

Meta analysis

The weakest link: sensitivity to climate extremes across life stages of marine invertebrates



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Predicting the effects of climate change on Earth's biota becomes even more challenging when acknowledging that most species have life cycles consisting of multiple stages, each of which may respond differently to extreme environmental conditions. There is currently no clear consensus regarding which stages are most susceptible to increasing environmental stress, or 'climate extremes'. We used a meta-analytic approach to quantify variation in responses to environmental stress across multiple life stages of marine invertebrates. We identified 287 experiments in 29 papers which examined the lethal thresholds of multiple life stages (embryo, larva, juvenile and adult) of both holoplanktonic and meroplanktonic marine invertebrates subjected to the same experimental conditions of warming, acidification and hypoxia stress. Most studies considered short acute exposure to stressors. We calculated effect sizes (log response ratio) for each life stage (unpaired analysis) and the difference in effect sizes between stages of each species (paired analysis) included in each experiment. In the unpaired analysis, all significant responses were negative, indicating that warming, acidification and hypoxia tended to increase mortality. Furthermore, embryos, larvae and juveniles were more negatively affected by warming than adults. The paired analysis revealed that, when subjected to the same experimental conditions, younger life stages were more negatively affected by warming than older life stages, specifically among pairings of adults versus juveniles and larvae versus embryos. Although responses to warming are well documented, few studies of the effects of acidification and hypoxia met the criteria for inclusion in our analyses. Our results suggest that while most life stages will be negatively affected by climate change, younger stages of marine invertebrates are more sensitive to extreme heating events.

Keywords: acidification, climate change, complex life cycle, extreme events, hypoxia, life stage

Synthesis

This study addresses the critical unanswered question of how vulnerability to climate extremes varies across life cycle stages. We focus on marine invertebrates as a diverse group composed overwhelmingly of species with complex life cycles. We take a novel paired approach to meta-analysis, comparing differences between life stages of the same species subjected to the same experimental conditions of extreme temperature, pH, and hypoxia. Our results indicated that, while most life stages will be negatively affected by climate change, younger stages of marine invertebrates are most sensitive to extreme heating events, making them 'weak links' in the life cycle.



Introduction

Anthropogenic climate change has already impacted systems worldwide, causing alterations from organismal physiology to community composition, ecosystem functioning and species ranges (Walther et al. 2002, Parmesan and Yohe 2003, Harley et al. 2006, Sorte et al. 2010, Chen et al. 2011, IPCC 2014). Over the next century, it is likely that the global average temperature will increase by 2–5°C (IPCC 2014) and ocean pH will decline by 0.4 pH units (Caldeira and Wickett 2005, IPCC 2014). Additionally, extreme events, including heat waves (Meehl and Tebaldi 2004, IPCC 2014) and ocean hypoxia (Justić et al. 1996, Diaz and Rosenberg 2008), are expected to become more frequent. Given these projections, it is increasingly important to understand the impacts of climate extremes on natural populations and their sensitivity (i.e. thresholds of physiological tolerance) to abiotic stressors.

Predicting such responses is complicated for species with complex life cycles (Werner and Gilliam 1984, Kingsolver et al. 2011, Pankhurst and Munday 2011), as physiological mechanisms of stress tolerance can vary throughout development (Conte 1984, Spicer 1995, Pörtner et al. 1998, 2004, Pörtner and Knust 2007, Pörtner and Farrell 2008). Complex life cycles involve progression through multiple ecologically distinct stages (Istock 1967, Wilbur 1980) and are present in 80% of extant animal taxa (Werner and Gilliam 1984, Hentschel 1999). As a group, marine invertebrates exhibit high phyletic diversity, in which complex life cycles are common (Roughgarden et al. 1988, Pechenik 1999). For example, intertidal bivalve mollusks progress through distinct life stages as follows (Fig. 1): gametes (eggs and sperm) form embryos via external fertilization, which develop into dispersive planktonic larvae, followed by sessile benthic (non-reproductive) juveniles and reproductively-mature adults. Similarly, many holoplanktonic organisms, such as pelagic copepods, exhibit complex life cycles, progressing through egg, naupliar and copepodite stages before reaching reproductive maturity (Peterson et al. 1979).

In marine systems, climate change exposes invertebrates to a variety of stressors, including warming, ocean

acidification and hypoxia in both a gradual, press-type change and extreme acute pulse events. Responses to these varying types and intensities of stressors may differ by life stage (Ceballos-Osuna et al. 2013, Tangwancharoen and Burton 2014). Vulnerability to climate change is a function of sensitivity and exposure, the former of which is the focus of this study. The impact of environmental stress on an organism, or sensitivity, can change during growth and development, as shown for the larvae of benthic species (Hamdoun and Epel 2007, Kapsenberg and Hofmann 2014). For example, embryonic stages of zooplankton can be resistant to acidification stress due to the presence of protective structures which isolate them from surrounding conditions (Sedlacek 2008, Hansen et al. 2012), and studies of copepods have shown that larvae can be more sensitive than embryos due to the high metabolic costs of undergoing developmental transitions (Kurihara et al. 2004a, b, Cripps et al. 2014). However, in many cases, stress tolerance is expected to increase with age. Maturation of regulatory functions occurs during development, including organisms' capacities to withstand environmental fluctuations in oxygen concentration (Spicer 1995), temperature (Pörtner et al. 2004, Pörtner and Knust 2007, Pörtner and Farrell 2008) and pH (Conte 1984). As organisms develop, they also accrue energy reserves, allowing them to withstand the costs (e.g. cellular repairs and increased metabolic rates) of sub-optimal conditions (Bulnheim 1974, Vetter et al. 1999). In addition to following typical developmental pathways, organisms can also develop stress tolerances that reflect their environmental histories: individuals exposed to greater levels of stress may be forced to either acclimate or perish (Hofmann and Somero 1995, Roberts et al. 1997, Giudice et al. 1999, Alfaro 2005, Kurihara and Ishimatsu 2008, Gleason and Burton 2013).

To date, there is no clear consensus on how sensitivity to climate extremes may differ across life stages of marine invertebrates (Russell et al. 2012, Kroeker et al. 2013, Cripps et al. 2014). The current literature both provides support for (Byrne 2012, Harvey et al. 2013) and against (Brunetti et al. 1985, Tangwancharoen and Burton 2014, Przeslawski et al. 2015) the hypothesis that younger life stages of marine invertebrates are more sensitive to climate change stressors than older stages, while others highlight inconsistencies among responses (Kroeker et al. 2010, 2013). Resolving this question has direct implications for predicting whether populations will persist versus go extinct under future climate change, as population growth rates of many ectotherms are related to environmental conditions such as temperature (Pepin 1991, O'Connor et al. 2007). For example, although adults of the butterfly *Boloria eunormia* are resistant to warming, the larval stage is negatively affected by warming which leads to decreases of up to 88% in population growth rate as compared to present day conditions (Radchuk et al. 2013). Similarly, nauplii of a calanoid copepod, *Acartia tonsa*, are more sensitive to acidification than older life stages (Cripps et al. 2014). Therefore, it is critical to understand how stage-specific demographic rates are affected by environmental stress to evaluate potential 'weak links' in life cycles,

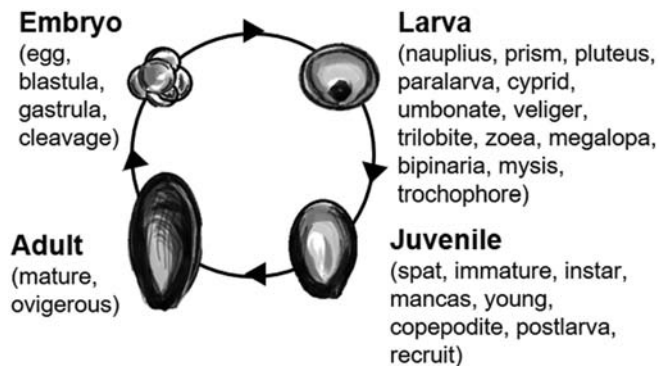


Figure 1. Life stages of marine invertebrates included in our analysis, with a mussel as a representative species. Stages (taxon specific) were categorized as in Pechenik (1999).

which can alter population trajectories under climate change (Russell et al. 2012).

In the current study, we address an important limitation of previous studies, which is that no prior publication has compared responses of multiple life stages across the same species evaluated in the same experiment under the same environmental conditions. We, therefore, take a within-species approach to test the hypothesis that younger life stages are more sensitive than older life stages. We use a meta-analysis framework that incorporates both unpaired (individual life stage) and paired (multiple life stage) comparisons in our analysis of the effects of three climate stressors (warming, acidification and hypoxia) across four life stages (embryo, larva, juvenile and adult) on the survival of marine invertebrates. Our specific questions were: 1) Do responses of marine invertebrates to climate change vary across life stages? 2) Are responses affected by treatment magnitude and treatment duration? 3) In experiments with two or more distinct life stages subjected to the same experimental conditions, are younger or older stages more sensitive to climatic stressors? Our goal in addressing these questions was to identify which stage is the most sensitive 'weakest link' under extreme climatic conditions.

Material and methods

Study identification and data extraction

We searched ISI web of science for studies documenting the effects of three climate stressors – warming, acidification and hypoxia – on marine invertebrates (Supplementary material Appendix 1 for search terms). Our search through 1 January 2017 yielded ca 56 000 papers. After excluding ca 53 000 based on titles, we reviewed 2637 abstracts. Of these, we selected papers which: 1) considered multiple life stages of a species subjected to the same experimental conditions (including stressor magnitude and duration), 2) presented extractable data, and 3) recorded a response with direct impacts on population demographic rates (e.g. we did not include metrics such as heat-shock protein expression because this can indicate both increased metabolic cost or increased survival under stress; Feder and Hofmann 1999). Although we focus here on studies that investigated lethal thresholds, we also present analyses based on condition metrics (e.g. growth and physiological indicators of stress) in Supplementary material Appendix 2. Ultimately, we included 287 experiments reported in 29 peer-reviewed papers (published between 1981 and 2016), all of which presented results of laboratory experiments (i.e. no field studies met our criteria for inclusion) across three stressors (213/38/38 for warming/acidification/hypoxia).

We extracted data for responses to control and treatment levels of climate variables utilizing WebPlotDigitizer ver. 3.9 (Rohatgi 2011). In cases where use of WebPlotDigitizer might not be accurate, such as overlapping data points, raw data were requested from authors and included when available. In all cases, we used the author's definitions of ambient

(control) conditions. While each publication was considered a distinct 'paper', we defined 'experiment' as addressing the effect of distinct parameters on a discrete set of individuals. Therefore, a single paper could include multiple experiments. For example, if authors performed tolerance experiments on two life stages (juveniles and adults) of three different species, this one paper would include three distinct 'experiments' for the paired analysis, and six distinct 'experiments' considered in the unpaired analysis. If experiments included response measures at multiple time points, only the final time point was included in our database. If more than one species was considered in the same experiment, both species were used, and if an experiment involved the manipulation of more than one stressor, the impacts of both stressors were considered by comparing the impact of each independent stressor while the other was held at ambient conditions. If organisms were raised in laboratory conditions, only individuals naïve to experimental conditions were considered in our analyses. While extracting data, we also recorded the species and habitat type (intertidal or pelagic, for the adult stage) of the study organism and experimental treatment magnitude (in °C or pH units for warming and acidification, respectively), duration (in hours), and latitude (degrees from equator).

We condensed the life stages of both holoplanktonic and meroplanktonic marine invertebrates into four stages (embryo, larva, juvenile and adult) based on the author's descriptions and with reference to Pechenik (1999) (Fig. 1). If multiple responses were reported per stage, the average value was used in our analyses. The complete dataset is included in the Supplementary materials (Supplementary material Appendix 3). Given that median experimental duration was 6 h, the data are most representative of acute responses.

Data analysis

This meta-analysis only includes experiments that quantified the responses of multiple life stages of a species to climatic extremes using identical experimental designs. Thus, we analyzed our dataset in two ways: 1) a paired analysis and 2) an unpaired analysis. In both analyses, we calculated the natural log of the response ratio [LRR = $\ln(\text{treatment response}/\text{control response})$] (Hedges et al. 1999) to quantify the impacts of extreme climate conditions on each life stage. We used this unweighted effect size metric because it allowed for the inclusion of the most experiments in our analysis (Englund et al. 1999), while we also calculated a weighted effect size metric (Hedges *d*; Hedges and Olkin 1985) for comparison. The results of these weighted analyses are presented in Supplementary material Appendix 4. We added a small positive number (+0.001 to lethal thresholds and +1 to condition metrics) before calculating LRRs to avoid response values ≤ 0 . All data analyses were conducted in R <www.r-project.org>.

In the unpaired analysis, we calculated mean effect sizes and bootstrapped (10 000 iterations) 95% confidence intervals (95% CIs) for each life stage (adult, juvenile, larva, embryo) of marine invertebrates responding to a given stressor (warming, acidification, hypoxia) (Adams et al. 1997) using

the boot package in R (Davison and Hinkley 1997, Cauty and Ripley 2017). If 95% CIs did not overlap zero, the effect was considered significant.

In the paired analysis, we quantified response differences across life stages using the LRR difference ($\text{LRR difference} = \text{LRR}_{\text{older life stage}} - \text{LRR}_{\text{younger life stage}}$) (Fig. 2). Most experiments included two life stages, so we calculated the difference between the older and younger life stage. In two papers, there were more than two life stages included in a single experiment, so we calculated the difference between all possible combinations of older and younger life stages. Here, positive effect sizes indicate that older life stages were more resistant to a given stressor, while negative effect sizes indicate that younger life stages were more resistant. For example, if the effect size (LRR) was -3 for adults and -7 for juveniles, the LRR difference would be $+4$, indicating that adult survival was higher than juvenile survival under the experimental conditions. As with the unpaired analysis, we calculated mean effect sizes and 95% bootstrapped CIs, and considered the effects where the CIs did not overlap zero to be significant.

In both the unpaired and paired analyses, a two-step model fitting approach was used in the metafor package in R (Raudenbush 2009, Viechtbauer 2010) to investigate how characteristics of study organisms and experimental design affected responses to climate change stressors. This approach included estimating heterogeneity (using restricted maximum-likelihood; REML), followed by parameter estimation (using linear mixed effects modeling) in order to test for the contributions of fixed effects (characteristics of interest) while accounting for the random effect of experiment (Viechtbauer 2005, Raudenbush 2009). Fixed effects tested included life stage, adult habitat type (intertidal or pelagic), and treatment magnitude, duration and latitude (as continuous variables). Experiment was included as a random effect to account for non-independence between comparisons (Bates et al. 2015). To assess whether patterns were driven by the response of the most studied species, we conducted a sensitivity analysis, as described in Supplementary material Appendix 5.

We assessed the possible impacts of publication bias on our analysis through calculation of unweighted fail-safe numbers (Rosenthal 1979, Orwin 1983, Rosenberg 2005) in the metafor package in R (Viechtbauer 2010) (Supplementary material Appendix 4 Table A1). These values indicate the

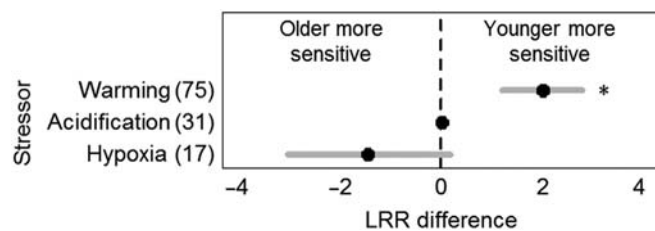


Figure 2. In the paired analysis, younger life stages were more sensitive than older life stages to lethal effects of warming (but not hypoxia and acidification). Means \pm bootstrap 95% CIs for effect sizes (LRR). *Significant difference. Sample sizes are adjacent to life stages on y-axis.

number of non-significant effect sizes that would be necessary to make significant patterns non-significant (Rosenthal 1979, Orwin 1983). Therefore, larger fail-safe numbers indicate more robust findings. As in Rosenthal (1979), fail-safe numbers greater than $5N + 10$, where N is the sample size, were considered to be robust to publication bias.

Data deposition

Data available from the University of California DASH Digital Repository: <<http://doi.org/10.15146/R3J09X>> (Pandori and Sorte 2018).

Results

Our database contains 287 measured lethal thresholds of marine invertebrates across the three stressors (213/38/38 for warming/acidification/hypoxia) from 29 published papers (Table 1, Supplementary material Appendix 3). Additional papers reporting non-lethal condition metrics are shown in Supplementary material Appendix 2. These metrics included measures of growth, metabolism and behavior that have direct impacts on population demographic rates. Study organisms spanned six phyla: Annelida, Arthropoda, Chordata, Cnidaria, Echinodermata and Mollusca. While all six phyla were represented in our warming comparisons, only two were represented in comparisons of acidification (Arthropoda, Echinodermata), and three were represented in comparisons of hypoxia (Annelida, Arthropoda, Mollusca).

In the paired analysis, younger life stages were more negatively affected than older life stages by warming (Fig. 2). However, no such effects were observed for acidification or hypoxia, for which our datasets contained fewer experiments (Fig. 2). Linear mixed effects (LME) models also revealed significant effects of life stage pairings on effect size differences for warming (LME $Z = 3.22$, $p = 0.001$), but not acidification or hypoxia (Z and p values for all analyses are reported in Supplementary material Appendix 6), and these differences were significant between adults and juveniles and between larvae and embryos (Fig. 3). We found no significant effects of treatment magnitude or duration in the paired analysis, but did find greater differences between effect sizes for organism that occupy intertidal habitats as adults than those that occupy pelagic habitats as adults (LME $Z = -2.64$, $p = 0.01$). These results were not driven by responses of the most studied species (Supplementary material Appendix 5).

In the unpaired analysis of lethal thresholds of warming, acidification and hypoxia, all significant effects were negative, with younger life stages often more negatively affected than older life stages (Fig. 4). Specifically, LME models revealed differences among life stages for warming (LME $Z = 3.94$, $p < 0.001$) but not acidification or hypoxia, for which fewer data were available (Supplementary material Appendix 6). There were also significant effects of treatment magnitude, but not duration (Supplementary material Appendix 6) or

Table 1. Summary of papers documenting survival of multiple life stages (embryo [E], larva [L], juvenile [J] and adult [A]) of marine invertebrates under three climate change stressors (warming [°C], acidification [pH] and hypoxia [DO]) included in our database.

Stressor	Life stage				Phylum	Species	Source	
	°C	pH	DO	E L J A				
X				X X	Mollusca	<i>Mytilus childressi</i>	Arellano and Young 2011	
X					X X	Chordata	<i>Molgula socialis</i> , <i>Molgula manhattensis</i>	Brunetti et al. 1985
X				X	X	Mollusca	<i>Crepidula fornicata</i>	Diederich and Pechenik 2013
X					X X	Cnidaria	<i>Ectopleura larynx</i>	Guenther et al. 2011
X					X X	Arthropoda	<i>Helice crassa</i>	Jones 1981
X				X X		Echinodermata	<i>Sterechinus neumayeri</i>	Kapsenberg and Hofmann 2014
X				X X		Cnidaria	<i>Paramuricea clavata</i>	Kipson et al. 2012
X					X X	Annelida	<i>Zeylanicobdella arugamensis</i>	Kua et al. 2014
X				X X		Cnidaria	<i>Porites astreoides</i>	Olsen et al. 2014
X				X X		Mollusca	<i>Spisula solidissima</i>	Roosenburg et al. 1984
X				X X		Mollusca	<i>Loligo vulgaris</i>	Rosa et al. 2014
X					X X	Arthropoda	<i>Gammarus tigrinus</i> , <i>Gammarus zaddachi</i>	Sareyka et al. 2011
X				X X		Echinodermata	<i>Echinometra lucunter</i>	Sewell and Young 1999
X					X X	Arthropoda	<i>Hyale crassicornis</i>	Tsoi et al. 2005
X				X X		Echinodermata	<i>Sterechinus neumayeri</i>	Tyler et al. 2000
X				X X		Mollusca	<i>Mytilopsis leucophaeata</i>	Verween et al. 2007
X				X X		Mollusca	<i>Argopecten irradians</i> , <i>Mercenaria mercenaria</i> , <i>Mulinia lateralis</i> , <i>Spisula solidissima</i>	Wright et al. 1983
X				X X		Arthropoda	<i>Farfantepenaeus duorarum</i>	Zink et al. 2013
X				X X		Arthropoda	<i>Petrolisthes cinctipes</i>	Ceballos-Osuna et al. 2013
X				X X X X		Arthropoda	<i>Acartia tonsa</i>	Cripps et al. 2014
X				X X		Arthropoda	<i>Artemia franciscana</i>	Doyle and McMahan 1995
X				X	X	Arthropoda	<i>Calanus glacialis</i> , <i>Calanus hyperboreus</i> , <i>Oithona similis</i>	Lewis et al. 2013
X				X X		Echinodermata	<i>Arbacia lixula</i>	Wangenstein et al. 2013
X				X X		Mollusca	<i>Perna canaliculus</i>	Alfaro 2005
X				X X X X		Arthropoda	<i>Petrolisthes laevigatus</i>	Alter et al. 2015
X				X X	X	Annelida	<i>Hydroides elegans</i>	Leung et al. 2013
X				X X		Arthropoda	<i>Callinectes sapidus</i>	Tankersley and Wieber 2000
X				X X		Arthropoda	<i>Idotea balthica</i> , <i>Idotea emarginata</i>	Vetter et al. 1999

latitude (Supplementary material Appendix 7), for warming (LME $Z = -11.6$, $p < 0.001$) and acidification (LME $Z = 3.09$, $p = 0.02$). More specifically, as the magnitude of acidification increased (decreasing pH), the effect size also became more negative, and this relationship was less pronounced for warming (Supplementary material Appendix 8 Fig. A2).

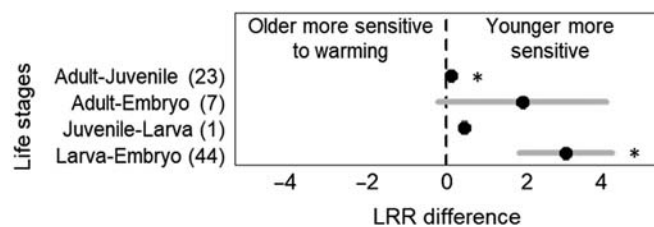


Figure 3. In the paired analysis of lethal warming thresholds, all life stage pairs had positive LRR differences, indicating that younger life stages were more sensitive. Means \pm bootstrap 95% CIs for effect size (LRR) differences. *Significant difference. Sample sizes are adjacent to life stages on y-axis, and the CI for adult-juvenile is ± 0.098 .

Fail-safe number calculations indicated the robustness of results against sampling bias. In the unpaired analysis, fail-safe numbers for all warming and hypoxia results were much greater than the $5N + 10$ threshold of Rosenthal (1979) to indicate robustness to sampling bias (Supplementary material Appendix 9 Table A3a), while those for acidification were often below the threshold. In the paired analysis, all fail-safe numbers were above the robustness threshold (Supplementary material Appendix 9 Table A3b). For example, fail-safe numbers for both paired warming and hypoxia were >200 (Supplementary material Appendix 9 Table A3b; i.e. >200 experiments with $LRR = 0$ would be needed to change the significant results to non-significant).

Discussion

Our results indicate that younger life stages, particularly embryonic and larval stages of marine invertebrates, were most sensitive to acute warming. This conclusion is supported

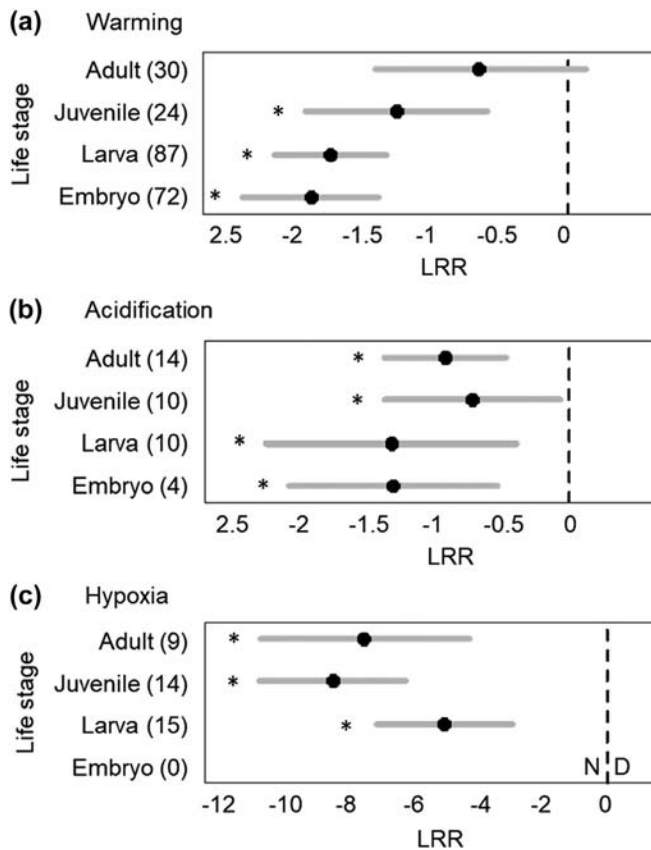


Figure 4. In the unpaired analysis, all significant lethal effects of climate change stressors on all life stages considered were negative. Note that LRR scales differ across panels. Means \pm bootstrap 95% CIs for effect sizes (LRR). *Significant difference, ND=no data. Sample sizes are adjacent to life stages on y-axis.

by two congruent findings, both of which are robust to sampling bias: 1) in the unpaired analysis, effect sizes were most negative for younger life stages, and 2) in the paired analysis, younger life stages were generally more sensitive than the older life stages, regardless of pairing. Additionally, life stage and life stage pairing were both significant factors in the linear mixed effects model analysis of the unpaired and paired warming data, respectively. Despite smaller sample sizes, response trends were similar for hypoxia. These results appeared to be robust to sampling bias. However, responses to acidification were both non-significant and prone to sampling bias.

We report results of the first meta-analysis investigating paired differences in responses of study organisms to climate change stressors across their life stages from embryos to adults and also the first meta-analysis to consider life stage differences in responses to hypoxia. The robustness of our findings is also supported by consistency with a prior meta-analysis (using an 'unpaired' approach), which demonstrated that younger life stages of marine invertebrates were more negatively affected by warming than older life stages (Harvey et al. 2013). More specifically, our results suggest that tolerance tends to increase as organisms progress through

their life stages (Fig. 4a–c; also see Dupont et al. 2010, Kroeker et al. 2010, 2013, Harvey et al. 2013). Kroeker et al. (2010, 2013) have also reported negative, yet variable, effects of acidification. Interestingly, our results differ from those of Przeslawski et al. (2015), who demonstrated that marine invertebrate larvae can be more sensitive to warming and acidification than embryos. This difference could partially be explained by variation in methods and data selection criteria, as we were specifically focused on studies allowing a paired analysis of differences between ages of single taxa.

While an increasing number of studies document the life stage-specific responses of marine invertebrates to climate extremes, many gaps still exist. There were few studies that met our selection criteria documenting responses to acidification and hypoxia as compared to the better studied warming responses (Table 1). These publication gaps were evident in our comparisons with low sample sizes and fail-safe numbers; notably, results for responses to acidification across life stages of marine invertebrates were not robust to sampling bias (Supplementary material Appendix 9 Table A3). The majority of papers which met inclusion criteria in our analyses were published after 2010, suggesting an increasing consideration of response differences across life stages. Additionally, we only addressed single stressors in this study, while, in natural environments, multiple stressors can occur simultaneously. For more complete assessments of climate change sensitivities of marine invertebrates, we call for more studies on the effects of acidification, hypoxia and multiple stressors across life stages.

In this study, we examined the sensitivity to climate change across life stages of organisms subject to the same treatment magnitudes and stressors. However, it is important to consider that under natural conditions, different life stages may be exposed to different levels of environmental stress. For example, life stages often utilize different resources and occupy separate habitats, influencing the levels and types of climate stressors they experience (Werner and Gilliam 1984). This variation in habitat is likely to determine differential stress acclimatization (which may have been displayed by individuals in our meta-analysis if they had been recently field-collected) as well as differential environmental exposure (Kingsolver et al. 2011, Pankhurst and Munday 2011). Variation in microclimates and acclimation that occur across life stages are common across both terrestrial (Kingsolver et al. 2011, Pincebourde and Casas 2015) and marine (Werner and Gilliam 1984, Schmidt and Rand 1999) invertebrates. For example, life stages of the hawkmoth, *Manduca sexta*, experience distinct thermal micro-environments, which may differ from ambient temperature by up to 10°C (Kingsolver et al. 2011, Woods 2013). Nocturnal adults lay eggs on plant leaves, which hatch into larvae, whose body temperatures transition from being governed by leaf temperature to being governed by ambient air temperature as they grow (Woods 2013). Similarly, intertidal mussels experience distinct thermal micro-environments as they progress through their life stages (Helmuth and Hofmann 2001, De Nesnera 2016, Jurgens and Gaylord 2016). Mussel larvae experience oceanic conditions, which might be correlated to their thermal

tolerance as intertidal recruits (Sorte et al. 2018). As benthic juveniles, mussels can occupy microhabitats with varying amounts of shelter from solar radiation and heat stress (Helmuth and Hofmann 2001, Jurgens and Gaylord 2016), which can give rise to differences in tolerance across life stages (Vetter et al. 1999, Lewis et al. 2013, Cripps et al. 2014, Alter et al. 2015). A key next step in determining vulnerability to climate change would be to pair measures of climate sensitivity (as collated here) with observations of climate exposure (body temperatures across habitats) between life stages, including across multiple stressors that occur simultaneously.

Mortality already tends to be high for early life stages of marine invertebrates under current climatic conditions (Rumrill 1990, Pechenik 1999). Our results suggest that unless exposure balances out differences in sensitivity, warming could disproportionately impact younger life stages, making this an even more pronounced bottleneck in population dynamics (O'Donnell et al. 2009, Findlay et al. 2010, Russell et al. 2012). Future studies would ideally investigate the physiological and ecological mechanisms of persistence across life stages, including potential for acclimation, adaptation and migration (Sorte et al. 2011, 2018, Suckling et al. 2014, 2015, Parker et al. 2015, Samani and Bell 2016), to predict the impacts of climate change on marine invertebrate species.

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Author contributions – LP and CS designed the project, LP collected and analyzed the data, LP wrote the manuscript, and LP and CS revised the manuscript.

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Supplementary material (available online as Appendix oik-05886 at <www.oikosjournal.org/appendix/oik-05886>). Appendix 1–9.