to 10 dph for *C. striata* reared under three $p\mathrm{CO}_2$ treatments: control, 400 µatm (gray); elevated, 2200 µatm (blue); and extreme, 3000 µatm (red). White circles represent means for each replicate, while the black circle and error bars represent the treatment mean (± SD). Note that percent survival means (± SD) in (B) exclude zero survival replicates

each $p\mathrm{CO}_2$ treatment, some replicates exhibited 100% mortality by 10 dph (i.e., control 8 of 12; elevated 7 of 12; extreme 7 of 16) and survival was not statistically different ($X^2 = 18.86$, df = 39, $P = 0.997$, Fig. 1B). Excluding these 100% mortality replicates, mean (SD) survival to 10 dph at control, elevated, and extreme $p\mathrm{CO}_2$ conditions was 22.6% (19.6%), 33.6% (24.4%), and 16.9% (14.3%) with an overall mean of 23% ± 19% (GLM, $P = 0.363$, Table 2). At 0 dph, mean TL was similar across pCO_2 treatments (1.8 mm; GLM, $P = 0.1$, Fig. 2A; Table 2), however, body depth at 0 dph increased with $p\mathrm{CO}_2$ (GLM, $P < 0.001$, Fig. 2C; Table 2), as larvae reared at control $p\mathrm{CO}_2$ conditions had a mean BD of 0.55 mm (SD, 0.10), while larvae reared at elevated and extreme $p\mathrm{CO}_2$ conditions had a mean BD of 0.59 mm (SD, 0.10). The BD to TL ratio at 0 dph did not vary between $p\mathrm{CO}_2$ treatments (SD, 0.09; GLM, $P = 0.94$,Fig. 2E; Table 2).

At 10 dph, *C. striata* larvae reared at the extreme $p\mathrm{CO}_2$ treatment measured 3.51 ± 0.55 mm, which was 1.2× larger than those reared at control conditions (2.84 ± 0.39 mm; GLM, $P = 0.001$, Fig. 2B; Table 2). BD was statistically unaffected by $p\mathrm{CO}_2$ treatments (0.67 ± 0.16 mm; GLM, $P = 0.239$, Fig. 2D; Table 2). The mean GR increased (GLM, $P = 0.0001$, Fig. 3; Table 2) from 0.11 mm day^{-1} (SD, 0.05) to 0.15 mm day^{-1} (SD, 0.06) to 0.17 mm day^{-1} (SD, 0.06) at control, elevated, and extreme $p\mathrm{CO}_2$ conditions, respectively. At 10 dph, all morphological traits were positively correlated with TL (SL: $R^2 = 0.82$, $P < 0.001$; BD: $R^2 = 0.51$, $P < 0.001$; ML: $R^2 = 0.25$, $P < 0.001$; ED: $R^2 = 0.51$, $P < 0.001$; Fig. 4). The residuals of these relationships showed no differences between $p\mathrm{CO}_2$ treatments for all four traits (Table 3). At 10 dph, the BD to TL ratio did not differ across $p\mathrm{CO}_2$ treatments at 10 dph (0.19 ± 0.03; GLM, $P = 0.94$, Fig. 2F; Table 2). However, the BD to TL ratio decreased by 42% from 0 to 10 dph (GLM, $P < 0.001$, Fig. 6E, F; Table 2) but there was no interaction of $p\mathrm{CO}_2$ and dph (GLM, $P = 0.65$, Fig. 2E, F; Table 2).

Discussion

We reared *C. striata* offspring from fertilization to 10 dph across a large range of $p\mathrm{CO}_2$ conditions, finding either neutral or positive CO_2 effects with regard to hatching success, larval survival, and growth. This apparent CO_2 tolerance is consistent

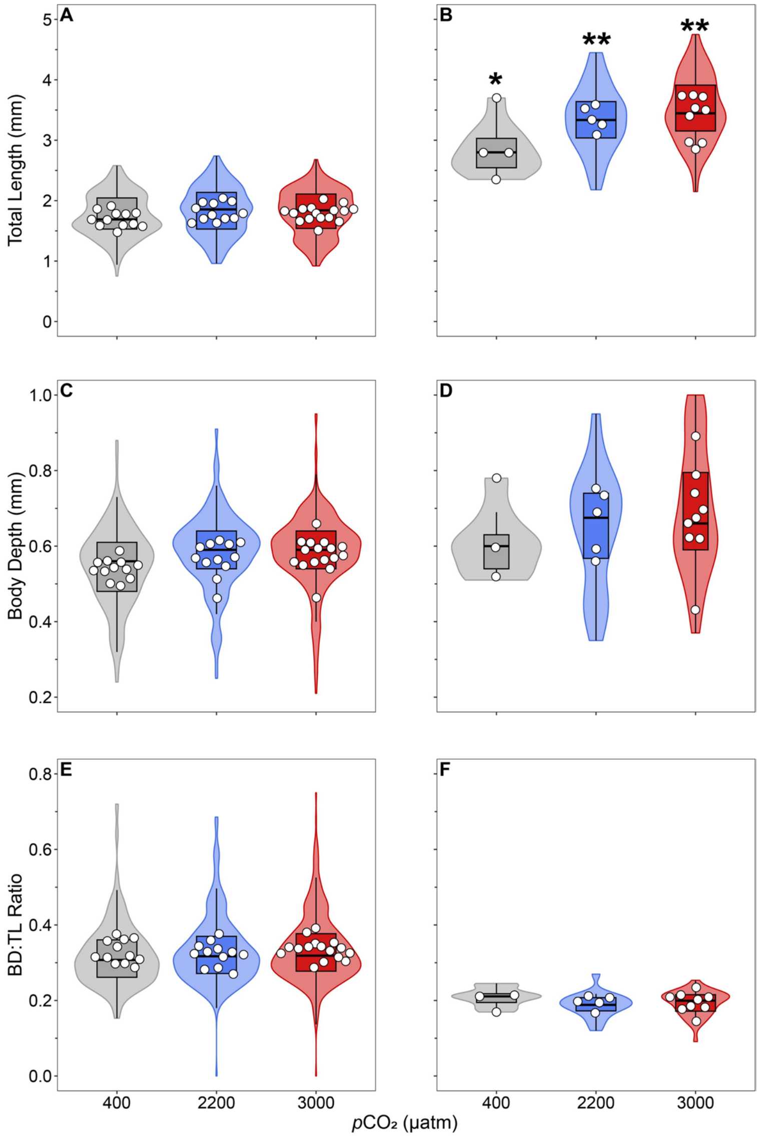

Fig. 2 Jittered violin and boxplots depicting total length at **A** 0 dph and **B** 10 dph, Body depth at **C** 0 dph and **D** 10 dph, and body depth: total length ratio (BD), a proxy for larval condition, at **E** 0 dph and **F** 10 dph for *C. striata* reared under three $p\mathrm{CO}_2$ treatments: control, 400 µatm (gray); elevated, 2200 µatm (blue); and extreme, 3000 µatm (red). Upper and lower whiskers represent the 90th and 10th percentile, respectively. While the upper and bottom edges of the boxplot represent the 75th and 25th percentile, respectively, and the bold center line represents the median. White circles represent means for each replicate with surviving larvae. Different numbers of asterisks indicate significant differences between treatments (Tukey HSD post-hoc test, $\alpha = 0.05$). We note that one replicate from the control treatment had only one surviving larva to 10 dph that could not be measured for BD, resulting in four replicates in panel B and three replicates in panels D and F

with Meseck et al. (2022), the only previous study on *C. striata* early life CO_2 sensitivity (Meseck et al. 2022), but our findings now extend it to ≥ 3000 µatm $p\mathrm{CO}_2$ and to feeding larvae at 10 dph. Meseck et al. (2022) produced offspring from adults that had been held in captivity for 265 to 630 days, which might have influenced offspring CO_2 tolerance via transgenerational plasticity (e.g., shellfish: Parker et al. 2011; copepods: Thor and Dupont 2015; fish: Miller et al. 2012; Murray et al. 2014; Donelson et al. 2018). Because our study used wild caught spawners and found similar results, it further strengthened the conclusion that *C. striata* early life stages are highly CO_2 resilient, regardless of prior parental exposure.

The high CO_2 tolerance of *C. striata* early life stages may be partially related to their rapid development, which is characteristic of serranids (Kendall Jr 1983). This is because direct, lethal CO_2 effects in fish early life stages occur mostly due to acidosis, i.e., organ failures due to underdeveloped acid-base competency and homeostatic regulation (Heuer and Grosell 2014; Dahlke et al. 2020), which is a cumulative process and therefore likely requires time (Baumann 2019). Other examples of fish species with fast development and also high early life CO_2 tolerance include

Table 2 General linear model (type III) results for the effects of pCO_2 on percent hatch (arcsine transformed), percent survival (excluding replicates with 100% mortality; arcsine transformed), total length (TL; 0 and 10 dph), body depth (BD; 0 and 10 dph), and growth rate in length between 0 and 10 dph (GR). In addition, GLM (type III) results for the effects of pCO_2, dph, and their interaction on body depth: total length ratio (BD to TL), a proxy for larval condition. Significant effects are in bold

Trait	Fixed effect	DF	SS	*F* value	*P*
Percent hatch	pCO_2	2	0.059	0.903	0.414
Percent survival	pCO_2	2	0.114	1.086	0.363
TL (0 dph)		2	0.640	2.304	0.1000
TL (10 dph)	pCO_2	2	4.183	7.400	**0.001**
BD (0 dph)	pCO_2	2	0.258	12.949	**< 0.001**
BD (10 dph)	pCO_2	2	0.071	1.461	0.239
GR	pCO_2	2	9.037	1114.1	**< 0.00001**
BD to TL	pCO_2	2	0.001	0.067	0.935
	dph	1	0.890	100.63	**< 0.001**
	pCO_2 × dph	2	0.008	0.432	0.649

mahi-mahi (*Coryphaena hippurus*, Bignami et al. 2014) and yellowtail kingfish (*Seriola lalandi*, Munday et al. 2016), while species with longer embryonic periods appear more sensitive (e.g., Atlantic cod, *Gadus morhua*, Frommel et al. 2012; Stiasny et al. 2016; northern sandlance, *Ammodytes dubius*, Murray et al. 2019; Baumann et al. 2022). In *C. striata*, hatching occurred at 48 h post-fertilization regardless of CO_2 level, which is consistent with aquaculture rearing studies at similar temperatures (Perry et al. 2007; Watanabe et al. 2021).

The observed early life stage high resiliency to elevated CO_2 may also arise from adult pre-adaptation to a high CO_2 environment. Northern stock *C. striata* currently overwinter on the mid-Atlantic bight shelf break off New Jersey (Miller et al. 2016) where winter temperatures remain > 10 °C, and ambient pCO_2 levels are believed to be only slightly increased (~400–600 µatm; Wright-Fairbanks et al. 2020; Lima et al. 2023), although bottom water pCO_2 data are notoriously limited. Storm-induced downwelling (Guzik et al. 2022) could potentially bring CO_2

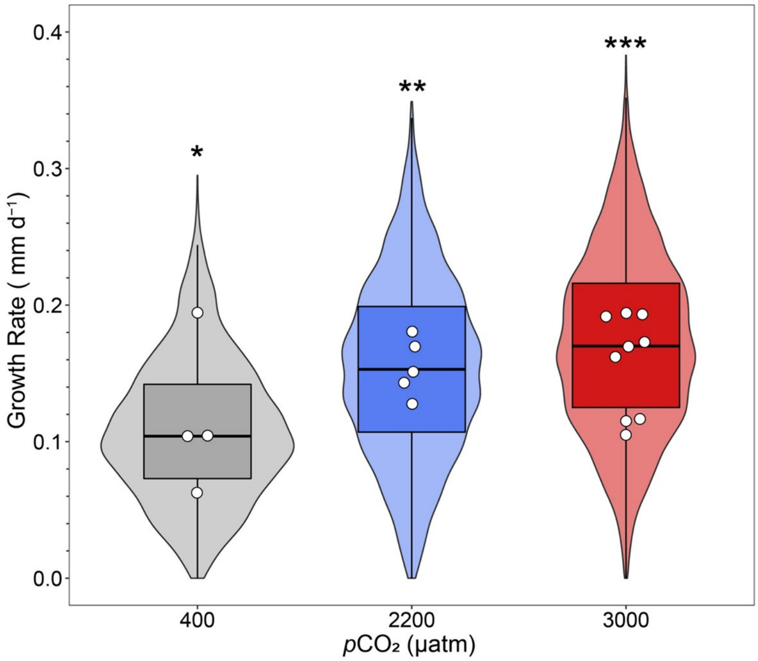

Fig. 3 Jittered violin and boxplots depicting theoretical growth rate distributions in length between 0 and 10 dph for *C. striata* reared under three pCO_2 treatments: Control, 400 µatm (gray); elevated, 2200 µatm (blue), and extreme, 3000 µatm (red). Upper and lower whiskers represent the 90th and 10th percentile, respectively. Upper and bottom edges of each boxplot represent the 75th and 25th percentile, respectively, and the bold center line represents the median. White circles represent means for each replicate that had surviving larvae at 10 dph. Different numbers of asterisks indicate significant differences between treatments (Tukey HSD post-hoc test, $\alpha = 0.05$)

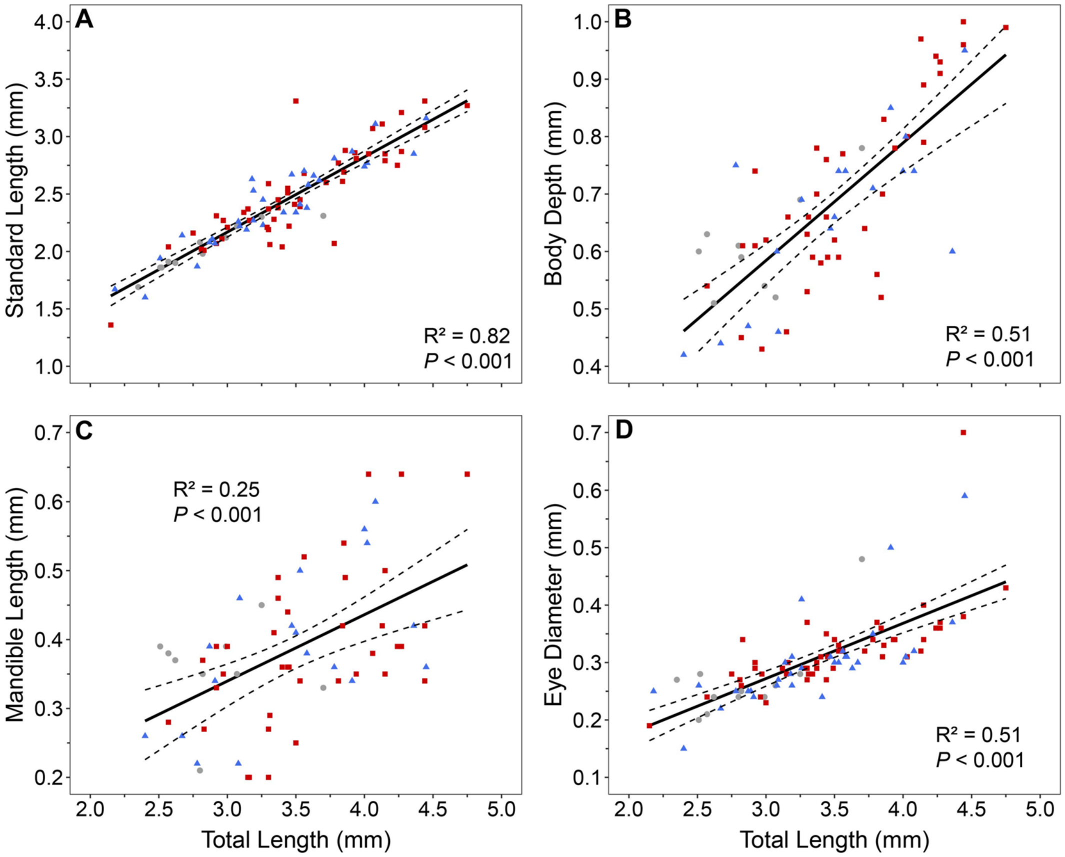

Fig. 4 Relationship between total length (TL) and **A** standard length, **B** body depth, **C** mandible length, and **D** eye diameter for 10 dph *C. striata* larvae reared under three contrasting $p\mathrm{CO_2}$ treatments: control, 400 µatm (gray circles); elevated, 2200 µatm (blue triangles), and extreme, 3000 µatm (red squares). The dashed lines represent the 95% C.I. for each relationship

Table 3 General linear model (type III) results for the effects of $p\mathrm{CO_2}$ on 10 dph standard length (SL), body depth (BD), eye diameter (ED), and mandible length (ML) residuals. Residuals were extracted from linear regressions of TL vs. each morphological trait

Trait	DF	SS	*F* value	*P*
SL	2	0.990	0.495	0.611
BD	2	1.968	0.999	0.374
ML	2	1.625	0.820	0.445
ED	2	0.681	0.339	0.713

rich water to the bottom and thus pre-expose adults to more elevated $\mathrm{CO_2}$-levels, but this has yet to be explicitly demonstrated. Alternatively, pre-adaptation could also occur to equip BSB offspring for the high and variable $\mathrm{CO_2}$ conditions which they encounter during summer in their nearshore settlement habitats (~330 to ~4000 µatm within single tidal cycles; Baumann et al. 2015). Such mitigating effect of parental conditioning due to seasonal $p\mathrm{CO_2}$ fluctuations has previously been proposed for Atlantic silversides (*Menidia menidia*, Murray et al. 2014).

Hatching success was surprisingly variable between replicates (but independent of $\mathrm{CO_2}$ treatment) ranging from ~6 to 67%. Similar variability across treatments was observed by Meseck et al. (2022) with the percentage of hatched larvae ranging from 6 to 63% in their 2013 experiment to 16–70% and 36–95% in their 2014 and 2015 experiments, respectively. This variability may be inherent to serial spawners, including *C. striata*, and other marine species (e.g., *Chrysophrys auratus*, Sabetian et al. 2020; *Clupea harengus*, Lambert and Ware 1984; *Engraulis* *ringens*, Castro et al. 2010; *Sciaenops ocellatus*, Fuiman et al. 2005) in which maternal investment varies both within and among spawns, producing a "batch effect," i.e., a "bet-hedging strategy" (Sabetian et al. 2020), thereby generating large variability in hatching success. This potential batch effect in *C. striata* may be caused by changes in the investment of triglycerides (Sabetin et al. 2020) and/or by changes in diet fatty acid composition over the spawning season which is known to affect embryo and larval performance (Hou and Fuiman 2021; Hou et al. 2022). *C. striata* are mixed breeders that incorporate both somatic energy and energy from their diet while spawning (Slesinger et al. 2022). Laboratory strip-spawning may further contribute to inconsistent hatch rates in broadcast spawning fish (e.g. *Lutjanus campechanus*, Bardon-Albaret and Sailant 2017). However, given that Meseck et al. (2022) did not strip-spawn fish but collected embryos spawned in tanks and still observed similar levels of variability in hatching success, differences in maternal investment appear the more likely explanation. While bet-hedging has not been described for *C. striata*, individuals might use a diversified bet-hedging strategy where phenotypic variance in, e.g., egg quality or offspring size is increased (Marshall et al. 2008; Crean and Marshall 2009; Olofsson et al. 2009). The resultant variations in hatching success could be advantageous for recruitment success under fluctuating environmental conditions (Hočevar et al. 2021), especially under increasing climate variability (Shama 2015).

Rearing *C. striata* larvae to 10 dph showed no statistical $p\mathrm{CO}_2$ effects on mean survival rates (range 0 to 69%), which therefore adds another empirical data point to suggest that direct, lethal effects of elevated CO_2 conditions are the exception (Chambers et al. 2014; Bromhead et al. 2015; Pimentel et al. 2016), not the rule among fish species (Pope et al. 2014; Sswat et al. 2018; McMahon et al. 2020). We also found that fish reared under extreme CO_2 conditions were longer in length, which has been observed in other CO_2 studies on larval fishes (e.g., Atlantic cod, Frommel et al. 2012; summer flounder, Chambers et al. 2014). Still, multiple studies have observed that larger larvae can be in poorer energetic condition, regardless of condition being measured morphometrically or via RNA to DNA ratios (Franke and Clemmesen 2011; Frommel et al. 2012; Chambers et al. 2014). Here, we examined another condition proxy, the body depth to total length ratio, but found no treatment differences in *C. striata*, only an ontogenetic decrease from 0 to 10 dph. Whether alternative, potentially more sensitive condition proxies (e.g. RNA: DNA; Clemmesen 1994) might have revealed negative $p\mathrm{CO}_2$ effects in larval *C. striata* remains speculative (Buckley et al. 1999; Raedemaecker et al. 2012). Future studies need to rear larval *C. striata* throughout the remainder of the larval stage in order to identify potential tradeoffs in energetic condition across the larval phase to better identify larger fitness implications. For example, Chambers et al. (2014) reared larval summer flounder under differing $p\mathrm{CO}_2$ treatments, finding altered ontogenetic trajectories under elevated $p\mathrm{CO}_2$ that could impact survival and recruitment.

While TL to BD ratios could be useful proxies for larval condition when similar life stages are compared (e.g., Koenker et al. 2018), comparisons across early life stages need to be interpreted with caution. For *C. striata*, the pronounced change in the TL to BD ratio from 0 to 10 dph clearly reflected an ontogenetic shift from the more compact form of an underdeveloped hatchling to the more elongated shape of an actively feeding larva. This also coincided with a diet shift from small zooplankton (e.g. rotifers) to larger prey items (e.g. *Artemia*), which occurs between 10 and 21 dph depending on culture conditions (Watanabe et al. 2021; Zavell and Baumann, pers obs.). Previous research on larval *Clupea harengus* found that condition indices decreased at a critical size, which corresponded to a diet shift from an omnivorous to carnivorous diet, which constituted a critical step in larval survival (Denis et al. 2017). Future studies should rear *C. striata* larvae under contrasting environmental conditions through settlement to the juvenile stage and employ a suite of different proxies to infer changes in larval condition (Peck et al. 2015).

We found no statistical differences in morphological traits (BD, ML, ED) at 10 dph across all CO_2 treatments. This was also observed in spiny damselfish reared at 450 to 850 µatm $p\mathrm{CO}_2$ (Munday et al. 2011), whereas Chambers et al. (2014) observed CO_2 effects on numerous morphological traits up to 4714 µatm. In our case, the absence of CO_2 effects appears to support the high resiliency of larval *C. striata*. Whether larger sample sizes and a larger breadth of morphological trait measurements might have revealed any CO_2 effects remains speculative. Nevertheless, the development of larval morphological traits is strongly linked to length (Peck et al. 2012), and this was true for *C. striata* larvae as well, regardless of CO_2 treatment. This scaling plays an important role in ontogeny and ontogenetic diet shifts, especially mouth and body size that impact larval feeding success (Pepin 2023). We did not observe any signs of skeletal anomalies in BSB larvae, as reported by Meseck et al. (2022) but which might have been an artifact of fixation. Fixation is known to cause specimen shrinkage and morphological changes (Hay 1982; Sotola et al. 2019), particularly in species like *C. striata* that hatch as underdeveloped larvae without cartilage/bone tissues and an undefined notochord (Zavell and Baumann, pers obs.).

High CO_2 levels appeared to positively affect growth, which in the wild would confer reduced mortality risk (Anderson 1988; Houde 1997), as fish reared under extreme CO_2 grew at a rate 55% faster than those in control conditions. Faster larval growth at higher CO_2 conditions is a common finding in fish early life CO_2 sensitivity experiments (Hurst et al. 2012, 2013; Bignami et al. 2014; Schade et al. 2014; McMahon et al. 2020; Siegfried and Johnson 2023b). It may in part result from increased feeding, which is difficult to quantify in very early fish larvae. In the present study, we used an ad libitum feeding regime of L-type rotifers; hence, fish at high CO_2 treatments could have compensated or overcompensated for increased energy demands by simply eating more, which is consistent with other studies that showed food availability to ameliorate CO_2 effects on fish early life survival, growth, and physiology (Stiasny et al. 2018).

The observed faster growth and larger individuals at elevated pCO_2 conditions could be due to faster metabolic rates and subsequently higher feeding rates and/or that larger individuals have a larger physiological capacity allowing them to cope with higher pCO_2 (Ishimatsu et al. 2008; Melzner et al. 2009; Pan et al. 2014). In turn, this could be favorable given that larval size correlates positively with predator avoidance and prey capture abilities (Miller et al. 1988; Takasuka et al. 2004; Robert et al. 2023). Overall, early life stages of *C. striata* may therefore be resilient to ocean acidification, as now indicated by two independent studies with different tested pCO_2 levels, parental provenance, and methodology. In this study, the generally low number of larvae surviving to 10 dph indicates potential for improved rearing that may still corroborate or falsify these conclusions. Overall, the northwest Atlantic shelf is rapidly warming (Kavanaugh et al. 2017) in addition to changes in Gulf Stream dynamics (Gangopadhyay et al. 2019), which are altering primary productivity, species compositions, and zooplankton prey items (Kleisner et al. 2017; Record et al. 2018; Suca et al. 2021; Benedetti et al. 2021; Balch et al. 2022). This could result in adverse effects for *C. striata* — independent of ocean acidification — perhaps via match/mismatch of larvae and their prey (Laurel et al. 2021) and/or a decrease in zooplankton nutritional quality (Rossoll et al. 2012). Thus, we emphasize that while *C. striata* larvae may appear resilient to ocean acidification, multi-stressor studies are required to more comprehensively understand the species' vulnerability to marine climate change and to better inform future management decisions.

Acknowledgements We thank C. Mills and L. Jones for assistance with collecting spawning adult specimens and C. Woods for assistance in the seawater laboratory. D. Barnum and M. Mouland assisted throughout the experiment, and C. Matassa gave statistical advice.

Author contribution Conceptualization: Max D. Zavell, Hannes Baumann; Methodology: Max D. Zavell, Hannes Baumann; Investigation: Max D. Zavell; Formal analysis and investigation: Max D. Zavell, Hannes Baumann; Writing – original draft preparation: Max D. Zavell; Writing – review and editing: Hannes Baumann, Max D. Zavell; Funding acquisition: Hannes Baumann, Max D. Zavell; Resources: Max D. Zavell.

Funding This study was partially funded by National Science Foundation, Division of Ocean Sciences grant #1536336, #1756316, and Connecticut SeaGrant R/LR-30 to Hannes Baumann and a University of Connecticut, Department of Marine Sciences Predoctoral award to Max D. Zavell.

Data availability Replicate-specific survival and growth data as well individual morphometrics data are available from the BCO-DMO repository, Project #650184 (DOI: https://doi.org/10.26008/1912/bco-dmo.927786.1; DOI: https://doi.org/10.26008/1912/bco-dmo.927800.1).

Declarations

Ethics approval All animal husbandry and methodology were conducted in accordance with the University of Connecticut's Institutional Animal Care and Use Committee protocol # A20-046.

Consent to participate Not applicable.

Consent for publication Not applicable.

Conflict of interest The authors declare no competing interests.

References

Anderson JT (1988) A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. J Northwest Atl Fish Sci 8:55–66. https://doi.org/10.2960/J.v8.a6

Ashur MM, Johnston NK, Dixson DL (2017) Impacts of ocean acidification on sensory function in marine organisms. Integr Comp Biol 57:63–80. https://doi.org/10.1093/icb/icx010

Balch WM, Drapeau DT, Bowler BC, Record NR, Bates NR, Pinkham S, Garley R, Michell C (2022) Changing hydrographic, biogeochemical, and acidification properties in the gulf of maine as measured by the Gulf of Maine North Atlantic Time Series, GNATS, between 1998 and 2018. J Geophys Res G: Biogeosciences 127:e2022JG006790. https://doi.org/10.1029/2022JG006790

Bandara RMWJ, Curchitser E, Pinsky ML (2023) The importance of oxygen for explaining rapid shifts in a marine fish. Glob Change Biol E 17008. https://doi.org/10.1111/gcb.17008

Bardon-Albaret A, Sailant E (2017) Egg quality traits and predictors of embryo and fry viability in red snapper *Lutjanus campechanus*. Aquacult Rep 7:48–56. https://doi.org/10.1016/j.aqrep.2017.05.004

Baumann H, Wallace R, Tagliaferri T, Gobler CJ (2015) Large natural pH, CO_2 and O_2 fluctuations in a temperate tidal salt marsh on diel, seasonal and interannual time scales. Estuar Coasts 38:220–231

Baumann H (2019) Experimental assessments of marine species sensitivities to ocean acidification and co-stressors: how far have we come? Can J Zool 97:399–408. https://doi.org/10.1139/cjz-2018-0198

Baumann H, Talmage SC, Gobler CJ (2012) Reduced early life growth and survival in a fish in direct response to increased carbon dioxide. Nat Clim Change 2:38–41. https://doi.org/10.1038/nclimate1291

Baumann H, Jones LF, Murray CS, Siedlecki SA, Alexander M, Cross EL (2022) Impaired hatching exacerbates the high CO_2 sensitivity of embryonic sand lance *Ammodytes dubius*. Mar Ecol Prog Ser 687:147–162. https://doi.org/10.3354/meps14010

Bell RJ, Richardson DE, Hare JA, Lynch PD, Fratantoni PS (2015) Disentangling the effects of climate, abundance, and size on the distribution of marine fish: an example based on four stocks from the Northeast US shelf. ICES J Mar Sci 72:1311–1322. https://doi.org/10.1093/icesjms/fsu217

Benedetti F, Vogt M, Elizondo UH, Righetti D, Zimmermann NE, Gruber N (2021) Major restructuring of marine plankton assemblages under global warming. Nat Commun 12:5226. https://doi.org/10.1038/s41467-021-25385-x

Berlinsky DL, Taylor JC, Howell RA, Bradley TM, Smith TIJ (2004) The effects of temperature and salinity on early life stages of black sea bass *Centropristis striata*. J World Aquacult Soc 35:335–344. https://doi.org/10.1111/j.1749-7345.2004.tb00097.x

Bignami S, Sponaugle S, Cowen RK (2014) Effects of ocean acidification on the larvae of a high-value pelagic fisheries species, mahi-mahi *Coryphaena hippurus*. Aquat Biol 21:249–260. https://doi.org/10.3354/ab00598

Bromhead D, Scholey V, Nicol S, Margulies D, Wexler J, Stein M, Lennert-Cody C, Williamson J, Havenhand J, Ilyina T, Lehodey P (2015) The potential impact of ocean acidification upon eggs and larvae of yellowfin tuna (*Thunnus albacares*). Deep Sea Res II Top Stud Oceanogr 113:268–279. https://doi.org/10.1016/j.dsr2.2014.03.019

Buckley L, Caldarone E, Ong T-L (1999) RNA-DNA ratio and other nucleic acid-based indicators for growth and condition of marine fishes. Hydrobiologia 401:265–277. https://doi.org/10.1023/A:1003798613241

Caldeira K, Wickett ME (2003) Anthropogenic carbon and ocean pH. Nature 425:365

Caldeira K, Wickett M (2005) Ocean model predictions of chemistry changes from carbon dioxide emissions to the atmosphere and ocean. J Geophys Res Oceans 110. https://doi.org/10.1029/2004JC002671. C09S04

Castro LR, Claramunt G, González HE, Krautz MC, Llanos-Rivera A, Méndez J, Schneider W, Soto S (2010) Fatty acids in eggs of anchoveta *Engraulis ringens* during two contrasting winter spawning seasons. Mar Ecol Prog Ser 420:193–205. https://doi.org/10.3354/meps08819

Chambers RC, Candelmo AC, Habeck EA, Poach ME, Wieczorek D, Cooper KR, Greenfield CE, Phelan BA (2014) Effects of elevated CO_2 in the early life stages of summer flounder, *Paralichthys dentatus*, and potential consequences of ocean acidification. Biogeosciences 11:1613–1626. https://doi.org/10.5194/bg-11-1613-2014

Clemmesen C (1994) The effect of food availability, age or size on the RNA/DNA ratio of individually measured herring larvae: laboratory calibration. Mar Biol 118:377–382. https://doi.org/10.1007/BF00350294

Concannon C, Cross E, Jones L, Murray C, Matassa C, McBride R, Baumann H (2021) Temperature-dependent effects on fecundity in a serial broadcast spawning fish after whole-life high CO_2 exposure. ICES J Mar Sci 78:3724–3734. https://doi.org/10.1093/icesjms/fsab217

Crean AJ, Marshall DJ (2009) Coping with environmental uncertainty: dynamic bet hedging as a maternal effect. Phil Trans R Soc B 364:1087–1096. https://doi.org/10.1098/rstb.2008.0237

Dahlke F, Lucassen M, Bickmeyer U, Wohlrab S, Puvanendran V, Mortensen A, Chierici M, Pörtner H-O, Storch D (2020) Fish embryo vulnerability to combined acidification and warming coincides with a low capacity for homeostatic regulation. J Exp Biol 223:jeb212589. https://doi.org/10.1242/jeb.212589

Denis J, Mahe K, Tavernier E, Monchy S, Vincent D, Vallet C, Marchal P, Antajan E, Caboche J, Lefebvre V, Cordier R, Loots C (2017) Ontogenetic changes in the larval condition of Downs herring: use of a multi-index approach at an individual scale. Mar Biol 164:154. https://doi.org/10.1007/s00227-017-3180-3

Donelson JM, Salinas S, Munday PL, Shama LNS (2018) Transgenerational plasticity and climate change experiments: where do we go from here. Glob Change Biol 24:13–34. https://doi.org/10.1111/gcb.13903

Doney SC, Fabry VJ, Feely RA, Kleypas JA (2008) Ocean acidification: the other CO_2 problem. Ann Rev Mar Sci 1:169–192. https://doi.org/10.1146/annurev.marine.010908.163834

Ellis RP, Urbina MA, Wilson RW (2016) Lessons from two high CO_2 worlds - future oceans and intensive aquaculture. Glob Change Biol 23:2141–2148. https://doi.org/10.1111/gcb.13515

Ferron A, Leggett WC (1994) An appraisal of condition measures for marine fish larvae. In: Blaxter JHS, Southward AJ (eds) Advances in Marine Biology, vol 30. Elsevier, Amsterdam, pp 217–303

Franke A, Clemmesen C (2011) Effect of ocean acidification on early life stages of Atlantic herring (*Clupea harengus* L). Biogeosciences 8:3697–3707. https://doi.org/10.5194/bg-8-3697-2011

Frommel AY, Maneja R, Lowe D, Malzahn AM, Geffen AJ, Folkvord A, Piatkowski U, Reusch TBH, Clemmesen C (2012) Severe tissue damage in Atlantic Cod larvae under increasing ocean acidification. Nat Clim Change 2:42–46. https://doi.org/10.1038/nclimate1324

Fuiman LA, Cowan JHJR, Smith ME, O'Neal J (2005) Behavior and recruitment success in fish larvae: variation with growth rate and the batch effect. Can J Fish Aquat Sci 62:1337–1349. https://doi.org/10.1139/f05-053

Gangopadhyay A, Gawarkiewicz G, Silva ENS, Monim M, Clark J (2019) An observed regime shift in the formation of warm core rings from the gulf stream. Sci Rep 9:12319. https://doi.org/10.1038/s41598-019-48661-9

Gotelli NJ, Ellison AM (2012) A primer of ecological statistics. Oxford University Press, UK

Guzik M, Saba G, Wright-Fairbanks E (2022) Observing winter carbonate chemistry throughout the Mid-atlantic Bight shelf using novel glider technology. Aresty Rutgers Undergrad Res J 1(4)

Hay DE (1982) Fixation shrinkage of herring larvae: effects of salinity, formalin concentration, and other factors. Can J Fish Aquat Sci 39:1138–1143. https://doi.org/10.1139/f82-151

Heuer RM, Grosell M (2014) Physiological impacts of elevated carbon dioxide and ocean acidification on fish. Am J Physiol Regul Integr Comp Physiol 307:R1061–R1084. https://doi.org/10.1152/ajpregu.00064.2014

Hočevar S, Hutchings JA, Kuparinen A (2021) Multiple-batch spawning as a bet-hedging strategy in highly stochastic environments: an exploratory analysis of Atlantic Cod. Evol Appl 14:1980–1992. https://doi.org/10.1111/eva.13251

Hou Z, Fuiman LA (2021) Maternal diet affects utilization of endogenous lipids by red drum *Sciaenops ocellatus* embryos and early larvae. Comp Biochem Physiol B: Biochem Mol Biol 256:110639. https://doi.org/10.1016/j.cbpb.2021.110639

Hou Z, Lu X, Tiziani S, Fuiman LA (2022) Nutritional programming by maternal diet alters offspring lipid metabolism in a marine teleost. Fish Physiol Biochem 48:535–553. https://doi.org/10.1007/s10695-022-01069-1

Houde ED (1997) Patterns and trends in larval-stage growth and mortality of teleost fish. J Fish Biol 51:52–83. https://doi.org/10.1111/j.1095-8649.1997.tb06093.x

Hurst TP, Fernandez ER, Mathis JT, Miller JA, Stinson CM, Ahgeak EF (2012) Resiliency of juvenile walleye pollock to projected levels of ocean acidification. Mar Ecol Prog Ser 17:247–259. https://doi.org/10.3354/ab00483

Hurst TP, Fernandez ER, Mathis JT (2013) Effects of ocean acidification on hatch size and larval growth of walleye pollock (*Theragra chalcogramma*). ICES J Mar Sci 70:812–822. https://doi.org/10.1093/icesjms/fst053

Ishimatsu A, Hayashi M, Kikkawa T (2008) Fishes in a high CO_2 acidified ocean. Mar Ecol Prog Ser 373:295–302. https://doi.org/10.3354/meps07823

Jansen H, Zeebe RE, Wolf-Gladrow DA (2002) Modeling the dissolution of settling $CaCO_3$ in the ocean: dissolution of settling $CaCO_3$. Glob Biogeochem Cycles 16. https://doi.org/10.1029/2000GB001279. 11-1-11–16

Kavanaugh MT, Rheuban JE, Luis KMA, Doney SC (2017) Thirty-three years of ocean benthic warming along the U.S. Northeast Continental Shelf and Slope: patterns, drivers, and ecological consequence. J Geophys Res Oceans 122:9399–9414. https://doi.org/10.1002/2017JC012953

Kelly MW, Padilla-Gamiño JL, Hofmann GE (2013) Natural variation and the capacity to adapt to ocean acidification in the keystone sea urchin *Strongylocentrotus purpuratus*. Glob Change Biol 19:2536–2546. https://doi.org/10.1111/gcb.12251

Kendall AW Jr (1983) Serranidae: Development and relationships. In: Moser HG, Richards WJ, Cohe DM, Fahay MP, Kendall AW Jr, Richardson SL (eds) Ontogeny and Systematics of fishes. American Society of Ichthyologists and Herpetologists, La Jolla, CA, pp 499–510

Kleisner KM, Fogarty MJ, McGee S, Hare JA, Moret S, Perretti CT, Saba VS (2017) Marine species distribution shifts on the US Northwest continental shelf under continued ocean warming. Prog Oceanogr 153:24–36. https://doi.org/10.1016/j.pocean.2017.04.001

Koenker BL, Copeman LA, Laurel BJ (2018) Impacts of temperature and food availability on the condition of larval Arctic cod (*Boreogadus saida*) and walleye pollock (*Gadus chalcogrammus*). ICES J Mar Sci 75:2370–2385. https://doi.org/10.1093/icesjms/fsy052

Kwan GT, Shen SG, Drawbridge M, Checkley DM Jr, Tresguerres M (2021) Ion-transporting capacity and aerobic respiration of larval white seabass (*Atractoscion nobilis*) may be resilient to ocean acidification conditions. Sci Total Environ 791:148285. https://doi.org/10.1016/j.scitotenv.2021.148285

Lambert TC, Ware DM (1984) Reproductive strategies of demersal and pelagic spawning fish. Can J Fish Aquat Sci 41:1565–1569. https://doi.org/10.1139/f84-194

Laurel BJ, Hunsicker ME, Ciannelli L, Hurst TP, Duffy-Anderson J, O'Malley R, Behrenfeld M (2021) Regional warming exacerbates match/mismatch vulnerability for cod larvae in Alaska. Prog Oceanogr 193:102555. https://doi.org/10.1016/j.pocean.2021.102555

Lewis ER, Wallace DWR (1998) Program developed for CO_2 system calculations. No. cdiac: CDIAC-105.

Environmental system science data infrastructure for a virtual ecosystem (ESS-DIVE) (United States)

Lima ID, Wang ZA, Cameron LP, Grabowski JH, Rheuban JE (2023) Predicting carbonate chemistry on the northwest Atlantic shelf using neural networks. J Geophys-Res: Biogeosciences 128. https://doi.org/10.1029/2023JG007536. e2023JG007536

Lotterhos KE, Láruson ÁJ, Jiang L-Q (2021) Novel and disappearing climates in the global surface ocean from 1800 to 2100. Sci Rep 11:15535. https://doi.org/10.1038/s41598-021-94872-4

Marshall DJ, Bonduriansky R, Bussiére LF (2008) Offspring size variation within broods as a bet-hedging strategy in unpredictable environments. Ecology 89:2506–2517. https://doi.org/10.1890/07-0267.1

McBride RS, Tweedie MK, Oliveira K (2018) Reproduction, first-year growth, and expansion of spawning and nursery grounds of black sea bass (*Centropristis striata*) into a warming Gulf of Maine. Fish Bull 116:323–336

McMahon SJ, Parsons DM, Donelson JM, Pether SMJ, Munday PL (2020) Elevated temperature and CO_2 have positive effects on the growth and survival of larval Australasian snapper. Mar Environ Res 161:105054. https://doi.org/10.1016/j.marenvres.2020.105054

Melzner F, Gutowska MA, Langenbuch M, Lucassen M, Thorndyke MC, Bleich M, Pörtner HO (2009) Physiological basis for high CO_2 tolerance in marine ectothermic animals: pre-adaptation through lifestyle and ontogeny? Biogeosciences 6:2313–2331. https://doi.org/10.5194/bg-6-2313-200

Mercer LP (1978) The reproductive biology and population dynamics of black sea bass, *Centropristis striata*. Doctoral dissertation. College of William and Mary, Williamsburg, VA

Mercer LP (1989) Species profile: life histories and environmental requirements of coastal fishes and invertebrates (South Atlantic) - black sea bass. U.S. Fish and Wildlife Service Biological Report 82(11.99). U.S. Army Corps of Engineers, TR EL-82-4. 16 pp

Meseck S, Redman D, Mercaldo-Allen R, Clark P, Rose JM, Perry D (2022) Resilience of black sea bass embryos to increased levels of carbon dioxide. Mar Coast Fish Dyn Manag Ecosyst Sci 14:e10200. https://doi.org/10.1002/mcf2.10200

Miller TJ, Crowder LB, Rice JA, Marschall EA (1988) Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Can J Fish Aquat Sci 45:1657–1670. https://doi.org/10.1139/f88-197

Miller GM, Watson S-A, Donelson JM, McCormick MI, Munday PL (2012) Parental environment mediates impacts of increased carbon dioxide on a coral reef fish. Nat Clim Change 2:858–861. https://doi.org/10.1038/nclimate1599

Miller AS, Shepherd GR, Fratantoni PS (2016) Offshore habitat preference of overwintering juvenile and adult black sea bass, *Centropristis striata*, and the relationship to year-class success. PLoS ONE 11:e0147627. https://doi.org/10.1371/journal.pone.0147627

Moser J, Shepherd GR (2009) Seasonal distribution and movement of black sea bass (*Centropristis striata*) in the Northwest Atlantic as determined from a mark-recapture experiment. J Northwest Atl Fish Sci 40:17–28. https://doi.org/10.2960/J.v40.m638

Munday PL, Gagliano M, Donelson JM, Dixson DL, Therrold SR (2011) Ocean acidification does not affect the early life history development of a tropical marine fish. Mar Ecol Prog Ser 423:211–221. https://doi.org/10.3354/meps08990

Munday PL, Watson S-A, Parsons DM, King A, Barr NG, Mcleod IM, Allan BJM, Pether SMJ (2016) Effects of elevated CO_2 on early life history development of the yellowtail kingfish, *Seriola lalandi*, a large pelagic fish. ICES J Mar Sci 73:641–649. https://doi.org/10.1093/icesjms/fsv210

Murray C, Baumann H (2015) The performance of a fully automated system for testing the combined effects of acidification and hypoxia on fish early life stages. 145th Annual Meeting of the American Fisheries Society

Murray C, Baumann H (2018) You better repeat it: complex CO_2 x temperature effects in Atlantic silverside offspring revealed by serial experimentation. Diversity 10:69. https://doi.org/10.3390/d10030069

Murray CS, Baumann H (2020) Are long-term growth responses to elevated pCO_2 sex-specific in fish? PLoS ONE 15:e0235817. https://doi.org/10.1371/journal.pone.0235817

Murray CS, Malvezzi A, Gobler CJ, Baumann H (2014) Offspring sensitivity to ocean acidification changes seasonally in a coastal marine fish. Mar Ecol Prog Ser 504:1–11. https://doi.org/10.3354/meps10791

Murray CS, Wiley D, Baumann H (2019) High sensitivity of a keystone forage fish to elevated CO_2 and temperature. Conserv Physiol 7:coz084. https://doi.org/10.1093/conphys/coz084

Olofsson H, Ripa J, Jonzén N (2009) Bet-hedging as an evolutionary game: the trade-off between egg size and number. Proc R Soc B 276:2963–2969. https://doi.org/10.1098/rspb.2009.0500

Pan TCF, Applebaum SL, Manahan DT (2014) Experimental ocean acidification alters the allocation of metabolic energy. Proc Natl Acad Sci U S A 112:4696–4701. https://doi.org/10.1073/pnas.1416967112

Parker LM, Ross PM, O'Connor WA, Borysko L, Raftos L, Pörtner H-O (2011) Adult exposure influences offspring response to ocean acidification in oysters. Glob Change Biol 18:82–92. https://doi.org/10.1111/j.1365-2486.2011.02520.xPepin

Pepin, P (2023) Feeding by larval fish: how taxonomy, body length, mouth size, and behaviour contribute to differences among individuals and species from a coastal ecosystem. ICES J Mar Sci 80:91–106

Peck MA, Huebert KB, Llopiz JK (2012) Intrinsic and extrinsic factors driving match-mismatch dynamics during the early life history of marine fishes. In: Woodward G, Jacob U, O'Gorman EJ (eds) Advances in Ecological Research, vol 47. Elsevier, London, pp 177–302

Peck MA, Baumann H, Clemmesen C, Herrmann J-P, Moyano M, Temming A (2015) Calibrating and comparing somatic-, nucleic acid-, and otolith-based indicators of growth and condition in young juvenile European sprat (*Sprattus sprattus*). J Exp Mar Biol Ecol 471:217–225. https://doi.org/10.1016/j.jembe.2015.06.011

Perry D, Nelson DA, Redman DH, Metzler S, Katersky R (2007) Growth of black sea bass (*Centropristis striata*) in recirculating aquaculture systems. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northeast Fisheries Science Center

Pimentel MS, Faleiro F, Marques T, Bispo R, Dionísio G, Faria AM, Machado J, Peck MA, Pörtner H-O, Pousão-Ferreira P, Gonçalves EJ, Rosa R (2016) Foraging behaviour, swimming performance and malformations of early stages of commercially important fishes unde ocean acidification and warming. Clim Change 137:495–509. https://doi.org/10.1007/s10584-016-1682-5

Pope EC, Ellis RP, Scolamacchia M, Scolding JWS, Keay A, Chingombe P, Shields RJ, Wilcox R, Speirs DC, Wilson RW, Lewis C, Flynn KJ (2014) European sea bass, *Dicentrarchus labrax*, in a changing ocean. Biogeosciences 11:2519–2530. https://doi.org/10.5194/bg-11-2519-2014

Raedemaecker F, De, Brophy D, O'Connor I, O'Neill B (2012) Dependence of RNA:DNA ratios and fultons k condition indices on environmental characteristics of plaice and dab nursery grounds. Estuar Coast Shelf Sci 98:60–70. https://doi.org/10.1016/j.ecss.2011.11.033

Record NR, Ji R, Maps F, Varpe Ø, Runge JA, Petrik CM, Johns D (2018) Copepod diapause and the biogeography of the marine lipidscape. J Biogeogr 45:2238–2251

Robert D, Shoji J, Sirois P, Takasuka A, Catalàn IA, Folkvord A, Ludsin SA, Peck MA, Sponaugle S, Ayón PM, Brodeur RD, Campbell EY, D'Alessandro EK, Dower JF, Fortier L, García AG, Huebert KB, Hufngal M, Ito S-I, Joh M, Juanes F, Nyuji M, Oozeki Y, Plaza G, Takahashi M, Tanaka Y, Tojo N, Watari S, Yasue N, Pepin P (2023) Life in the fast lane: revisiting the fast growth - high survival paradigm during the early life stages of fishes. Fish Fish 24:863–888. https://doi.org/10.1111/faf.12774

Rossoll D, Bermúdez R, Hauss H, Schulz KG, Riebesell U, Sommer U, Winder M (2012) Ocean acidification-induced food quality deterioration constrains trophic transfer. PLoS ONE 7:e34737. https://doi.org/10.1371/journal.pone.0034737

Sabetian A, Cullen D, Hoang LH, Lilkendey J (2020) Diversified bet-hedging explains the batch effect in New Zealand snapper Chrysophrys auratus. Aquaculture 522:735135. https://doi.org/10.1016/j.aquaculture.2020.735135

Salisbury JE, Jönsson BF (2018) Rapid warming and salinity changes in the Gulf of Maine alter surface ocean carbonate parameters and hide ocean acidification. Biogeochemistry 141:401–418

Schade FM, Clemmesen C, Wegner KM (2014) Within- and transgenerational effects of ocean acidification on life history of marine three-spined stickleback (*Gasterosteus aculeatus*). Mar Biol 161:1667–1676. https://doi.org/10.1007/s00227-014-2450-6

Schwemmer T, Baumann H, Murray C, Molina A, Nye J (2020) Acidification and hypoxia interactively affect metabolism in embryos, but not larvae, of the coastal forage fish *Menidia menidia*. J Exp Biol 223:jeb228015. .org/10.1242/jeb.228015

Shama LNS (2015) Bet hedging in a warming ocean: predictability of maternal environment shapes offspring size variation in marine sticklebacks. Glob Change Biol 21:4382–4400. https://doi.org/10.1111/gcb.13041

Siegfried E, Johnson DW (2023a) Effects of ocean acidification and warming on the specific dynamic action of California grunion (*Leuresthes tenuis*) larvae. J Exp Mar Biol Ecol 563:151893. https://doi.org/10.1016/j.jembe.2023.151893

Siegfried E, Johnson DW (2023b) Experimental ocean acidification and food limitation reveals altered energy budgets and synergistic effects on mortality of larvae of a coastal fish. Front Mar Sci 10:1240404. https://doi.org/10.3389/fmars.2023.1240404

Slesinger E, Jensen O, Saba G (2021) Spawning phenology of a rapidly shifting marine fish species throughout its range. ICES J Mar Sci 78:1010–1022. https://doi.org/10.1093/icesjms/fsaa252

Slesinger E, Bates K, Wuenschel M, Saba GK (2022) Regional differences in energy allocation of black sea bass (*Centropristis striata*) along the U.S. Northeast Shelf (36°N to 42°N) and throughout the spawning season. J Fish Biol 100:918–934. https://doi.org/10.1111/jfb.15023

Sokal RR, Rohlf FJ (1995) Biometry: principles and practices of statistics in biological research. W.H. Freeman and Co., New York

Sotola AV, Craig CA, Pfaff PJ, Maikoetter JD, Martin NH, Bonner TH (2019) Effect of preservation on fish morphology over time: implications for morphological studies. PLoS ONE 14:e0213915. https://doi.org/10.1371/journal.pone.0213915

Sswat M, Stiasny MH, Jutfelt F, Riebesell U, Clemmesen C (2018) Growth performance and survival of larval Atlantic herring, under the combined effects of elevated temperature and CO_2. PLoS ONE 13:e0191947. https://doi.org/10.1371/journal.pone.0191947

Stiasny MH, Miteermayer FH, Sswat M, Voss R, Jutfelt F, Chierici M, Puvanendran V, Mortensen A, Reusch TBH, Clemmesen C (2016) Ocean acidifcation effects on Atlantic Cod larval survival and recruitment to the fished population. PLoS ONE 11:e0155448. https://doi.org/10.1371/journal.pone.0155448

Stiasny MH, Mittermayer FH, Göttler G, Bridges CR, Falk-Petersen I-B, Puvanendran V, Mortensen A, Reusch TBH, Clemmesen C (2018) Effects of parental acclimation and energy limitation in response to high CO_2 exposure in Atlantic Cod. Sci Rep 8:8348. https://doi.org/10.1038/s41598-018-26711-y

Stiasny MH, Sswat M, Mittermayer F, Falk-Petersen I-B, Schnell NK, Puvanendran V, Mortensen A, Reusch TBH, Clemmesen C (2019) Divergent responses of Atlantic cod to ocean acidification and food limitation. Glob Change Biol 25:839–849. https://doi.org/10.1111/gcb.14554

Suca J, Wiley D, Silva T, Robuck A, Richardson DE, Glancy S, Clancey E, Giandonato T, Solow A, Thompson M, Hong P, Baumann H, Kaufman L, Llopiz J (2021) Sensitivity of sand lance to shifting prey and hydrography indicates forthcoming change to the northeast US shelf forage fish complex. ICES J Mar Sci 78:1023–1037. https://doi.org/10.1093/icesjms/fsaa251

Takasuka A, Oozeki Y, Kimura R, Kubota H, Aoki I (2004) Growth-selective predation hypothesis revisted for larval anchovy in offshore waters: cannibalism by juveniles versus predation by skipjack tunas. Mar Ecol Prog Ser 278:297–302. https://doi.org/10.3354/meps278297

Tasoff AJ, Johnson DW (2019) Can larvae of a marine fish adapt to ocean acidification? Evaluating the evolutionary potential of the California grunion (*Leuresthes tenuis*). Evol Appl 12:560–571. https://doi.org/10.1111/eva.12739

Thor P, Dupont S (2015) Transgenerational effects alleviate severe fecundity loss during ocean acidification in a ubiquitous planktonic copepod. Glob Change Biol 21:2261–2271. https://doi.org/10.1111/gcb.12815

Vargas CA, Lagos NA, Lardies MA, Duarte C, Manríquez PH, Aguilera VM, =Broitman B, Widdicombe S, Dupont S (2017) Species-specific responses to ocean acidification should account for local adaptation and adaptive plasticity. Nat Ecol Evol 1:0084. https://doi.org/10.1038/s41559-017-0084

Wallace RB, Baumann H, Grear JS, Aller RC, Gobler CJ (2014) Coastal ocean acidification: the other eutrophication problem. Estuar Coast Shelf Sci 148:1–13. https://doi.org/10.1016/j.ecss.2014.05.027

Watanabe W, Carroll P, Alam S, Dumas C, Gabel J, Davis T, Bentley C (2021) The status of black sea bass, *Centropristis striata*, as a commercially ready species for U.S. marine aquaculture. J World Aquac Soc 52:541–565. https://doi.org/10.1111/jwas.12803

Wright-Fairbanks EK, Miles TN, Cai W-J, Chen B, Saba GK (2020) Autonomous observations of seasonal carbonate chemistry dynamics in the Mid-atlantic Bight. J GeophysRes: Oceans 125. https://doi.org/10.1029/2020JC016505. e2020JC016505

Zar JH (1998) Biotatistical analysis. Prentice Hall, New Jersey

Zavell MD, Mouland MEP, Matassa CM, Schultz ET, Baumann H (2023) Temperature- and ration-dependent winter growth in northern stock black sea bass juveniles. Trans Am Fish Soc 153:163–179. https://doi.org/10.1002/tafs.10452