Received: 5 August 2020 | Revised: 20 January 2021 | Accepted: 8 April 2021
DOI: 10.1111/geb.13318

META ANALYSIS

Global Ecology and Biogeography A Journal of Macroecology

WILEY

Non-native species outperform natives in coastal marine ecosystems subjected to warming and freshening events

Ella McKnight[1] | Rebecca Spake[2] | Amanda Bates[1,3] | Dan A. Smale[4] | Marc Rius[1,5]

[1]School of Ocean and Earth Science, University of Southampton, National Oceanography Centre, Southampton, United Kingdom

[2]School of Geography and Environmental Science, University of Southampton, Southampton, United Kingdom

[3]Department of Ocean Sciences, Memorial University of Newfoundland, St. John's, Newfoundland, Canada

[4]Marine Biological Association of the United Kingdom, The Laboratory, Plymouth, United Kingdom

[5]Department of Zoology, Centre for Ecological Genomics and Wildlife Conservation, University of Johannesburg, Johannesburg, South Africa

Correspondence
Ella McKnight, School of Ocean and Earth Science, University of Southampton, National Oceanography Centre, European Way, Southampton SO14 3ZH, UK.
Email: Ella.mcknight@soton.ac.uk

Funding information
Natural Environment Research Council, Grant/Award Number: NE/L002531/1; UKRI Future Leaders Fellowship, Grant/Award Number: MR/S032827/1; Canada Research Chairs

Editor: Fabien Leprieur

Abstract

Aims: Contemporary climate change and biological invasions are two main drivers of biodiversity redistribution. Interactive effects between these drivers have been reported in a variety of studies, yet results are conflicting. Some studies find that contemporary climate change facilitates the spread and success of non-native species, especially those with broad physiological tolerances. Other studies conclude that non-natives are vulnerable to current and future changes in climatic conditions. Given that most studies have focused on terrestrial species, here we contribute to this debate by analysing responses of marine native and non-native fauna and flora to key climate-related stressors, namely increased temperature (warming) and decreased salinity (freshening).

Location: Global.

Time period: 2002–2019.

Major taxa studied: Marine benthic macrophytes and invertebrates.

Methods: We conducted a meta-analysis of experiments investigating the performance (e.g. growth, survival and reproduction) of benthic species in response to warming and freshening.

Results: We found that non-native species tended to respond positively to elevated temperature, whereas the performance of native species declined. Similarly, decreased salinity negatively affected the biological processes of native species, but non-natives showed neutral or negative overall responses to freshening.

Main conclusions: We find evidence that non-native species outperform natives under a wide variety of warming and freshening conditions. The growth and reproduction of non-natives are enhanced by warmer temperatures, and thus ocean warming is expected to facilitate future spread and success of non-native species. Increased freshening along future coastal areas, however, will likely have a negative impact in both native and non-native species and thus is expected to be a driver of significant change in coastal marine ecosystems. Our comprehensive analysis highlighted the need to expand our understanding of climate change effects beyond warming and specifically, studies focusing on salinity changes.

KEYWORDS

biofouling, coastal ecosystems, epibenthic, global change, invasive, marine biodiversity, quantitative synthesis

1 | INTRODUCTION

Ecosystems around the globe are increasingly threatened by contemporary climate change and the spread of non-native species (Early et al., 2016). Altered temperature and precipitation regimes (Pfleiderer et al., 2019) lead to profound effects on species' performances and distributions (Pecl et al., 2017). For example, climate change drivers are directly responsible for altering species phenology and ecosystem functioning (Smale et al., 2019; Wernberg et al., 2013; Wolkovich & Cleland, 2010). In addition, non-native species affect native populations, transforming entire recipient communities and leading to major redistributions of local and regional biota (Ehrenfeld, 2010; Katsanevakis et al., 2014). A growing number of studies suggest that these drivers can act synergistically leading to negative ecosystem effects and exacerbating the impacts of non-natives (Hulme, 2017). Indeed, environmental variability has been shown to enhance the performance of non-natives relative to native species, either directly by improving abiotic conditions (Hellmann et al., 2008) or indirectly by inhibiting the fitness of native competitors or potential predators (Hillebrand, 2011; Wolkovich & Cleland, 2010). Understanding how different taxonomic and functional groups respond to climate change is then critical, especially as they play different ecological roles and therefore shifts in their distribution and abundance may have contrasting wider impacts on ecosystems (Karatayev et al., 2014; Kumschick et al., 2014; Layton et al., 2019).

Recent reviews and meta-analyses have focused on assessing the effects of climate change drivers on both native and non-native species' performance. Sorte et al. (2013) found that non-natives consistently outperform natives in aquatic ecosystems. Similarly, Bates et al. (2013) found greater heat tolerance in non-natives than closely related natives across different aquatic ecosystems. In turn, Stephens et al. (2019) reported overall negative effects of both temperature and CO_2 increases on non-native performance in both marine and freshwater ecosystems. These conflicting results suggest further analysis of the effects of climate change on native and non-native species is needed. In addition, previous meta-analyses (e.g. Sorte et al., 2013; Stephens et al., 2019) considered a limited number of studies focusing on aquatic ecosystems and thus the inclusion of more studies is needed to confirm or refute the generality of previous findings. Moreover, previous meta-analyses did not examine variation in species' responses across life-history stages (i.e. larva, adult or juvenile), even though experimental studies stress the need to consider multiple life-history stages to fully understand species' abilities to tolerate climate change stressors (Hudson et al., 2020; Pandori & Sorte, 2018). Furthermore, the synthesis of Stephens et al. (2019) was geographically limited to North America, in line with the majority of ecological experiments that are performed in the Northern Hemisphere and temperate regions (see Cameron et al., 2019; Martin et al., 2012). Finally, previous analyses (e.g. Bates et al., 2013) primarily focused on animals, largely ignoring other ecologically important species such as macroalgae and angiosperms. Taken together, a more comprehensive analysis is needed to consider geographical and taxonomic biases and strengthen generalizations made by previous studies.

Coastal marine ecosystems have significant ecological and socioeconomic value (Martínez et al., 2007), and as a result of several stressors impacting these ecosystems, considerable management actions (e.g. protected areas, control of non-native species) are required. Understanding how coastal species respond to climate change is critical for developing predictions of future biodiversity scenarios (Harvey et al., 2013; Ummenhofer & Meehl, 2017). Coastal ecosystems are naturally subjected to significant environmental variability, where fluctuations in parameters such as temperature and salinity can be marked (Borero, 1993; Gade et al., 1983). However, variability signals are increasing in frequency and intensity, with heatwave events and storm activity being more prevalent now than in the recent past (Coumou et al., 2013; Oliver et al., 2019). Storms bring more frequent and intense precipitation that can combine with changes in coastal land use to increase freshwater influxes into estuaries and coastal seas (Coumou et al., 2013; Gillanders & Kingsford, 2002). The consequences of changing temperature and salinity on both natives and non-natives are ultimately driven by their underlying physiology and their ability to tolerate both short-term and long-term environmental variability (Smyth & Elliott, 2016). As such, organisms within shallow-water benthic communities, specifically those taxa that are sessile (e.g. invertebrates and macroalgae), may be particularly vulnerable and susceptible to predicted future changes in thermal and salinity regimes (Dobretsov et al., 2019; Gillanders & Kingsford, 2002).

Here, we performed a meta-analysis to investigate how two key climate-related stressors – increased temperature (hereafter 'warming') and reduced salinity (hereafter 'freshening') – influence different biological processes (e.g. growth, survival, reproduction) in both native and non-native coastal marine and brackish species. We explored variation in biological processes across several factors that might mediate the effect of these stressors, including geographical distribution and broad taxonomic grouping. We expected that the magnitude and direction of the effects of stressors on biological processes would vary with species nativeness, type of organism (plant or animal), and between warming and freshening. Specifically we tested four predictions: (a) both warming and freshening will exert more negative effects on native species than non-natives across different biological processes (Kordas et al., 2015), (b) non-natives will respond positively to warming (e.g. Sorte et al., 2013; Stephens et al., 2019), and be more tolerant to freshening compared to native species (Diez et al., 2012; Velasco et al., 2018), (c) early life-history stages will be more adversely affected by climate-related stressors than adults, as early life-history stages are often more vulnerable to variability in abiotic factors (Pineda et al., 2012), and (d) non-native plants (i.e. macroalgae or angiosperms) will respond positively to climate-related stressors (in line with Stephens et al., 2019 who found that non-native terrestrial plants benefited from increased climatic variability).

2 | METHODOLOGY

2.1 | Study scope and inclusion criteria

We used the ISI Web of Science (Thomson Reuters) to search the peer-reviewed published literature for papers using the following search terms: ('climate change' OR 'global warming' OR 'ocean warming') AND (experiment* OR manipul*) AND (temperature* OR thermal OR salin* OR freshen*) AND (marine OR coastal OR sea OR ocean), with no restriction on publication year. Additional literature was identified by 'snowballing' (i.e. searching for references within retrieved articles and reviews). We chose papers that measured biological responses of native and/or non-native species to experimentally controlled changes in temperature (warming) and reduced salinity (freshening). We included papers that measured any biological processes that relate to changes in biological rates (i.e. metabolism and respiration), health or performance (i.e. growth, survival, reproduction) at either the individual organism or population levels. We restricted our search to studies of sessile or sedentary marine and brackish organisms that inhabit depths of up to 10 m, and thus included species typical of shallow seas that are subjected to variation in abiotic stressors. Papers were included if they focused on laboratory or field-based manipulative experiments, either in separate experimental units or together in a community mixture, and measured biological processes among replicated control (ambient) and treatment groups subjected to elevated temperature and/or decreases in salinity. Studies were excluded if experiments did not include replicates or did not provide measures of variation. Multi-driver experiments that explored other variables (e.g. hypoxia or nutrients) for which the independent effects of temperature and freshening could not be measured were excluded.

2.2 | Data extraction

All studies were coded according to the following covariates: manipulated stressor (warming or freshening), measured biological process (see details in Table 1), nativeness [native or non-native, identified according to the authors' descriptions or through the World Register of Introduced Marine Species (Ahyong et al., 2020)], the experimental duration (number of days), type of organism (i.e. plant or animal), life-history stage (i.e. larva, adult or juvenile), and geographical location (absolute latitude). Finally, we calculated the 'stress exposure' of each study, the absolute difference between experimental and a control level exposure (in degrees Celsius or practical salinity units). For studies that measured environmental variables other than

TABLE 1 Classification of biological responses and covariates used within the meta-analyses. Biological responses were categorized as processes measured among studies

Biological processes	
Critical biological rate	Photosynthesis (chlorophyll a concentration, average optimum quantum yield) and calcification
Metabolic indicators[a]	Heat shock proteins, free radical activity, lipidperoxidation (malondialdehyde) levels$^{\text{(inverse)}}$, % eosinophils, lysozyme activity, number of haemocytes in haemolymph
Growth	Growth rate, abundance, biomass, growth efficiency, elongation
Feeding ability	Feeding rate, clearance rate, nutrient uptake
Health	Condition index, tissue health, tissue composition, palatability, concentration of soluble phlorotannins
Reproduction	Gonad index, receptacle development, formation of reproductive cells, viable larvae
Respiration[a]	Oxygen consumption$^{\text{(inverse)}}$
Survival[a]	Survival, mortality$^{\text{(inverse)}}$
Covariates of interest	
Climatic stressor	Warming or freshening
Nativeness	Organism is native or non-native to the area of study
Life-history stage	Adult, juvenile or larval
Species type	Plants or animals[b]

[a] The direction of the effect size was reversed for some processes for intuitive purposes (e.g. increased mortality under stress is equivalent to decreased survival).

[b] Macroalgae were included with angiosperms as 'plants' as similar ecological function.

warming and freshening (such as hypoxia or nutrient variation), data were taken from only the experiments where these variables were considered at 'ambient' or 'control' levels, as determined or described by the authors. The control conditions of the focal environmental stressors (warming or freshening) needed to represent current ambient seawater at the time of collection and study or based on the authors' knowledge and understanding of ambient conditions for the study organism(s) and area.

For each biological response (here distinguished as a 'process' – see Table 1) reported from each paper, we extracted values of mean, sample size (number of replicates) and variance (standard deviation, standard error, or confidence interval) for control and treatment groups. Where articles reported separate values for two or more study locations, species and biological process categories, we regarded each as an independent 'study'. When studies reported several metrics for the same biological process category (e.g. growth expressed as changes in length and biomass) only one process was selected randomly from the most conservative results. For studies that included time-series data, measurements were taken from the final experimental time point. Data were extracted from tables or figures using the software DataThief III, v1.7 (Tummers, 2006).

2.3 | Data analysis

We estimated Hedges' *d* (Rosenberg et al., 2013; see Supporting Information Table S1 for equation and model details) and its variance for each study to estimate the magnitude and direction of the biological process to changes in warming and/or freshening. All analyses were carried out using R v3.6.2 (R Core Team, 2018) and we used R package 'metaphor' (Viechtbauer, 2010) to compute summary effect sizes.

The studies were highly heterogeneous; therefore, we split data into two core subgroups, according to stressor and nativeness. First, we separated studies according to stressor, warming and freshening, because these stressors exerted different effects on organisms through different physiological pathways. We then further subgrouped studies according to nativeness because we hypothesized natives and non-natives would respond differently to stressors. Next, for each of these four categories, we subgrouped by categorical variables of interest: the biological process measured, species-type and life-history stages (described in more detail in Supporting Information Figure S1).

We set out to compare the magnitude, direction and heterogeneity of effect sizes, representing responses to stressors, across the subgroups. To account for known sources of variability in the study attributes, we constructed global mixed-effect meta-regression models for each subgroup, consisting of the three continuous moderator variables: the level of stress exposure, experimental duration and absolute latitude. Continuous moderators were converted to z-scores to improve the interpretability and comparability of meta-regression coefficients (Schielzeth, 2010). In each analysis, studies were precision-weighted by the inverse of the sum of their within-study variance (V_d) and between-study variance (τ^2), assuming that studies with lower within-study variance were more precise (Hedges & Olkin, 1985). In all models, article and species identifiers were included as random effects, as effect sizes from the same research study or species may be more similar than effects from different groups. For the subgroups divided by life-history stage and species-type, the measured biological process was specified as a random effect. From these global models, we generated a full set of nested models, all to be compared with Akaike's information criterion (AIC) using R (v3.6.2; R Core Team, 2018). We identified a single, minimum adequate model as the one with the lowest AIC value (Burnham & Anderson, 2002). From these models, we interpreted mean effect sizes as the model intercepts, conditioned on mean values of covariates.

Summary effect sizes were interpreted according to Cohen's benchmark (Cohen, 1962) of small, moderate and large effects from values of *d* in the regions of .2, .5 and .8, respectively. Statistical significance was attributed if bias-corrected 95% confidence intervals (Hedges & Olkin, 1985) did not overlap zero. Given the heterogeneity typical of ecological studies (Senior et al., 2016), our focus was on the overall direction and magnitude of summary effects, rather than the statistical significance. A total heterogeneity statistic (I^2) was calculated, where I^2 is the percentage of variance between effect sizes that cannot be attributed to sampling error (Higgins et al., 2003).

3 | RESULTS

In total, 96 peer-reviewed articles met our study inclusion criteria (see Supporting Information Table S2 for list) and these articles were published between 2002 and 2019. Studies were distributed globally from Alaska to the Antarctic, although the vast majority of studies occurred in the Northern Hemisphere. Non-native species did not appear in polar, sub-polar or tropical latitudes (see Supporting Information Figure S2 for a map of study distribution and Figure S3b for nativeness distribution). A total of 27 non-natives and 104 natives were identified across the articles, with the distribution of taxa covering 12 phyla/subphyla of both plants and animals (Supporting Information Table S3, Figure S3a). The most commonly studied non-natives were the ascidians *Styela plicata* and *Ciona intestinalis*, and the macroalga *Undaria pinnatifida* (see Supporting Information Table S3). The 96 articles contributed a total of 575 effect sizes (studies) for different biological processes with greater representation of warming ($n = 453$) than freshening ($n = 123$). Growth was the most commonly studied biological response under both stressors ($n = 190$), and reproduction and feeding ability were the least frequently reported. There were more native ($n = 431$) than non-native studies ($n = 144$) and more studies on plants and algae ($n = 318$) than animals ($n = 257$). Experiments comprised a wide range of intensities of stress exposure, with temperature elevations (from ambient) ranging between 0.67 and 25 degrees, and declines in salinity between 2 and 29 practical salinity units (see Supporting Information Figure S3). The distribution of native and non-native species between ecosystem (i.e. marine or estuarine) and magnitude of stress exposure are provided in Supporting Information Figure S4.

3.1 | Variation among biological processes

Critical biological rate, growth, respiration and survival decreased with freshening but were not affected by warming (Figure 1a). The magnitude of the negative effect size was particularly large for survival and growth under freshening. In contrast, reproductive measures decreased with both freshening and warming, and metabolic indicators increased with warming but had no overall change with freshening (Figure 1a). Warming decreased health measures but exerted no overall effect on feeding ability (Figure 1a). High levels of heterogeneity among these mean effect size estimates (I^2 between 50 and 95%) indicated a need to explore sources of variation among effect sizes.

3.2 | Differential responses by nativeness

Under warming, growth increased for non-native species but decreased for native species, while metabolic indicators increased for both natives and non-natives (Figure 1b). Warming reduced the health of native species, but had no effect on non-natives. Reproductive success decreased in response to warming for natives, whereas non-native reproductive success increased (Figure 1b). Finally, there was no overall effect on survival and respiration for both native and non-native species (Figure 1b). Due to the unbalanced nature of the subgroups, not all of the three continuous covariates were used as moderators in the mixed-effects meta-regressions (see Supporting Information Table S4). The levels of temperature stress exposure had an influence on natives and non-natives, with greater stress yielding a more strongly negative effect size for survival, and more positive for respiration. Experimental duration influenced non-native metabolic indicators negatively while absolute latitude influenced non-native species positively (see Supporting Information Table S4 for more information on the meta-regression models).

Under freshening treatments, critical biological rate, growth, reproduction and survival all decreased for natives, but did not for non-natives (Figure 1c). For metabolic indicators, there was no overall effect under freshening (Figure 1c). Stress exposure negatively influenced growth and survival of natives. Experimental duration positively influenced the growth of both native and non-natives, and absolute latitude negatively affected the growth of non-natives and the metabolic indicators of natives (see Supporting Information

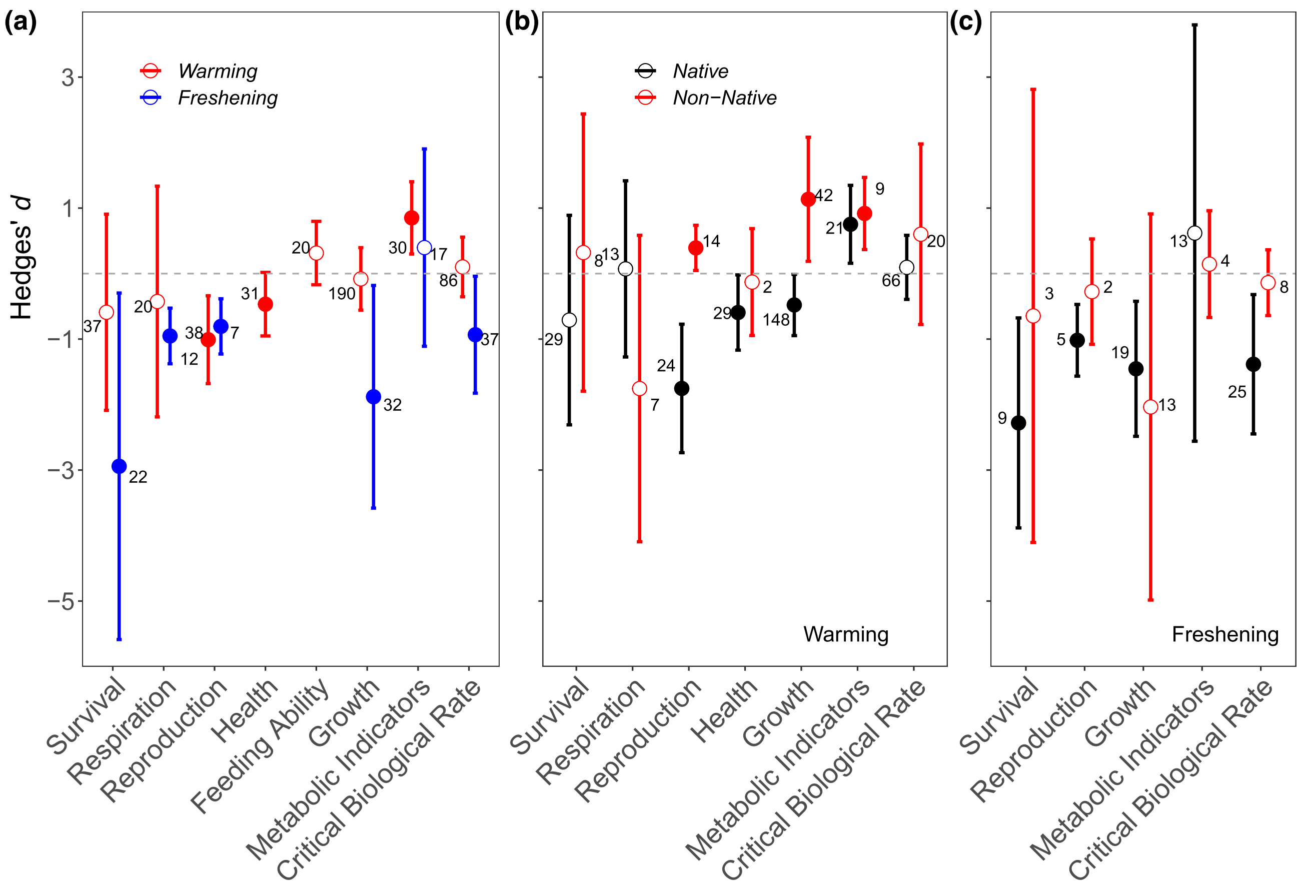

FIGURE 1 Effects of (a) temperature (red) and salinity (blue) on biological processes, and effects of (b) temperature and (c) salinity between native (black) and non-native (red) species on marine/brackish biological processes. Numbers indicate the number of observations (*n*) in each analysis. Mean effect sizes as Hedges' *d* and ±95% confidence intervals estimated using mixed-effects meta-regressions are shown. The dashed line indicates zero effect. The confidence intervals of significant mean effect sizes (filled circles) do not overlap zero

Table S4 for model outputs). Heterogeneity among studies was very high among these mean effect size estimates (Supporting Information Table S4, I^2 between 37 and 99%). Subgrouping by process and nativeness yielded small sample sizes for some subgroups, so we have cautiously interpreted effect sizes with small sample sizes (shown in Figure 1c).

3.3 | Effect size variation among covariates

Our analyses revealed variable effects across the covariates considered (Figure 2). Although adult and juvenile life-history stages were generally not affected by warming, native larval stages were negatively affected (Figure 2a). The overall positive effect of warming on non-native larvae was not different from zero (Figure 2a). Under freshening, native and non-native adult and native larval stages responded negatively (Figure 2a), while native juvenile and non-native larval stages were not affected overall. Plants and animals displayed contrasting results; non-native plants responded positively to warming and did not have an overall response to freshening, whereas native plants were not affected by warming but responded negatively to freshening (Figure 2b). Both native and non-native animals were not affected by warming or freshening (Figure 2b). Despite having explored sources of heterogeneity (e.g. stress intensity, nativeness, duration, taxa, etc.), a high degree of heterogeneity remained (see Supporting Information Table S4).

4 | DISCUSSION

Our meta-analysis provided new insights into the directionality of the effects of climate-related stressors across a wide range of native and non-native species and coastal ecosystems, greatly expanding the breadth of taxa and ecosystems considered in previous studies (e.g. Bates et al., 2013; Sorte et al., 2013; Stephens et al., 2019). We found that warming and freshening had greater detrimental effects on key biological processes of natives compared to those of non-native species. In particular, growth and reproduction of non-native species responded positively to warming (Figure 1b), suggesting that a warming climate will continue to enhance the spread and performance of non-natives in the near future.

From the diverse set of performance metrics included, metabolic processes responded positively to warming in both native and non-native species groupings (Figure 1a). This finding was consistent with theory, as moderate warming near thermal optima is known to increase metabolic rates, particularly in ectotherms (Dahlhoff, 2004; Deutsch et al., 2008), influencing key biological processes and performance traits (O'Connor et al., 2007). Indeed, a number of studies on aquatic plants that subjected organisms to modest warming documented increased growth (e.g. Graba-Landry et al., 2018; Poore et al., 2016; Werner et al., 2016) and photosynthetic rates (e.g. Bender et al., 2014; Schoenrock et al., 2016), which are consistent with greater phenology changes of plants (Thackeray et al., 2016). Furthermore, warming promoted the growth of non-native species in our analysis (Figure 2a). Indeed studies have reported that growth is important to the success of non-natives in both terrestrial and marine/brackish systems, even when compared to native counterparts under normal conditions (McKnight et al., 2016). More specifically, rapid growth can underpin the capacity of non-native species to take advantage of increased resources, such as open space following mass mortality events, and also survival after extreme climatic events (Diez et al., 2012).

The growth, health and reproduction of native species responded negatively to warming (Figure 1b). When thermal conditions exceed physiological thresholds, organisms redistribute their energy to protective mechanisms in order to survive, such as with the upregulation of heat shock proteins (Dahlhoff, 2004). Thus, health and performance can decline in acute and even chronic exposures (Bergmann et al., 2010), but individuals can still persist (e.g. Bennett et al., 2015). Although non-natives may have broader environmental tolerance and greater capacity for short-term acclimatization to environmental

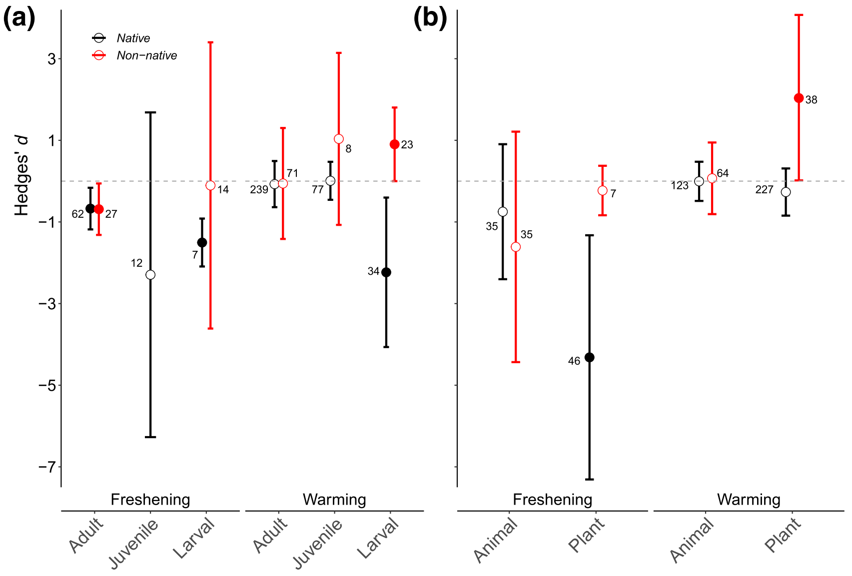

FIGURE 2 Subgroup parameter estimates for (a) life-history stages and (b) species type. Forest plots showing mixed-effects models of life stages or species type separated by stress and native status. Numbers indicate number of observations (n) in each analysis. Mean effect sizes and ±95% confidence intervals estimated using mixed-effects meta-regression are shown. The dashed line indicates zero effect. The confidence intervals of significant mean effect sizes (filled circles) do not overlap zero

variability than natives (Hulme, 2017), shifts in competitive interactions can also be important (Occhipinti-Ambrogi, 2007). For example, a number of studies included experiments conducted on multi-species assemblages, which captured shifts in interspecific interactions driven by warming, such as competition for space between natives and non-natives on warmed settlement panels (e.g. Smale & Wernberg, 2012) where warmer waters promoted non-native abundance. However, the vast majority of experiments were conducted on one or a few species in isolation and, as such, it is not possible to disentangle the relative importance of direct and indirect effects of warming on the interaction between native and non-native species. Further work on the influence of climate change drivers on the outcomes of ecological interactions in complex communities is needed to better understand responses to future climate change conditions.

The reproductive success of non-natives increased under warming, whereas native reproduction declined (Figure 1b). Reproduction for many species is temperature-sensitive (Andrews et al., 2014; Rothausler et al., 2018) and increased temperatures can either suppress or enhance reproduction (Harris et al., 2017; Lawrence & Soame, 2004). Among life-history stages, the magnitude and direction of responses also differed, with non-native larvae generally benefiting, while the performance of natives was impeded. This supports evidence that many non-natives have broad thermal tolerances (Bates et al., 2013; Somero, 2010) and this advantage may manifest at early developmental stages. Thus, extreme events such as heatwaves, which cause widespread mortality (e.g. Smale & Wernberg, 2013; Wernberg et al., 2016), may displace native species and provide free space for colonization and recruitment of non-native larvae.

The performance of non-natives can be promoted through recruitment, growth and reproduction, particularly for non-native plants, where these components can potentially affect abundance, range size and per capita effects (Bradley et al., 2019). Theoretically, climatic fluctuations could cause invading marine and brackish plants to propagate into dense monospecific stands, smothering other vegetation and altering biodiversity (Epstein et al., 2019) and ecosystem functioning (Pyšek et al., 2012; Vila et al., 2011). As the frequency and magnitude of extreme climatic events are predicted to increase, attention should also be directed towards greater understanding of the impacts of variables other than temperature on ecological interaction under climate change.

Under freshening only metabolic indicators lacked a systematic response across both native and non-native species groupings (Figure 1c). Freshening stress can cause organisms to engage homeostatic and excretory mechanisms in order to regulate internal osmolarity (Smyth & Elliott, 2016). However, adoption of osmoregulatory processes comes at a high energetic cost, and many marine species are not capable of performing this process (Rivera-Ingraham & Lignot, 2017). While we did not detect a trend in the direction of metabolic responses, we found a mix of highly adept and inept osmoregulatory strategies, whereby organisms were capable of maintaining homeostasis via quick metabolic pathways, or little reaction, thus osmoconforming to the salinity in their surrounding environmental conditions (Rivera-Ingraham & Lignot, 2017).

Critical biological rates (i.e. photosynthesis or calcification), growth, reproduction and survival were dampened by seawater freshening in native species. By contrast, there was no overall effect on these processes for non-natives (Figure 1c). Those experiments investigating critical biological rates on non-native organisms were represented primarily by aquatic plants and photosynthesis as the focal response. Greater resilience of the cellular photosynthetic machinery at low salinity may explain the apparent tolerance of photosynthetic non-natives. For instance, under decreasing salinity stress, the highly invasive macroalga *Undaria pinnatifida* upregulates resilient antioxidants, but native comparators do not (Bollen et al., 2016). In addition, this may explain the negative trend of native plants under freshening (Figure 2b), where an inability to efficiently photosynthesize under stressful conditions would disrupt organismal physiology and functionality (Scherner et al., 2013).

Native species displayed negative trends for growth, reproduction and survival (Figure 1c). Extreme exposures to freshwater can result in cellular damage in marine and brackish fauna and flora (e.g. Gröner et al., 2011; Newcomer et al., 2018), and while some organisms are capable of tolerating a range of fluctuating salinities, once their osmoregulatory limits are exceeded, organismal fitness traits are reduced (Hofmann & Todgham, 2010; Somero, 2010). In contrast, these biological processes showed no overall effect of freshening for non-natives consequently indicating a possible adaptation to osmotic stress (Yang et al., 2016) and that non-natives may further benefit from the negative effects on neighbouring native species. The disparity between native and non-native species is also extended to life-history stages, where native and non-native larvae differed in their responses (Figure 2a). The fact that non-native species tolerate severe osmotic stress indicates that short-term treatment with freshwater, which has been used for the control of invasive seaweeds such as *Caulerpa taxifolia* (Anderson, 2007), may not be an effective measure to eradicate problematic species. Nevertheless, there is a lack of studies that focus on freshening stress, and areas such reproductive success, survival and metabolic mechanisms of non-native species should be explored further.

Recent decades have seen an intensification of precipitation regimes in many regions that has led to increased frequency and magnitude of floods and freshening events (Stott et al., 2016). In the nearshore shallow benthos, freshening may have a greater negative impact than warming, and in fact, the extreme intensities of treatments for the climate change experiments reflects the severe freshening events seen in nature and explains the larger effect sizes in comparison to the warming treatments (see Supporting Information Figure S4a). Long-term freshening due to climate change also has the potential to alter coastal communities, since salinity regimes are known to influence species' presence and distributions (Wilkinson et al., 2007). This finding, combined with recent studies (e.g. Velasco et al., 2018), highlights the potential for freshening to drive significant changes in coastal marine ecosystems.

Our analysis of the available literature on shallow-water marine and estuarine species revealed several knowledge gaps. The analysed data were relatively unbalanced among phyla, biological responses and native and non-native species (Supporting Information Figures S3 and S4). In particular, non-native species were only represented at temperate latitudes and often by relatively few well-studied species, leading to some bias in the distribution of species across our comparisons. Given that effect sizes for some biological processes were generated from relatively few studies, and the high heterogeneity observed within subgroups, the results of our analysis should be taken with caution and cannot lead to major management recommendations, but rather point to general trends in responses and highlight key areas for future research.

5 | CONCLUSIONS

Here we contribute to the debate surrounding the effects of contemporary climate change on non-native species performance, by examining the responses of a wide variety of marine and brackish species to freshening and warming treatments. The addition of many previously understudied native and non-native taxa and the inclusion of freshening as a focal parameter address previously identified knowledge gaps and support the hypothesis that marine and brackish non-natives are poised to prosper under contemporary climate change (Sorte et al., 2013). We found across all species that warming induced both positive and negative responses in a range of biological processes. Responses to freshening were, however, primarily negative, illustrating the strong influence of salinity regime on estuarine and marine species. Acute freshening events may represent a more extreme climate-related stressor in the coastal environment than moderate warming, with low salinity values typical of extreme precipitation events more likely to lead to sublethal effects and even mortality (Bible et al., 2017; Cheng et al., 2015). Given that freshening events are predicted to intensify in some regions, salinity reduction has the potential to drive marked ecological shifts in coastal communities. Even so, our comprehensive synthesis revealed a paucity of data on the impacts of osmotic stress and the interaction between warming and freshening in shallow coastal systems, which represents a key knowledge gap. Our results indicate predominantly greater gains for non-native than native species under future climate conditions. This disparity in performance has the potential to exacerbate the negative effects that some non-native species have on natives. For example, predicted climatic fluctuations of temperature and precipitation may reduce the effects of biotic resistance, increasing the likelihood of non-natives spreading and becoming established. With the frequency and magnitude of extreme climatic events predicted to increase, attention should be directed towards a greater understanding of the impacts of erratic trends of variables (other than temperature) on ecological responses to climate change.

ACKNOWLEDGEMENTS

E.M.K. was supported by the Natural Environmental Research Council (grant number NE/L002531/1). Salary to A.B. was through the Canada Research Chairs Program. D.A.S. was supported by a UK Research and Innovation Future Leaders Fellowship (MR/S032827/1).

DATA AVAILABILITY STATEMENT

A list of the references from which the data were extracted can be found in the Appendix: Data Sources and all the data used in the meta-analysis are provided in Supporting Information Table S2. Data are also deposited in the Dryad repository: (https://doi.org/10.5061/dryad.mcvdncjzb).

ORCID

Ella McKnight https://orcid.org/0000-0003-3313-3910
Rebecca Spake https://orcid.org/0000-0003-4671-2225
Amanda Bates https://orcid.org/0000-0002-0198-4537
Dan A. Smale https://orcid.org/0000-0003-4157-541X
Marc Rius https://orcid.org/0000-0002-2195-6605

REFERENCES

Ahyong, S., Costello, M. J., Galil, B. S., Gollasch, S., Hutchings, P., Katsanevakis, S., Lejeusne, A., Marchini, A., Occhipinti, A., Pagad, S., Poore, G. C. B., Rius, M., Robinson, T. B., Sterrer, W., Turon, X., Willan, R. C., & Zhan, A. (2020). *World Register of Introduced Marine Species (WRiMS)*. http://www.marinespecies.org/introduced

Anderson, L. W. J. (2007). Control of invasive seaweeds. *Botanica Marina*, *50*(5–6), 418–437. https://doi.org/10.1515/BOT.2007.045

Andrews, S., Bennett, S., & Wernberg, T. (2014). Reproductive seasonality and early life temperature sensitivity reflect vulnerability of a seaweed undergoing range reduction. *Marine Ecology Progress Series*, *495*, 119–129. https://doi.org/10.3354/meps10567

Bates, A. E., McKelvie, C. M., Sorte, C. J. B., Morley, S. A., Jones, N. A. R., Mondon, J. A., Bird, T. J., & Quinn, G. (2013). Geographical range, heat tolerance and invasion success in aquatic species. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1772), 20131958. https://doi.org/10.1098/rspb.2013.1958

Bender, D., Diaz-Pulido, G., & Dove, S. (2014). Warming and acidification promote cyanobacterial dominance in turf algal assemblages. *Marine Ecology Progress Series*, *517*, 271–284. https://doi.org/10.3354/meps11037

Bennett, S., Wernberg, T., Arackal Joy, B., de Bettignies, T., & Campbell, A. H. (2015). Central and rear-edge populations can be equally vulnerable to warming. *Nature Communications*, *6*, 10280. https://doi.org/10.1038/ncomms10280

Bergmann, N., Winters, G., Rauch, G., Eizaguirre, C., Gu, J., Nelle, P., Fricke, B., & Reusch, T. B. H. (2010). Population-specificity of heat stress gene induction in northern and southern eelgrass *Zostera marina* populations under simulated global warming. *Molecular Ecology*, *19*(14), 2870–2883. https://doi.org/10.1111/j.1365-294X.2010.04731.x

Bible, J. M., Cheng, B. S., Chang, A. L., Ferner, M. C., Wasson, K., Zabin, C. J., Latta, M., Sanford, E., Deck, A., & Grosholz, E. D. (2017). Timing of stressors alters interactive effects on a coastal foundation species. *Ecology*, *98*(9), 2468–2478. https://doi.org/10.1002/ecy.1943

Bollen, M., Pilditch, C. A., Battershill, C. N., & Bischof, K. (2016). Salinity and temperature tolerance of the invasive alga *Undaria pinnatifida* and native New Zealand kelps: Implications for competition. *Marine Biology*, *163*(9), 163–194. https://doi.org/10.1007/s00227-016-2954-3

Borero, F. (1993). Fluctuations and variations in coastal marine environments. *Marine Ecology*, *15*(1), 3–25. https://doi.org/10.1111/j.1439-0485.1994.tb00038.x

Bradley, B. A., Laginhas, B. B., Whitlock, R., Allen, J. M., Bates, A. E., Bernatchez, G., Diez, J. M., Early, R., Lenoir, J., Vilà, M., & Sorte, C. J. B. (2019). Disentangling the abundance-impact relationship for invasive species. *Proceedings of the National Academy of Sciences USA*, *116*(20), 9919–9924. https://doi.org/10.1073/pnas.1818081116

Burnham, K. P., & Anderson, D. R. (2002). Model selection and multimodel inference: A practical information-theoretic approach. *Sociological Methods & Research*, *33*(2), 261–304. https://doi.org/10.1177/0049124104268644

Cameron, E. K., Sundqvist, M. K., Keith, S. A., CaraDonna, P. J., Mousing, E. A., Nilsson, K. A., Metcalfe, D. B., & Classen, A. T. (2019). Uneven global distribution of food web studies under climate change. *Ecosphere*, *10*(3), e02645. https://doi.org/10.1002/ecs2.2645

Cheng, B. S., Bible, J. M., Chang, A. L., Ferner, M. C., Wasson, K., Zabin, C. J., Latta, M., Deck, A., Todgham, A. E., & Grosholz, E. D. (2015). Testing local and global stressor impacts on a coastal foundation species using an ecologically realistic framework. *Global Change Biology*, *21*(7), 2488–2499. https://doi.org/10.1111/gcb.12895

Cohen, J. (1962). The statistical power of abnormal-social psychological research: A review. *The Journal of Abnormal and Social Psychology*, *65*(3), 145–153. https://doi.org/10.1037/h0045186

Coumou, D., Robinson, A., & Rahmstorf, S. (2013). Global increase in record-breaking monthly-mean temperatures. *Climate Change*, *118*, 771–782. https://doi.org/10.1007/s10584-012-0668-1

Dahlhoff, E. P. (2004). Biochemical indicators of stress and metabolism: Applications for marine ecological studies. *Annual Review of Physiology*, *66*, 183–207. https://doi.org/10.1146/annurev.physiol.66.032102.114509

Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences USA*, *105*(18), 6668–6672. https://doi.org/10.1073/pnas.0709472105

Diez, J. M., D'Antonio, C. M., Dukes, J. S., Grosholz, E. D., Olden, J. D., Sorte, C. J. B., Blumenthal, D. M., Bradley, B. A., Early, R., Ibáñez, I., Jones, S. J., Lawler, J. J., & Miller, L. P. (2012). Will extreme climatic events facilitate biological invasions? *Frontiers in Ecology and the Environment*, *10*(5), 249–257. https://doi.org/10.1890/110137

Dobretsov, S., Coutinho, R., Rittschof, D., Salta, M., Ragazzola, F., & Hellio, C. (2019). The oceans are changing: Impact of ocean warming and acidification on biofouling communities. *Biofouling*, *35*(5), 585–595. https://doi.org/10.1080/08927014.2019.1624727

Early, R., Bradley, B. A., Dukes, J. S., Lawler, J. J., Olden, J. D., Blumenthal, D. M., Gonzalez, P., Grosholz, E. D., Ibañez, I., Miller, L. P., Sorte, C. J. B., & Tatem, A. J. (2016). Global threats from invasive alien species in the twenty-first century and national response capacities. *Nature Communications*, *7*, 12485. https://doi.org/10.1038/ncomms12485

Ehrenfeld, J. G. (2010). Ecosystem consequences of biological invasions. *Annual Review of Ecology, Evolution, and Systematics*, *41*(1), 59–80. https://doi.org/10.1146/annurev-ecolsys-102209-144650

Epstein, G., Foggo, A., & Smale, D. A. (2019). Inconspicuous impacts: Widespread marine invader causes subtle but significant changes in native macroalgal assemblages. *Ecosphere*, *10*(7), e02814. https://doi.org/10.1002/ecs2.2814

Gade, H. G., Edwards, A. J., & Svendsen, H. (1983). *Coastal oceanography*. Springer Science.

Gillanders, B. M., & Kingsford, M. J. (2002). Impact of changes in flow of freshwater on estuarine and open coastal habitats and the associated organisms. *Oceanography and Marine Biology, An Annual Review*, *40*(40), 233. https://doi.org/10.1201/9780203180594.ch5

Graba-Landry, A., Hoey, A. S., Matley, J. K., Sheppard-Brennand, H., Poore, A. G. B., Byrne, M., & Dworjanyn, S. A. (2018). Ocean warming has greater and more consistent negative effects than ocean acidification on the growth and health of subtropical macroalgae. *Marine Ecology Progress Series*, *595*, 55–69. https://doi.org/10.3354/meps12552

Gröner, F., Lenz, M., Wahl, M., & Jenkins, S. R. (2011). Stress resistance in two colonial ascidians from the Irish Sea: The recent invader *Didemnum vexillum* is more tolerant to low salinity than the cosmopolitan *Diplosoma listerianum*. *Journal of Experimental Marine Biology and Ecology*, *409*(1–2), 48–52. https://doi.org/10.1016/j.jembe.2011.08.002

Harris, M., Moore, A., Lowen, B., & DiBacco, C. (2017). Seasonal reproduction of the non-native vase tunicate *Ciona intestinalis* (Linnaeus, 1767) in Nova Scotia, Canada, in relation to water temperature. *Aquatic Invasions*, *12*(1), 33–41. https://doi.org/10.3391/ai.2017.12.1.04

Harvey, B. P., Gwynn-Jones, D., & Moore, P. J. (2013). Meta-analysis reveals complex marine biological responses to the interactive effects of ocean acidification and warming. *Ecology and Evolution*, *3*(4), 1016–1030. https://doi.org/10.1002/ece3.516

Hedges, L. V., & Olkin, I. (1985). *Statistical methods for meta-analysis*. Academic Press.

Hellmann, J. J., Byers, J. E., Bierwagen, B. G., & Dukes, J. S. (2008). Five potential consequences of climate change for invasive species. *Conservation Biology*, *22*(3), 534–543. https://doi.org/10.1111/j.1523-1739.2008.00951.x

Higgins, J. P. T., Thompson, S. G., Deeks, J. J., & Altman, D. G.(2003). Measuring inconsistency in meta-analyses. *British Medical Journal*, *327*, 557–560. https://doi.org/10.1136/bmj.327.7414.557

Hillebrand, H. (2011). Temperature mediates competitive exclusion and diversity in benthic microalgae under different N: P stoichiometry. *Ecological Research*, *26*(3), 533–539. https://doi.org/10.1007/s11284-011-0810-y

Hofmann, G. E., & Todgham, A. E. (2010). Living in the now: Physiological mechanisms to tolerate a rapidly changing environment. *Annual Review of Physiology*, *72*, 127–145. https://doi.org/10.1146/annurev-physiol-021909-135900

Hudson, J., McQuaid, C. D., & Rius, M. (2020). Contemporary climate change hinders hybrid performance of ecologically dominant marine invertebrates. *Journal of Evolutionary Biology*, *34*, 60–72. https://doi.org/10.1111/jeb.13609

Hulme, P. E. (2017). Climate change and biological invasions: Evidence, expectations, and response options. *Biological Reviews of the Cambridge Philosophical Society*, *92*(3), 1297–1313. https://doi.org/10.1111/brv.12282

Karatayev, A. Y., Burlakova, L. E., & Padilla, D. K. (2014). Zebra versus quagga mussels: A review of their spread, population dynamics, and ecosystem impacts. *Hydrobiologia*, *746*(1), 97–112. https://doi.org/10.1007/s10750-014-1901-x

Katsanevakis, S., Wallentinus, I., Zenetos, A., Leppäkoski, E., Çinar, M. E., Oztürk, B., Grabowski, M., Golani, D., & Cardoso, A. C. (2014). Impacts of invasive alien marine species on ecosystem services and biodiversity: A pan-European review. *Aquatic Invasions*, *9*(4), 391–423. https://doi.org/10.3391/ai.2014.9.4.01

Kordas, R. L., Dudgeon, S., Storey, S., & Harley, C. D. G. (2015). Intertidal community responses to field-based experimental warming. *Oikos*, *124*(7), 888–898. https://doi.org/10.1111/oik.00806

Kumschick, S., Gaertner, M., Vilà, M., Essl, F., Jeschke, J. M., Pyšek, P., Ricciardi, A., Bacher, S., Blackburn, T. M., Dick, J. T. A., Evans, T., Hulme, P. E., Kühn, I., Mrugała, A., Pergl, J., Rabitsch, W., Richardson, D. M., Sendek, A., & Winter, M. (2014). Ecological impacts of alien species: Quantification, scope, caveats, and recommendations. *BioScience*, *65*(1), 55–63. https://doi.org/10.1093/biosci/biu193

Lawrence, A. J., & Soame, J. M. (2004). The effects of climate change on the reproduction of coastal invertebrates. *Ibis*, *14*, 29–39. https://doi.org/10.1111/j.1474-919X.2004.00325.x

Layton, C., Shelamoff, V., Cameron, M. J., Tatsumi, M., Wright, J. T., & Johnson, C. R. (2019). Resilience and stability of kelp forests: The importance of patch dynamics and environment-engineer feedbacks. *PLoS ONE*, *14*(1), e0210220. https://doi.org/10.1371/journal.pone.0210220

Martin, L. J., Blossey, B., & Ellis, E. (2012). Mapping where ecologists work: Biases in the global distribution of terrestrial ecological observations. *Frontiers in Ecology and the Environment*, *10*(4), 195–201. https://doi.org/10.1890/110154

Martínez, M. L., Intralawan, A., Vázquez, G., Pérez-Maqueo, O., Sutton, P., & Landgrave, R. (2007). The coasts of our world: Ecological, economic and social importance. *Ecological Economics*, *63*(2–3), 254–272. https://doi.org/10.1016/j.ecolecon.2006.10.022

McKnight, E., Garcia-Berthou, E., Srean, P., & Rius, M. (2016). Global meta-analysis of native and nonindigenous trophic traits in aquatic ecosystems. *Global Change Biology*, *23*, 1861–1870. https://doi.org/10.1111/gcb.13524

Newcomer, K., Marraffini, M. L., Chang, A. L. (2018). Distribution patterns of the introduced encrusting bryozoan *Conopeum chesapeakensis* (Osburn 1944; Banta et al. 1995) in an estuarine environment in upper San Francisco Bay. *Journal of Experimental Marine Biology and Ecology*, *504*, 20–31. https://doi.org/10.1016/j.jembe.2018.04.001

Occhipinti-Ambrogi, A. (2007). Global change and marine communities: Alien species and climate change. *Marine Pollution Bulletin*, *55*(7–9), 342–352. https://doi.org/10.1016/j.marpolbul.2006.11.014

O'Connor, M. I., Bruno, J. F., Gaines, S. D., Halpern, B. S., Lester, S. E., Kinlan, B. P., & Weiss, J. M. (2007). Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proceedings of the National Academy of Sciences USA*, *104*(4), 1266–1271. https://doi.org/10.1073/pnas.0603422104

Oliver, E. C. J., Burrows, M. T., Donat, M. G., Sen Gupta, A., Alexander, L. V., Perkins-Kirkpatrick, S. E., Benthuysen, J. A., Hobday, A. J., Holbrook, N. J., Moore, P. J., & Thomsen, M. S. (2019). Projected marine heatwaves in the 21st century and the potential for ecological impact. *Frontiers in Marine Science*, *6*, 734. https://doi.org/10.3389/fmars.2019.00734

Pandori, L. L. M., & Sorte, C. J. B. (2018). The weakest link: Sensitivity to climate extremes across life stages of marine invertebrates. *Oikos*, *128*(5), 621–629. https://doi.org/10.1111/oik.05886

Pecl, G. T., Araujo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I. C., Clark, T. D., Colwell, R. K., Danielsen, F., Evengård, B., & Falconi, L. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, *355*(355), 6332. https://doi.org/10.1126/science.aai9214

Pfleiderer, P., Schleussner, C.-F., Kornhuber, K., & Coumou, D. (2019). Summer weather becomes more persistent in a 2 °C world. *Nature Climate Change*, *9*(9), 666–671. https://doi.org/10.1038/s41558-019-0555-0

Pineda, M. C., McQuaid, C. D., Turon, X., Lopez-Legentil, S., Ordonez, V., & Rius, M. (2012). Tough adults, frail babies: An analysis of stress sensitivity across early life-history stages of widely introduced marine invertebrates. *PLoS ONE*, *7*(10), e46672. https://doi.org/10.1371/journal.pone.0046672

Poore, A. G. B., Graham, S. E., Byrne, M., & Dworjanyn, S. A. (2016). Effects of ocean warming and lowered pH on algal growth and palatability to a grazing gastropod. *Marine Biology*, *163*(5), 1–11. https://doi.org/10.1007/s00227-016-2878-y

Pyšek, P., Jarošík, V., Hulme, P. E., Pergl, J., Hejda, M., Schaffner, U., & Vilà, M. (2012). A global assessment of invasive plant impacts on resident species, communities and ecosystems: The interaction of impact measures, invading species' traits and environment. *Global Change Biology*, *18*(5), 1725–1737. https://doi.org/10.1111/j.1365-2486.2011.02636.x

R Core Team (2018). *R: A language and environment for statistical computing*. The R Development Core Team. http://www.r-project.org

Rivera-Ingraham, G. A., & Lignot, J. H. (2017). Osmoregulation, bioenergetics and oxidative stress in coastal marine invertebrates: Raising the questions for future research. *The Journal of Experimental Biology*, *220*(10), 1749–1760. https://doi.org/10.1242/jeb.135624

Rosenberg, M., Rothstein, H. R., & Gurevitch, J. (2013). Effect sizes: Conventional choices and calculations. In J. Koricheva, J. Gurevitch & K. Mengersen (Eds.), *Handbook of meta-analysis in ecology and evolution* (pp. 61–71). Princeton University Press.

Rothausler, E., Rugiu, L., & Jormalainen, V. (2018). Forecast climate change conditions sustain growth and physiology but hamper reproduction in range-margin populations of a foundation rockweed species. *Marine Environmental Research*, *141*, 205–213. https://doi.org/10.1016/j.marenvres.2018.09.014

Scherner, F., Ventura, R., Barufi, J. B., & Horta, P. A. (2013). Salinity critical threshold values for photosynthesis of two cosmopolitan seaweed species: Providing baselines for potential shifts on seaweed assemblages. *Marine Environmental Research*, *91*, 14–25. https://doi.org/10.1016/j.marenvres.2012.05.007

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, *1*(2), 103–113. https://doi.org/10.1111/j.2041-210X.2010.00012.x

Schoenrock, K. M., Schram, J. B., Amsler, C. D., McClintock, J. B., Angus, R. A., & Vohra, Y. K. (2016). Climate change confers a potential advantage to fleshy Antarctic crustose macroalgae over calcified species. *Journal of Experimental Marine Biology and Ecology*, *474*, 58–66. https://doi.org/10.1016/j.jembe.2015.09.009

Senior, A. M., Grueber, C. E., Kamiya, T., Lagisz, M., O'Dwyer, K., Santos, E. S. A., & Nakagawa, S. (2016). Heterogeneity in ecological and evolutionary meta-analyses: Its magnitude and implications. *Statistical Reports*, *97*(12), 3293–3299. https://doi.org/10.1002/ecy.1591

Smale, D. A., & Wernberg, T. (2012). Short-term in situ warming influences early development of sessile assemblages. *Marine Ecology Progress Series*, *453*, 129–136. https://doi.org/10.3354/meps09680

Smale, D. A., & Wernberg, T. (2013). Extreme climatic event drives range contraction of a habitat-forming species. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1754), 20122829. https://doi.org/10.1098/rspb.2012.2829

Smale, D. A., Wernberg, T., Oliver, E. C. J., Thomsen, M. S., Harvey, B. P., Straub, S. C., Burrows, M. T., Alexander, L. V., Benthuysen, J. A., Donat, M. G., & Feng, M. (2019). Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nature Climate Change*, 306–312. https://doi.org/10.1038/s41558-019-0412-1

Smyth, K., & Elliott, M. (2016). Effects of changing salinity on the ecology of the marine environment. In M. Solan & N. Whiteley (Eds.), *Stressors in the Marine Environment: Physiological and Ecological Responses; Societal Implications* (pp. 161–174). Oxford, GB: Oxford University Press.

Somero, G. N. (2010). The physiology of climate change: How potentials for acclimatization and genetic adaptation will determine "winners" and "losers". *The Journal of Experimental Biology*, *213*(6), 912–920. https://doi.org/10.1242/jeb.037473

Sorte, C. J., Ibanez, I., Blumenthal, D. M., Molinari, N. A., Miller, L. P., Grosholz, E. D., Diez, J. M., D'Antonio, C. M., Olden, J. D., Jones, S. J., & Dukes, J. S. (2013). Poised to prosper? A cross-system comparison of climate change effects on native and non-native species performance. *Ecology Letters*, *16*(2), 261–270. https://doi.org/10.1111/ele.12017

Stephens, K. L., Dantzler-Kyer, M. E., Patten, M. A., & Souza, L. (2019). Differential responses to global change of aquatic and terrestrial invasive species: Evidences from a meta-analysis. *Ecosphere*, *10*(4), e02680. https://doi.org/10.1002/ecs2.2680

Stott, P. A., Christidis, N., Otto, F. E., Sun, Y., Vanderlinden, J. P., van Oldenborgh, G. J., Vautard, R., von Storch, H., Walton, P., Yiou, P., & Zwiers, F. W. (2016). Attribution of extreme weather and climate-related events. *Wiley Interdisciplinary Reviews Climate Change*, *7*(1), 23–41. https://doi.org/10.1002/wcc.380

Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., Helaouet, P., Johns, D. G., Jones, I. D., Leech, D. I., & Mackay, E. B. (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature*, *535*(7611), 241–245. https://doi.org/10.1038/nature18608

Tummers, B. (2006). *DataThief III*. https://datathief.org/

Ummenhofer, C. C., & Meehl, G. A. (2017). Extreme weather and climate events with ecological relevance: A review. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1723), 20160135. https://doi.org/10.1098/rstb.2016.0135

Velasco, J., Gutierrez-Canovas, C., Botella-Cruz, M., Sanchez-Fernandez, D., Arribas, P., Carbonell, J. A., Millán, A., & Pallares, S. (2018). Effects of salinity changes on aquatic organisms in a multiple stressor context. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *374*(1764), 20180011. https://doi.org/10.1098/rstb.2018.0011

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, *36*(3), 1–48. https://doi.org/10.18637/jss.v036.i03

Vila, M., Espinar, J. L., Hejda, M., Hulme, P. E., Jarosik, V., Maron, J. L., Pergl, J., Schaffner, U., Sun, Y., & Pysek, P. (2011). Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, *14*(7), 702–708. https://doi.org/10.1111/j.1461-0248.2011.01628.x

Wernberg, T., Bennett, S., Babcock, R. C., Bettignies, T., Cure, K., Depczynski, M., Dufois, F., Fromont, J., Fulton, C. J., Hovey, R. K., & Harvey, E. S. (2016). Climate driven regime shift of a temperate marine ecosystem. *Science*, *353*(6295), 169–172. https://doi.org/10.1126/science.aad8745

Wernberg, T., Smale, D. A., Tuya, F., Thomsen, M. S., Langlois, T. J., de Bettignies, T., Bennett, S., & Rousseaux, C. S. (2013). An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nature Climate Change*, *3*(1), 78–82. https://doi.org/10.1038/nclimate1627

Werner, F. J., Graiff, A., & Matthiessen, B. (2016). Temperature effects on seaweed-sustaining top-down control vary with season. *Oecologia*, *180*(3), 889–901. https://doi.org/10.1007/s00442-015-3489-x

Wilkinson, M., Wood, P., Wells, E., & Scanlan, C. (2007). Using attached macroalgae to assess ecological status of British estuaries for the European Water Framework Directive. *Marine Pollution Bulletin*, *55*(1–6), 136–150. https://doi.org/10.1016/j.marpolbul.2006.09.004

Wolkovich, E. M., & Cleland, E. E. (2010). The phenology of plant invasions: A community ecology perspective. *Frontiers in Ecology and the Environment*, *9*(5), 287–294. https://doi.org/10.1890/100033

Yang, C. Y., Sierp, M. T., Abbott, C. A., Li, Y., & Qin, J. G. (2016). Responses to thermal and salinity stress in wild and farmed Pacific oysters *Crassostrea gigas*. *Comparative Biochemistry and Physiology*, *201*, 22–29. https://doi.org/10.1016/j.cbpa.2016.06.024

BIOSKETCH

The research interests of this team include macroecology, community ecology, invasion science and global change biology. The shared interests in these fields were combined to advance our understanding of future changes on coastal benthic communities. More detailed profiles can be found on the following individual web pages: www.riuslab.com, https://www.physiologicaldiversitylab.com/, https://www.mba.ac.uk/fellows/smale-group, https://www.southampton.ac.uk/geography/about/staff/rs15g08.page.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

How to cite this article: McKnight E, Spake R, Bates A, Smale DA, Rius M. Non-native species outperform natives in coastal marine ecosystems subjected to warming and freshening events. *Global Ecol Biogeogr*. 2021;00:1–15. https://doi.org/10.1111/geb.13318

APPENDIX

DATA SOURCES

Ab Lah, R., Kelaher, B. P., Bucher, D., & Benkendorff, K. (2018). Ocean warming and acidification affect the nutritional quality of the commercially-harvested turbinid snail *Turbo militaris*. *Marine Environmental Research*, *141*, 100–108. https://doi.org/10.1016/j.marenvres.2018.08.009

Agius, B. P. (2007). Spatial and temporal effects of pre-seeding plates with invasive ascidians: Growth, recruitment and community composition. *Journal of Experimental Marine Biology and Ecology*, *342*(1), 30–39. https://doi.org/10.1016/j.jembe.2006.10.012

Basso, L., Hendriks, I., Steckbauer, A., & Duarte, C. (2015). Resistance of juveniles of the Mediterranean pen shell, (*Pinna nobilis*) to hypoxia and interaction with warming. *Estuarine, Coastal and Shelf Science*, *165*, 199–203. https://doi.org/10.1016/j.ecss.2015.05.016

Bender, D., Diaz-Pulido, G., & Dove, S. (2014a). Warming and acidification promote cyanobacterial dominance in turf algal assemblages. *Marine Ecology Progress Series*, *517*, 271–284. https://doi.org/10.3354/meps11037

Bender, D., Diaz-Pulido, G., & Dove, S. (2014b). The impact of CO2 emission scenarios and nutrient enrichment on a common coral reef macroalga is modified by temporal effects. *Journal of Phycology*, *50*(1), 203–215. https://doi.org/10.1111/jpy.12153

Bennett, S., Wernberg, T., Arackal Joy, B., de Bettignies, T., & Campbell, A. H. (2015). Central and rear-edge populations can be equally vulnerable to warming. *Nature Communications*, *6*, 10280. https://doi.org/10.1038/ncomms10280

Bergmann, N., Winters, G., Rauch, G., Eizaguirre, C., Gu, J., Nelle, P., Fricke, B., & Reusch, T. B. (2010). Population-specificity of heat stress gene induction in northern and southern eelgrass *Zostera marina* populations under simulated global warming. *Molecular Ecology*, *19*(14), 2870–2883. https://doi.org/10.1111/j.1365-294X.2010.04731.x

Best, R. J., Stone, M. N., Stachowicz, J. J., & Beaumont, L. (2015). Predicting consequences of climate change for ecosystem functioning: Variation across trophic levels, species and individuals. *Diversity and Distributions*, *21*(12), 1364–1374. https://doi.org/10.1111/ddi.12367

Bible, J. M., Cheng, B. S., Chang, A. L., Ferner, M. C., Wasson, K., Zabin, C. J., Latta, M., Sanford, E., Deck, A., & Grosholz, E. D. (2017). Timing of stressors alters interactive effects on a coastal foundation species. *Ecology*, *98*(9), 2468–2478. https://doi.org/10.1002/ecy.1943

Bible, J. M., & Sanford, E. (2016). Local adaptation in an estuarine foundation species: Implications for restoration. *Biological Conservation*, *193*, 95–102. https://doi.org/10.1016/j.biocon.2015.11.015

Biscere, T., Lorrain, A., Rodolfo-Metalpa, R., Gilbert, A., Wright, A., Devissi, C., Peignon, C., Farman, R., Duvieilbourg, E., Payri, C., & Houlbreque, F. (2017). Nickel and ocean warming affect scleractinian coral growth. *Marine Pollution Bulletin*, *120*(1–2), 250–258. https://doi.org/10.1016/j.marpolbul.2017.05.025

Bollen, M., Pilditch, C. A., Battershill, C. N., & Bischof, K. (2016). Salinity and temperature tolerance of the invasive alga *Undaria pinnatifida* and native New Zealand kelps: Implications for competition. *Marine Biology*, *163*(9), 163–194. https://doi.org/10.1007/s00227-016-2954-3

Brown, M. B., Edwards, M. S., & Kim, K. Y. (2014). Effects of climate change on the physiology of giant kelp, *Macrocystis pyrifera*, and grazing by purple urchin, *Strongylocentrotus purpuratus*. *Algae*, *29*(3), 203–215. https://doi.org/10.4490/algae.2014.29.3.203

Burgess, S. C., & Marshall, D. J. (2011). Temperature-induced maternal effects and environmental predictability. *Journal of Experimental Biology*, *214*(14), 2329–2336. https://doi.org/10.1242/jeb.054718

Bussell, J. A., Gidman, E. A., Causton, D. R., Gwynn-Jones, D., Malham, S. K., Jones, M. L. M., Reynolds, B., & Seed, R. (2008). Changes in the immune response and metabolic fingerprint of the mussel, *Mytilus edulis* (Linnaeus) in response to lowered salinity and physical stress. *Journal of Experimental Marine Biology and Ecology*, *358*(1), 78–85. https://doi.org/10.1016/j.jembe.2008.01.018

Campbell, J. E., Fisch, J., Langdon, C., & Paul, V. J. (2015). Increased temperature mitigates the effects of ocean acidification in calcified green algae (*Halimeda* spp.). *Coral Reefs*, *35*(1), 357–368. https://doi.org/10.1007/s00338-015-1377-9

Capdevila, P., Hereu, B., Salguero-Gómez, R., Rovira, G. l., Medrano, A., Cebrian, E., Garrabou, J., Kersting, D. K., Linares, C., & Hughes, A. R. (2018). Warming impacts on early life stages increase the vulnerability and delay the population recovery of a long-lived habitat-forming macroalga. *Journal of Ecology*, *107*(3), 1129–1140. https://doi.org/10.1111/1365-2745.13090

Cebrian, E., Uriz, M. J., Garrabou, J., & Ballesteros, E. (2011). Sponge mass mortalities in a warming Mediterranean Sea: Are cyanobacteria-harboring species worse off? *PLoS ONE*, *6*(6), e20211. https://doi.org/10.1371/journal.pone.0020211

Chakravarti, L. J., Jarrold, M. D., Gibbin, E. M., Christen, F., Massamba-N'Siala, G., Blier, P. U., & Calosi, P. (2016). Can trans-generational experiments be used to enhance species resilience to ocean warming and acidification? *Evolutionary Applications*, *9*(9), 1133–1146. https://doi.org/10.1111/eva.12391

Chan, V. B., Thiyagarajan, V., Lu, X. W., Zhang, T., & Shih, K. (2013). Temperature dependent effects of elevated CO2 on shell composition and mechanical properties of *Hydroides elegans*: Insights from a multiple stressor experiment. *PLoS ONE*, *8*(11), e78945. https://doi.org/10.1371/journal.pone.0078945

Chen, B., & Zou, D. (2014). Growth and photosynthetic activity of *Sargassum henslowianum* (Fucales, Phaeophyta) seedlings in responses to different light intensities, temperatures and CO2 levels under laboratory conditions. *Marine Biology Research*, *10*(10), 1019–1026. https://doi.org/10.1080/17451000.2013.872798

Cheng, B. S., Bible, J. M., Chang, A. L., Ferner, M. C., Wasson, K., Zabin, C. J., Latta, M., Deck, A., Todgham, A. E., & Grosholz, E. D. (2015). Testing local and global stressor impacts on a coastal foundation species using an ecologically realistic framework. *Global Change Biology*, *21*, 2488–249. https://doi.org/10.1111/gcb.12895

Chi, X., Mueller-Navarra, D. C., Hylander, S., Sommer, U., & Javidpour, J. (2019). Food quality matters: Interplay among food quality, food quantity and temperature affecting life history traits of *Aurelia aurita* (Cnidaria: Scyphozoa) polyps. *Science of The Total Environment*, *656*, 1280–1288. https://doi.org/10.1016/j.scitotenv.2018.11.469

Cockrell, M. L., & Sorte, C. J. B. (2013). Predicting climate-induced changes in population dynamics of invasive species in a marine epibenthic community. *Journal of Experimental Marine Biology and Ecology*, *440*, 42–48. https://doi.org/10.1016/j.jembe.2012.11.008

De Marchi, L., Neto, V., Pretti, C., Chiellini, F., Morelli, A., Soares, A., Figueira, E., & Freitas, R. (2019). The influence of climate change on the fate and behavior of different carbon nanotubes materials and implication to estuarine invertebrates. *Comparative Biochemistry and Physiology*, *219*, 103–115. https://doi.org/10.1016/j.cbpc.2019.02.008

De Marchi, L., Neto, V., Pretti, C., Figueira, E., Chiellini, F., Morelli, A., Soares, A. M., & Freitas, R. (2018). Effects of multi-walled carbon nanotube materials on *Ruditapes philippinarum* under climate change: The case of salinity shifts. *Aquatic Toxicology*, *199*, 199–211. https://doi.org/10.1016/j.aquatox.2018.04.001

Duarte, C., Navarro, J. M., Acuña, K., Torres, R., Manríquez, P. H., Lardies, M. A., Vargas, C. A., Lagos, N. A., & Aguilera, V. (2014). Combined effects of temperature and ocean acidification on the juvenile individuals of the mussel *Mytilus chilensis*. *Journal of Sea Research*, *85*, 308–314. https://doi.org/10.1016/j.seares.2013.06.002

Ehlers, A., Worm, B., & Reusch, T. B. H. (2008). Importance of genetic diversity in eelgrass *Zostera marina* for its resilience to global warming. *Marine Ecology Progress Series*, *355*, 1–7. https://doi.org/10.3354/meps07369

Ellis, R. P., Widdicombe, S., Parry, H., Hutchinson, T. H., & Spicer, J. I. (2015). Pathogenic challenge reveals immune trade-off in mussels exposed to reduced seawater pH and increased temperature. *Journal of Experimental Marine Biology and Ecology*, *462*, 83–89. https://doi.org/10.1016/j.jembe.2014.10.015

Eriksson Wiklund, A. K., Dahlgren, K., Sundelin, B., & Andersson, A. (2009). Effects of warming and shifts of pelagic food web structure on benthic productivity in a coastal marine system. *Marine Ecology Progress Series*, *396*, 13–25. https://doi.org/10.3354/meps08290

Figueiredo, J., Baird, A. H., Harii, S., & Connolly, S. R. (2014). Increased local retention of reef coral larvae as a result of ocean warming. *Nature Climate Change*, *4*(6), 498–502. https://doi.org/10.1038/nclimate2210

Figueroa, F. L., Bonomi Barufi, J., Malta, E. J., Conde-Álvarez, R., Nitschke, U., Arenas, F., Mata, M., Connan, S., Abreu, M. H., Marquardt, R., & Stengel, D. B. (2014). Short-term effects of increasing CO2, nitrate and temperature on three Mediterranean macroalgae: Biochemical composition. *Aquatic Biology*, *22*, 177–193. https://doi.org/10.3354/ab00610

Gaitán-Espitia, J. D., Hancock, J. R., Padilla-Gamiño, J. L., Rivest, E. B., Blanchette, C. A., Reed, D. C., & Hofmann, G. E. (2014). Interactive effects of elevated temperature and pCO2 on early-life-history stages of the giant kelp *Macrocystis pyrifera*. *Journal of Experimental Marine Biology and Ecology*, *457*, 51–58. https://doi.org/10.1016/j.jembe.2014.03.018

Gao, G., Clare, A. S., Rose, C., & Caldwell, G. S. (2018). Ulva rigida in the future ocean: Potential for carbon capture, bioremediation and biomethane production. *Global Change Biology Bioenergy*, *10*(1), 39–51. https://doi.org/10.1111/gcbb.12465

Gao, X., Endo, H., & Agatsuma, Y. (2017). Comparative study on the physiological differences between three Chaetomorpha species from Japan in preparation for cultivation. *Journal of Applied Phycology*, *30*(2), 1167–1174. https://doi.org/10.1007/s10811-017-1306-0

Gao, X., Kim, J. H., Park, S. K., Yu, O. H., Kim, Y. S., & Choi, H. G. (2019). Diverse responses of sporophytic photochemical efficiency and gametophytic growth for two edible kelps, *Saccharina japonica* and *Undaria pinnatifida*, to ocean acidification and warming. *Marine Pollution Bulletin*, *142*, 315–320. https://doi.org/10.1016/j.marpolbul.2019.03.063

Gestoso, I., Arenas, F., & Olabarria, C. (2016). Ecological interactions modulate responses of two intertidal mussel species to changes in temperature and pH. *Journal of Experimental Marine Biology and Ecology*, *474*, 116–125. https://doi.org/10.1016/j.jembe.2015.10.006

Gouvea, L. P., Schubert, N., Martins, C. D. L., Sissini, M., Ramlov, F., Rodrigues, E. R. O., Bastos, E. O., Freire, V. C., Maraschin, M., Carlos Simonassi, J., & Varela, D. A. (2017). Interactive effects of marine heatwaves and eutrophication on the ecophysiology of a widespread and ecologically important macroalga. *Limnology and Oceanography*, *62*, 2056–2075. https://doi.org/10.1002/lno.10551

Graba-Landry, A., Hoey, A. S., Matley, J. K., Sheppard-Brennand, H., Poore, A. G. B., Byrne, M., & Dworjanyn, S. A. (2018). Ocean warming has greater and more consistent negative effects than ocean acidification on the growth and health of subtropical macroalgae. *Marine Ecology Progress Series*, *595*, 55–69. https://doi.org/10.3354/meps12552

Gröner, F., Lenz, M., Wahl, M., & Jenkins, S. R. (2011). Stress resistance in two colonial ascidians from the Irish Sea: The recent invader *Didemnum vexillum* is more tolerant to low salinity than the cosmopolitan *Diplosoma listerianum*. *Journal of Experimental Marine Biology and Ecology*, *409*(1–2), 48–52. https://doi.org/10.1016/j.jembe.2011.08.002

Gutow, L., Rahman, M. M., Bartl, K., Saborowski, R., Bartsch, I., & Wiencke, C. (2014). Ocean acidification affects growth but not nutritional quality of the seaweed *Fucus vesiculosus* (Phaeophyceae, Fucales). *Journal of Experimental Marine Biology and Ecology*, *453*, 84–90. https://doi.org/10.1016/j.jembe.2014.01.005

Hargrave, M. S., Foggo, A., Pessarrodona, A., & Smale, D. A. (2016). The effects of warming on the ecophysiology of two co-existing kelp species with contrasting distributions. *Oecologia*. https://doi.org/10.1007/s00442-016-3776-1

Huggett, M. J., McMahon, K., & Bernasconi, R. (2018). Future warming and acidification result in multiple ecological impacts to a temperate coralline alga. *Environmental Microbiology*, *20*(8), 2769–2782. https://doi.org/10.1111/1462-2920.14113

Jenewein, B. T., & Gosselin, L. A. (2013). Ontogenetic shift in stress tolerance thresholds of *Mytilus trossulus*: Effects of desiccation and heat on juvenile mortality. *Marine Ecology Progress Series*, *481*, 147–159. https://doi.org/10.3354/meps10221

Kaniewska, P., Chan, C. K., Kline, D., Ling, E. Y., Rosic, N., Edwards, D., Hoegh-Guldberg, O., & Dove, S. (2015). Transcriptomic changes in coral holobionts provide insights into physiological challenges of future climate and ocean change. *PLoS ONE*, *10*(10), e0139223. https://doi.org/10.1371/journal.pone.0139223

Kenworthy, J. M., Davoult, D., & Lejeusne, C. (2018). Compared stress tolerance to short-term exposure in native and invasive tunicates from the NE Atlantic: When the invader performs better. *Marine Biology*, *165*(10), 1-11. https://doi.org/10.1007/s00227-018-3420-1

King, N. G., Wilcockson, D. C., Webster, R., Smale, D. A., Hoelters, L. S., & Moore, P. J. (2018). Cumulative stress restricts niche filling potential of habitat-forming kelps in a future climate. *Functional Ecology*, *32*(2), 288–299. https://doi.org/10.1111/1365-2435.12977

Kordas, R. L., & Harley, C. D. G. (2016). Demographic responses of coexisting species to in situ warming. *Marine Ecology Progress Series*, *546*, 147–161. https://doi.org/10.3354/meps11620

Kram, S. L., Price, N. N., Donham, E. M., Johnson, M. D., Kelly, E. L. A., Hamilton, S. L., & Smith, J. E. (2016). Variable responses of temperate calcified and fleshy macroalgae to elevated *p*CO2 and warming. *ICES Journal of Marine Science*, *73*(3), 693–703. https://doi.org/10.1093/icesjms/fsv168

Lagos, N. A., Benítez, S., Duarte, C., Lardies, M. A., Broitman, B. R., Tapia, C., Widdicombe, S., & Vargas, C. A. (2016). Effects of temperature and ocean acidification on shell characteristics of *Argopecten purpuratus*: Implications for scallop aquaculture in an upwelling-influenced area. *Aquaculture Environment Interactions*, *8*, 357–370. https://doi.org/10.3354/aei00183

Li, H., Monteiro, C., Heinrich, S., Bartsch, I., Valentin, K., Harms, L., Glockner, G., Corre, E., & Bischof, K. (2019). Responses of the kelp

Saccharina latissima (Phaeophyceae) to the warming Arctic: From physiology to transcriptomics. *Physiologia Plantarum,168*(1), 5–26. https://doi.org/10.1111/ppl.13009

Li, S., Huang, J., Liu, C., Liu, Y., Zheng, G., Xie, L., & Zhang, R. (2016). Interactive effects of seawater acidification and elevated temperature on the transcriptome and biomineralization in the pearl oyster *Pinctada fucata*. *Environmental Science Technology*, *50*(3), 1157–1165. https://doi.org/10.1021/acs.est.5b05107

Lind, A. C., & Konar, B. (2017). Effects of abiotic stressors on kelp early life-history stages. *Algae*, *32*(3), 223–233. https://doi.org/10.4490/algae.2017.32.8.7

Liu, C., & Zou, D. (2014). Do increased temperature and CO2 levels affect the growth, photosynthesis, and respiration of the marine macroalga *Pyropia haitanensis* (Rhodophyta)? An experimental study. *Hydrobiologia*, *745*(1), 285–296. https://doi.org/10.1007/s10750-014-2113-0

Lockwood, B. L., Sanders, J. G., & Somero, G. N. (2010). Transcriptomic responses to heat stress in invasive and native blue mussels (genus Mytilus): Molecular correlates of invasive success. *Journal of Experimental Biology*, *213*(20), 3548–3558. https://doi.org/10.1242/jeb.046094

Lopes, A. R., Faleiro, F., Rosa, I. C., Pimentel, M. S., Trubenbach, K., Repolho, T., Diniz, M., & Rosa, R. (2018). Physiological resilience of a temperate soft coral to ocean warming and acidification. *Cell Stress Chaperones*, *23*(5), 1093–1100. https://doi.org/10.1007/s12192-018-0919-9

Lord, J., & Whitlatch, R. (2015). Predicting competitive shifts and responses to climate change based on latitudinal distributions of species assemblages. *Ecology*, *96*(5), 1264–1274. https://doi.org/10.1890/14-0403.1

Lord, J. P., Barry, J. P., & Graves, D. (2017). Impact of climate change on direct and indirect species interactions. *Marine Ecology Progress Series*, *571*, 1–11. https://doi.org/10.3354/meps12148

Mabin, C. J. T., Johnson, C. R., & Wright, J. T. (2019). Physiological response to temperature, light, and nitrates in the giant kelp *Macrocystis pyrifera*, from Tasmania, Australia. *Marine Ecology Progress Series*, *614*, 1–19. https://doi.org/10.3354/meps12900

Madariaga, D. J., Rivadeneira, M. M., Tala, F., & Thiel, M. (2014). Environmental tolerance of the two invasive species *Ciona intestinalis* and *Codium fragile*: Their invasion potential along a temperate coast. *Biological Invasions*, *16*, 2507–2527. https://doi.org/10.1007/s10530-014-0680-7

Madeira, C., Mendonça, V., Flores, A. A. V., Diniz, M. S., & Vinagre, C. (2018). High thermal tolerance does not protect from chronic warming—A multiple end-point approach using a tropical gastropod, *Stramonita haemastoma*. *Ecological Indicators*, *91*, 626–635. https://doi.org/10.1016/j.ecolind.2018.04.044

Magalhaes, L., de Montaudouin, X., Figueira, E., & Freitas, R. (2018). Trematode infection modulates cockles biochemical response to climate change. *Science of The Total Environment*, *637–638*, 30–40. https://doi.org/10.1016/j.scitotenv.2018.04.432

Malfant, M., Coudret, J., Le Merdy, R., & Viard, F. (2017). Effects of temperature and salinity on juveniles of two ascidians, one native and one invasive, and their hybrids. *Journal of Experimental Marine Biology and Ecology*, *497*, 180–187. https://doi.org/10.1016/j.jembe.2017.09.019

Martinez, B., Arenas, F., Rubal, M., Burgues, S., Esteban, R., Garcia-Plazaola, I., Figueroa, F. L., Pereira, R., Saldana, L., Sousa-Pinto, I., Trilla, A., & Viejo, R. M. (2012). Physical factors driving intertidal macroalgae distribution: Physiological stress of a dominant fucoid at its southern limit. *Oecologia*, *170*(2), 341–353. https://doi.org/10.1007/s00442-012-2324-x

Matozzo, V., Chinellato, A., Munari, M., Finos, L., Bressan, M., & Marin, M. G. (2012). First evidence of immunomodulation in bivalves under seawater acidification and increased temperature. *PLoS ONE*, *7*(3), e33820. https://doi.org/10.1371/journal.pone.0033820

Mrowicki, R. J., & O'Connor, N. E. (2015). Wave action modifies the effects of consumer diversity and warming on algal assemblages. *Ecology*, *96*(4), 1020–1029. https://doi.org/10.1890/14-0577.1

Navarro, J. M., Duarte, C., Manríquez, P. H., Lardies, M. A., Torres, R., Acuña, K., Vargas, C. A., & Lagos, N. A. (2016). Ocean warming and elevated carbon dioxide: Multiple stressor impacts on juvenile mussels from southern Chile. *ICES Journal of Marine Science: Journal du Conseil*, *73*(3), 764–771. https://doi.org/10.1093/icesjms/fsv249

Nejrup, L. B., Staehr, P. A., & Thomsen, M. S. (2013). Temperature- and light-dependent growth and metabolism of the invasive red algae *Gracilaria vermiculophylla*—a comparison with two native macroalgae. *European Journal of Phycology*, *48*(3), 295–308. https://doi.org/10.1080/09670262.2013.830778

Newcomer, K., Marraffini, M. L., & Chang, A. L. (2018). Distribution patterns of the introduced encrusting bryozoan *Conopeum chesapeakensis* (Osburn 1944; Banta et al. 1995) in an estuarine environment in upper San Francisco Bay. *Journal of Experimental Marine Biology and Ecology*, *504*, 20–31. https://doi.org/10.1016/j.jembe.2018.04.001

Nishizaki, M., Barron, S., & Carew, E. (2015). Thermal stress increases fluctuating asymmetry in marine mussels: Environmental variation and developmental instability. *Eosphere*, *6*(5), 85. https://doi.org/10.1890/ES14-00399.1

O'Connor, M. I. (2009). Warming strengthens an herbivore–plant interaction. *Ecology*, *90*(2), 388–398. https://doi.org/10.1890/08-0034.1

Olabarria, C., Arenas, F., Viejo, R. M., Gestoso, I., Vaz-Pinto, F., Incera, M., Rubal, M., Cacabelos, E., Veiga, P., & Sobrino, C. (2013). Response of macroalgal assemblages from rockpools to climate change: Effects of persistent increase in temperature and CO2. *Oikos*, *122*(7), 1065–1079. https://doi.org/10.1111/j.1600-0706.2012.20825.x

Pansch, C., Nasrolahi, A., Appelhans, Y. S., & Wahl, M. (2012). Impacts of ocean warming and acidification on the larval development of the barnacle *Amphibalanus improvisus*. *Journal of Experimental Marine Biology and Ecology*, *420–421*, 48–55. https://doi.org/10.1016/j.jembe.2012.03.023

Pineda, M. C., McQuaid, C. D., Turon, X., Lopez-Legentil, S., Ordonez, V., & Rius, M. (2012). Tough adults, frail babies: An analysis of stress sensitivity across early life-history stages of widely introduced marine invertebrates. *PLoS ONE*, *7*(10), e46672. https://doi.org/10.1371/journal.pone.0046672

Poore, A. G. B., Graham, S. E., Byrne, M., & Dworjanyn, S. A. (2016). Effects of ocean warming and lowered pH on algal growth and palatability to a grazing gastropod. *Marine Biology*, *163*(5), 1–11. https://doi.org/10.1007/s00227-016-2878-y

Provost, E. J., Kelaher, B. P., Dworjanyn, S. A., Russell, B. D., Connell, S. D., Ghedini, G., Gillanders, B. M., Figueira. W., & Coleman, M. A. (2017). Climate-driven disparities among ecological interactions threaten kelp forest persistence. *Global Change Biology*, *23*(1), 353–361. https://doi.org/10.1111/gcb.13414

Reynolds, L. K., DuBois, K., Abbott, J. M., Williams, S. L., & Stachowicz, J. J. (2016). Response of a habitat-forming marine plant to a simulated warming event is delayed, genotype specific, and varies with phenology. *PLoS ONE*, *11*(6), e0154532. https://doi.org/10.1371/journal.pone.0154532

Rius, M., Clusella-Trullas, S., McQuaid, C. D., Navarro, R. A., Griffiths, C. L., Matthee, C. A., von der Heyden, S., & Turon, X. (2014). Range expansions across ecoregions: Interactions of climate change, physiology and genetic diversity. *Global Ecology and Biogeography*, *23*(1), 76–88. https://doi.org/10.1111/geb.12105

Rothausler, E., Rugiu, L., & Jormalainen, V. (2018). Forecast climate change conditions sustain growth and physiology but hamper reproduction in range-margin populations of a foundation rockweed species. *Marine Environmental Research*, *141*, 205–213. https://doi.org/10.1016/j.marenvres.2018.09.014

Rugiu, L., Manninen, I., Sjöroos, J., & Jormalainen, V. (2017). Variations in tolerance to climate change in a key littoral herbivore. *Marine Biology*, *165*(1), 1–11. https://doi.org/10.1007/s00227-017-3275-x

Sampaio, E., Rodil, I. F., Vaz-Pinto, F., Fernandez, A., & Arenas, F. (2017). Interaction strength between different grazers and macroalgae mediated by ocean acidification over warming gradients. *Marine Environmental Research*, *125*, 25–33. https://doi.org/10.1016/j.marenvres.2017.01.001

Samperio-Ramos, G., Olsen, Y. S., Tomas, F., & Marba, N. (2015). Ecophysiological responses of three Mediterranean invasive seaweeds (*Acrothamnion preissii*, *Lophocladia lallemandii* and *Caulerpa cylindracea*) to experimental warming. *Marine Pollution Bulletin*, *96*(1–2), 418–423. https://doi.org/10.1016/j.marpolbul.2015.05.024

Scherner, F., Pereira, C. M., Duarte, G., Horta, P. A., Castro, C. B., Barufi, J. B., & Pereira, S. M. (2016). Effects of ocean acidification and temperature increases on the photosynthesis of tropical reef calcified macroalgae. *PLoS ONE*, *11*(5), e0154844. https://doi.org/10.1371/journal.pone.0154844

Scherner, F., Ventura, R., Barufi, J. B., & Horta, P. A. (2013). Salinity critical threshold values for photosynthesis of two cosmopolitan seaweed species: Providing baselines for potential shifts on seaweed assemblages. *Marine Environmental Research*, *91*, 14–25. https://doi.org/10.1016/j.marenvres.2012.05.007

Schoenrock, K. M., Bacquet, M., Pearce, D., Rea, B. R., Schofield, J. E., Lea, J., Mair, D., & Kamenos, N. (2018). Influences of salinity on the physiology and distribution of the Arctic coralline algae, *Lithothamnion glaciale* (Corallinales, Rhodophyta). *Journal of Phycology*, *54*(5), 690–702. https://doi.org/10.1111/jpy.12774

Schoenrock, K. M., Schram, J. B., Amsler, C. D., McClintock, J. B., & Angus, R. A. (2014). Climate change impacts on overstory *Desmarestia* spp. from the western Antarctic Peninsula. *Marine Biology*, *162*(2), 377–389. https://doi.org/10.1007/s00227-014-2582-8

Schoenrock, K. M., Schram, J. B., Amsler, C. D., McClintock, J. B., Angus, R. A., & Vohra, Y. K. (2016). Climate change confers a potential advantage to fleshy Antarctic crustose macroalgae over calcified species. *Journal of Experimental Marine Biology and Ecology*, *474*, 58–66. https://doi.org/10.1016/j.jembe.2015.09.009

Smale, D. A., & Wernberg, T. (2012). Short-term in situ warming influences early development of sessile assemblages. *Marine Ecology Progress Series*, *453*, 129–136. https://doi.org/10.3354/meps09680

Smale, D. A., Wernberg, T., Peck, L. S., & Barnes, D. K. (2011). Turning on the heat: ecological response to simulated warming in the sea. *PLoS ONE*, *6*(1), e16050. https://doi.org/10.1371/journal.pone.0016050

Stengel, D. B., Conde-Álvarez, R., Connan, S., Nitschke, U., Arenas, F., Abreu, H., Bonomi Baruf, J., Chow. F., Robledo, D., Malta, E. L., Mata, M., Konotchick, T., Nassar, C., Pérez-Ruzafa, Á., López, D., Marquardt, R., Vaz-Pinto, F., Celis-Plá, P. S. M., Hermoso, M., Ruiz, E., Ordoñez, G., Flores, P., Zanolla, M., Bañares-España, E., Altamirano, M., Korbee, N., Bischof, K., & Figueroa, F. L. (2014). Short-term effects of CO2, nutrients and temperature on three marine macroalgae under solar radiation. *Aquatic Biology*, *22*, 159–176. https://doi.org/10.3354/ab00576

Stevens, A. M., & Gobler, C. J. (2018). Interactive effects of acidification, hypoxia, and thermal stress on growth, respiration, and survival of four North Atlantic bivalves. *Marine Ecology Progress Series*, *604*, 143–161. https://doi.org/10.3354/meps12725

Strain, E. M., van Belzen, J., van Dalen, J., Bouma, T. J., & Airoldi, L. (2015). Management of local stressors can improve the resilience of marine canopy algae to global stressors. *PLoS ONE*, *10*(3), e0120837. https://doi.org/10.1371/journal.pone.0120837

Thiyagarajan, V., & Qian, P.-Y. (2003). Effect of temperature, salinity and delayed attachment on development of the solitary ascidian *Styela plicata* (Lesueur). *Journal of Experimental Marine Biology and Ecology*, *290*(1), 133–146. https://doi.org/10.1016/s0022-0981(03)00071-6

Vaz-Pinto, F., Olabarria, C., Gestoso, I., Cacabelos, E., Incera, M., & Arenas, F. (2013). Functional diversity and climate change: Effects on the invasibility of macroalgal assemblages. *Biological Invasions*, *15*(8), 1833–1846. https://doi.org/10.1007/s10530-013-0412-4

Werner, F. J., Graiff, A., & Matthiessen, B. (2016). Temperature effects on seaweed-sustaining top-down control vary with season. *Oecologia*, *180*(3), 889–901. https://doi.org/10.1007/s00442-015-3489-x

Yang, C. Y., Sierp, M. T., Abbott, C. A., Li, Y., & Qin, J. G. (2016). Responses to thermal and salinity stress in wild and farmed Pacific oysters *Crassostrea gigas*. *Comparative Biochemistry and Physiology*, *201*, 22–29. https://doi.org/10.1016/j.cbpa.2016.06.024