



A Regional View of the Response to Climate Change: A Meta-Analysis of European Benthic Organisms' Responses

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Climate change is impacting organisms in every region of the world ocean by acting through individuals in response to their local environments. Given projected future risks derived from these changes, it is becoming increasingly important to understand regional signals of how organisms respond to facilitate their governance and protection. Benthic organisms structure ecological compositions and ecosystem dynamics, therefore not only providing insights into their own response to climate change but also how ecosystems might respond to future conditions. European seas are transitional areas including boreal, warm-temperate, and subarctic waters with organisms frequently at limits of their distributions. Here, we use a meta-analytical approach to assess how calcification, growth, metabolism, photosynthesis, reproduction, and survival in European benthic organisms respond to ocean acidification and warming. Using meta-regression, we examine how study design factors influence effect-size outcomes. Longer experimental periods generally amplified the effects of climate change on taxonomic groupings and related physiological traits and against expectation do not result in acclimation. In agreement with global studies, we find that impacts vary considerably on different taxonomic groupings and their physiological traits. We found calcifying organisms are an at-risk taxon in European waters, with climate stressors decreasing growth rates, reproduction, and survival rates. Fleshy algal species demonstrate resilience to climate stressors, suggesting future European benthic ecosystems will undergo restructuring based on current climate emission pathways.

Keywords: climate change, benthic organisms, ocean acidification, ocean warming, meta-analysis, european ecosystems

1 INTRODUCTION

Atmospheric carbon dioxide concentration is currently ~412.5ppm (Friedlingstein et al., 2020), the highest level in 3.6 million years (Martínez-Botí et al., 2015). Depending on emission scenarios, likely global atmospheric air warming is projected to be 2.5°C – 4°C by 2100 (IPCC, 2021). These emissions drive changes to ocean properties, chiefly ocean acidification from excess CO₂ interacting with seawater (Doney et al., 2009) and increases to ocean temperature from

absorbing excess atmospheric heat (IPCC, 2021). Such warming is amplified in higher latitudes (Wu et al., 2011; Singh et al., 2017) but lower in the ocean due oceanic to thermal inertia (Abdussamatov et al., 2012). High latitudes are absorbing most CO₂ as cold water can naturally store more gasses (Cooley et al., 2022).

These changes in the ocean physico-chemical properties have consequences for marine organisms including changes to growth, calcification, reproduction, metabolic processes, and survival; these effects though are highly variable across taxonomic groups (Kroeker et al., 2013; Cattano et al., 2018; Bindoff et al., 2019; Sampaio et al., 2021). While the development of the climatic drivers over the next decades is broadly well understood (Cooley et al., 2022) and a vast range of responses of individuals and their developmental stages exemplified, upscaling to the response of larger groups, ecosystems and their services is a vast challenge, despite scientific literature on individual studies accumulating (Bass et al., 2021).

Meta-analyses help focus knowledge on how marine organisms may respond by condensing many independent studies into a standardised and comparable format allowing patterns to emerge, despite the variation between experiments, across taxonomic groups and latitudes. Agenda setting studies showed how climate change interacts with organisms and the physiological responses at a global scale (Hendriks et al., 2010; Harvey et al., 2013; Kroeker et al., 2013). These studies identified potential generalised trends like calcifying organisms' growth rates decreasing under ocean acidification.

Organism responses to climate change though are not homogenous and interregional variability is expected (Krumhansl et al., 2016). For example, a meta-analysis showed coral calcification rates to ocean acidification increase in the tropics, decreases in the subtropics, and are unaffected in temperate ecosystems in response to climate scenarios for 2100 (Kornder et al., 2018). The natural variability of the climate and environment, as well as the synergies between drivers, might predispose organisms to a wider range of impacts. Temperate regions, for example, record greater annual variability in temperature than tropical regions which may lead to different responses to climate stressors (Sheldon et al., 2011; Vergés et al., 2014).

Two recent meta-analyses have taken a different regional approach focussing on ocean acidification in the Southern Ocean (Hancock et al., 2020; Figuerola et al., 2021) finding potential to alter ecosystem interactions. Bove et al. (2020) investigated Caribbean coral calcification indicating ocean warming reduces calcification while ocean acidification and ocean acidification with warming, does not. A study of Mediterranean benthic organism responses to ocean acidification showed a replacement of calcifying algae and corals by fleshy algae (Zunino et al., 2017). Regional studies find trends that are less evident using global analyses (Parker et al., 2013) such as resilience in calcification or growth responses (Goethel et al., 2017; Zunino et al., 2017; Kornder et al., 2018; Bove et al., 2020) which are not identifiable when pooling studies globally (Hendriks et al., 2010; Kroeker et al., 2013; Harvey et al., 2013).

Given projected future risks derived from these changes, it is becoming increasingly important to understand regional signals of how organisms response. Here we use the approach of global studies in the context of European waters to determine vulnerability or resilience of taxonomic groupings to multiple climate stressors. This understanding will be important to prioritise conservation efforts and identify governance needs in an international context. Across Europe multiple biogeographic regions are in close proximity with organisms at the edges of their distributions (Narayanaswamy et al., 2013; Kotta et al., 2017). Large volumes of experimental work analysing organism responses to climate change exist for Europe, augmented by long-time series data sets assessing natural variation of presence and absence e.g. MarClim in the UK (Mieszkowska et al., 2006), and the Helgoland Roads time series (Wiltshire et al., 2010). Despite the large volume of data, studies assessing interactions across multiple stressors and their potential cumulative impacts within the wider context of European waters are lacking. It is not clear which habitats are most vulnerable or which services are most under pressure which hinders the effectiveness to conserve European marine ecosystems through protected area networks (Mazaris et al., 2019), and the sustainable development of coastal resources (Qiu and Jones, 2013).

We focus on benthic organisms as these are habitat formers, keystone species, and provide regulating and provisioning services which are fundamental in structuring ecosystems. Molluscs are food sources for other organisms (Coen et al., 2007), form biogenic habitats (Koivisto and Westerbom, 2010), and key economic resources (Mangi et al., 2018). Crustaceans are key components of food webs often serving as a trophic link between benthic and pelagic species (Szaniawska, 2018). Algal species fix carbon *via* photosynthesis (Tsai et al., 2017), stabilise shorelines (Currin et al., 2010), contribute to nutrient cycles (Smale et al., 2013), and provide habitat for epiphytic communities (Bates and DeWreede, 2007; King et al., 2021). Echinoderms are dominant grazing species in ecosystems that structure habitats (Norderhaug and Christie, 2009) and drive trophic interactions (Hughes et al., 2012). Calcifying algae build habitats both *via* their physical structures (Hofmann et al., 2012) and shaping surrounding sediment profiles (Coniglio and James, 1985), and host epiphytic species (Nelson, 2009).

Additionally, meta-analyses have moved on technically since earlier seminal studies. While the importance of study design in experimental outcomes has been acknowledged and suggestions for standardisation have been made (Riebesell et al., 2011), its relevance has rarely been explored in meta-analysis. The substantial increase in understanding of impacts of climate change on marine organisms since publication of earlier agenda setting work offers the chance to incorporate a larger volume of data and develop meta-analysis studies to improve understanding of the underlying mechanisms that may drive observations. Duration of exposure and acclimation periods are thought to impact how organisms respond to climate stressors (Evans and Hofmann, 2012; Griffith and Gobler, 2017). Short term experiments, often without days in the laboratory conditions allowing equilibration, are perceived as shock to the

physiology of the study organisms (Li et al., 2015) while long-term response allow for acclimation and therefore are considered to give a better idea of the responses to long term climate change (Leung et al., 2021). New longer duration datasets allow us to analyse the importance of these designs of experimental datasets expanding from previous meta-analyses.

Using a meta-analytical approach, we examine peer-reviewed literature focusing on how European benthic marine organisms respond to climate change drivers. We focus our analysis on organism calcification, growth, metabolism, reproduction, photosynthesis, and survival. Based on global analyses and understanding of the physiology of these taxa, we hypothesise that calcifying organism will be impacted more strongly, and that growth is negatively impacted while photosynthesis is enhanced. These traits capture a range of key organism physiological traits providing insights into organism fitness and allow of comparisons with previous meta-analyses. Using meta-regression, we examine how study design factors influence effect-size outcomes.

2 METHODS

2.1 Study and Selection Criteria

This study gathered articles published between 1st January 2000 – 1st January 2020 to cover most ocean acidification (OA) research articles (Riebesell and Gattuso, 2015). Web of Science and Scopus were used to find articles covering climate change impacts on native European benthic marine organisms using the keywords: “ocean acidification”, “acidification”, “ocean warming”, “climate change”, “global warming”, and combinations/permutations of these. The results were snowballed following recommendations made by Orr et al. (2020); article lists from previous comprehensive reviews (Harvey et al., 2013; Kroeker et al., 2013) and their reference

lists were used to locate additional studies. Article collection occurred between March 2019 – Jan 2020, article list available in **Supplementary Data**.

Data were limited to native European species (**Figure 1**), excluding invasive species. Minimum standards for reporting of meta data were: control condition, acidification and or warming manipulated individually or synergistically within possible for conditions for 2100 conditions in European seas. Plausible conditions were determined based on author knowledge of likely conditions at a study site or species might experience, allowing inclusion of local contexts not identifiable in large, averaged projections. We exclude unrealistic stress (i.e., conditions beyond high end emissions scenarios by 2100) experiments in the context of climate change designed to improve our understanding of physiology. Studies assessing interaction with other stressors (such as heavy metal pollution or nutrients) were included if they analysed the climate stressors separately. Studies examining multiple species, biological responses, seasons, or geographical locations were included if they could be disaggregated.

Data on calcification, growth, metabolism, reproduction, photosynthesis, and survival were extracted (**Supplementary Data**). When the same biological trait was measured in multiple ways (e.g. growth as organism length and biomass), one was chosen at random following standard methodology (Harvey et al., 2013; Kroeker et al., 2013; Sampaio et al., 2021). To avoid higher weighting, one parameter was chosen when multiple biological responses (e.g. length and biomass to determine growth) were reported. Survival data were converted from mortality for standardisation. Many identified articles reported survival rates. However, these were often reported as percentages and thereby did not provide variance, preventing us from computing an effect size consistent with the rest of these meta-analyses, resulting in exclusion from our study. Time-series data were attributed to the endpoint of that experiment.

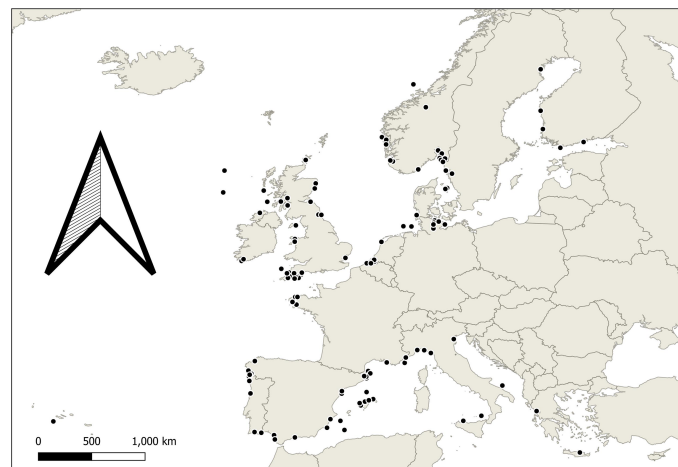


FIGURE 1 | A map of Europe detailing approximate collection locations of study organisms in identified articles for meta-analysis.

Datapoints, a form or variance (standard error, confidence intervals, or standard deviation), and sample size were extracted directly from either text or tables. Graphs were data mined using WebPlotDigitizer (Rohatgi, 2019, See SI). Acclimation period (experimental period whereby organisms were transitioned to climate stressors e.g., increasing water temperature by 0.5°C daily to reach temperature increase value), study duration (length of organism exposure to climate stressor excluding acclimation period), organism developmental stage (categorised as Egg/larva, Juvenile, and Adult), pH change or temperature change, organisms' size were extracted when possible. Size at the start of the experiment was converted to grams [g] or millimetres [mm]) based on the sample mean and log transformed. Insufficient data were extracted to allow for taxonomic-biological trait responses to organism size, so data were pooled combining biological traits to identify general trends on traits alone.

2.2 Statistical Analyses

All analyses were conducted using the R (version 4.0.0; R Development Core Team). The package “Metafor” (Viechtbauer, 2010) was used to calculate effect size using the “escalc” function and conduct the meta-analyses. Log Response Ratio (LnRR) was chosen to measure effect size (Koricheva et al., 2013).

Multivariate meta-analysis models (function “*rma.mv*”) were used to calculate the mean effect and sampling variance of a treatment on a biological response. Random intercepts of article and species for each treatment were incorporated to account for possible results correlation due to studies from the same article or organism and account for pseudo-replication. Data were subsetted into taxonomic groupings, calcifiers vs non-calcifiers, heterotrophic vs autotrophic, and developmental stage when possible. Climate stressors were used as model moderators (mods = stressor -1). A result is considered significant if the 95% confidence interval for the overall mean calculated by a model does not overlap zero. Tests for residual heterogeneity (Q_E) were used to ascertain if additional moderators not considered in the analysis might be influencing study results (Hedges and Olkin, 2014).

To examine the impact of study duration and acclimation period we modified the multivariate meta-analysis models to include either of these as moderators within the models. E.g: [model <- *rma.mv*(*yi*, *vi*, method=“REML”, test=“t”, random = ~1|Article/species, data=data, mods = ~duration: stressor -1)].

2.3 Publication Bias

Standardized diagnostic tests for multivariate meta-analytical methods are still evolving (Viechtbauer and Cheung, 2010; Hacheck and Schultz, 2015) and currently only applicable for univariate models (e.g. models of class “*rma*”). To detect publication bias within our data we modified our multivariate models in accordance with Hacheck and Schultz (2015) to calculate Egger's regression. Egger's regression detects funnel plot asymmetry, a common measure of publication bias, by looking if there are statistically absent studies based on the distribution of studies within meta-analysis datasets using

linear regression (Egger et al., 1997). Multivariate meta-analysis models were extended to include the square root on effect size variance as a model moderator variable to perform a regression test (Hacheck and Schultz, 2015). When this regression test intercept significantly deviates from zero, a data set is considered asymmetrical, thus biased (Sterne et al., 2005). Following previous recommendations (Egger et al., 1997; Hacheck and Schultz, 2015) an analysis is considered biased if the intercept differs from zero at $P = 0.10$. Results from tests for residual heterogeneity (Q_E) and publication bias are reported in **Supplementary Information**.

3 RESULTS

171 articles matched our inclusion criteria (**Figure 2**), totalling 791 experiments for meta-analysis (**Supplementary Data**). Most studies were molluscs ($n = 173$), acidification ($n = 423$) and the traits of calcification ($n = 126$), growth ($n = 266$), and metabolic response ($n = 202$). Average experimental duration was 86.3 (± 102.1) days, acclimation period 7.1 (± 20.4) days, pH change 0.26 (± 0.17) and temperature change = 2.69°C (± 2).

The responses of benthic organisms to climate stressors were highly variable across taxonomic groups (**Figure 3**). No stressor consistently produced positive or negative changes. Crustaceans were the most impacted with combined ocean acidification and warming decreasing calcification ($LnRR = -0.1448$, $P = 0.0111$, 95% confidence interval -0.2509 - -0.0387), reproduction ($LnRR = -0.144$, $P = 0.0014$, 95% confidence interval -0.2277 - -0.0604), and survival ($LnRR = -0.4057$, $P = 0.0001$, 95% confidence interval -0.4086 - -0.3604), but increasing metabolic rate ($LnRR = 0.2211$, $P = 0.0188$, 95% confidence interval 0.0425 - 0.3996). Ocean acidification alone lowered reproduction ($LnRR = -0.111$, $P = 0.0109$, 95% confidence interval -0.1945 - -0.0276). Warming increased metabolic rates ($LnRR = 0.3993$, $P = 0.0001$, 95% confidence interval 0.2344 - 0.5641) but decreased reproduction ($LnRR = -0.1272$, $P = 0.0042$, 95% confidence interval -0.2108 - -0.0436), and survival ($LnRR = -0.269$, $P = 0.0053$). Most calcifying organisms exhibit statistically significant responses when taxa were examined individually (**Figure 3**) and when data were aggregated to compare with non-calcifying organisms with respect to growth rates and metabolism (**Figure 4**).

Metabolism was both negatively and positively affected by at least one climate stressor in every taxon except algae (9 statistically significant observations in 5 taxa) (**Figure 3**). Fleishy algae are the most resilient with no statistically significant signals in growth, metabolism, photosynthesis, and reproduction (**Figure 3**). Ocean acidification caused decreases in metabolism in calcifying and heterotrophic organisms (**Figure 4**). Warming individually, and combined with ocean acidification, increase metabolic rates except corals where metabolic rate decreased and algae where no statistical signal was detected. Egg/larval growth rates across all taxa increased in response to combined acidification and warming ($LnRR =$

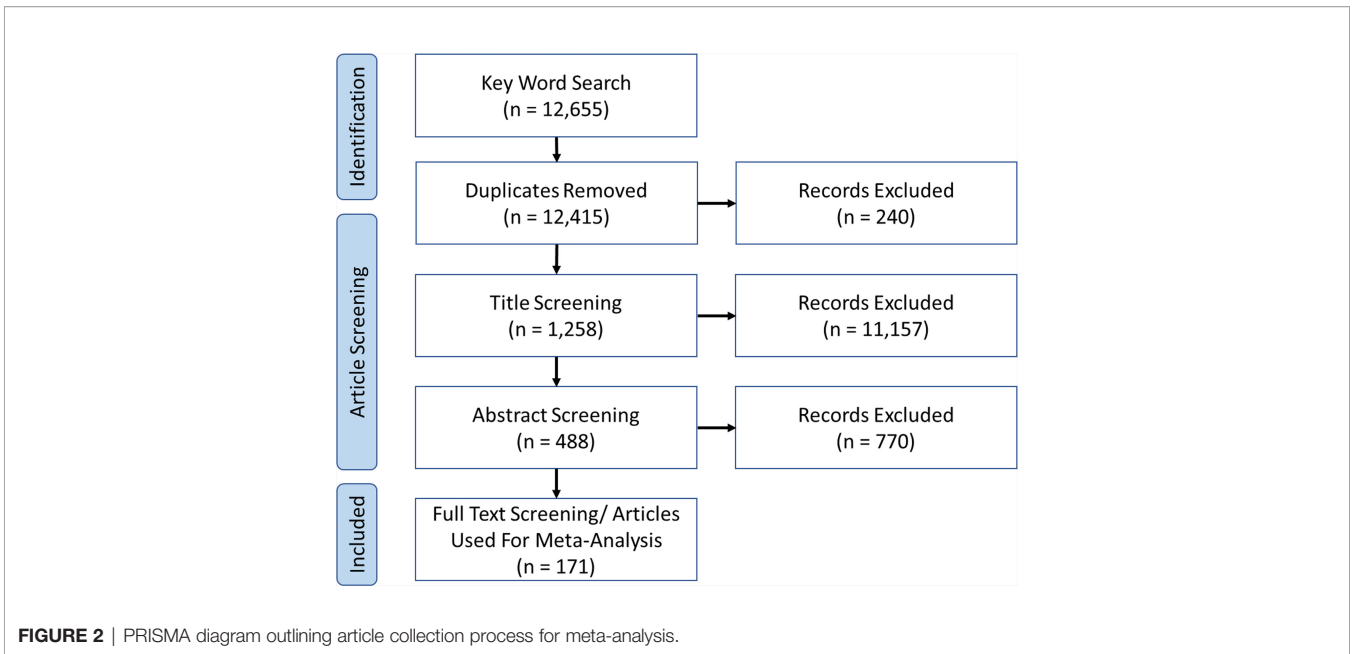
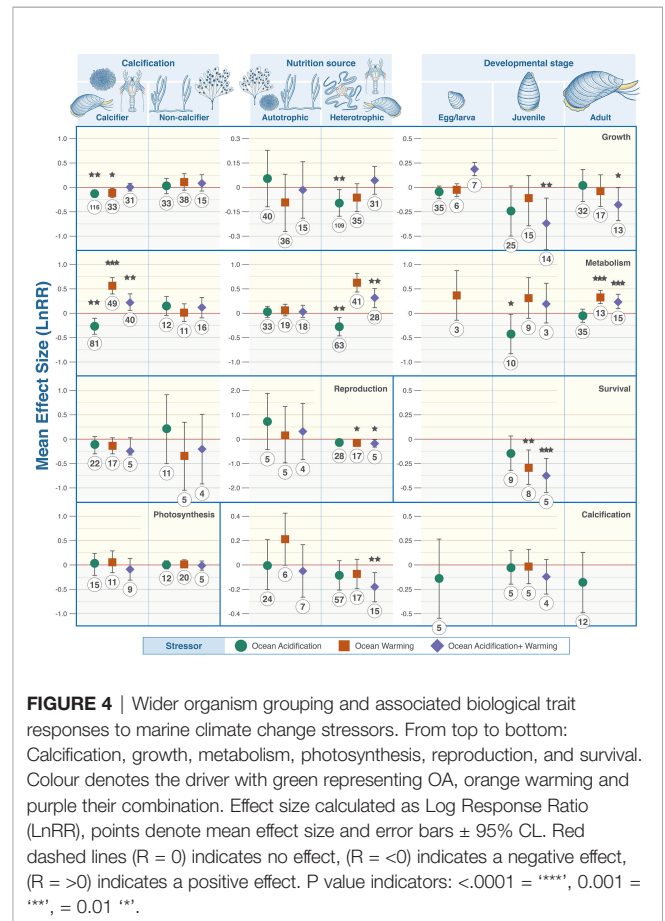
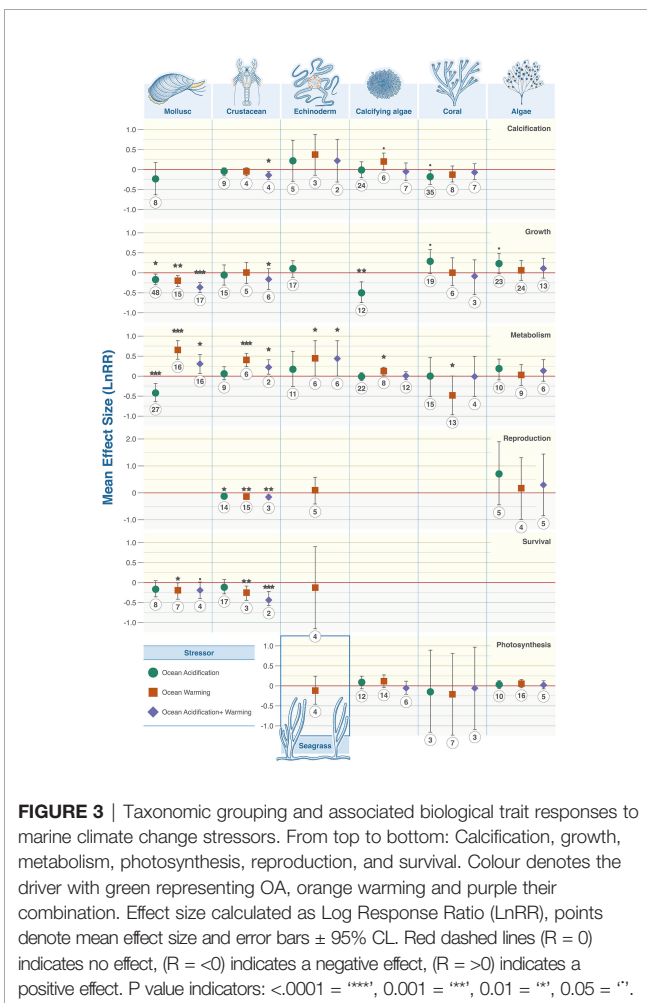


FIGURE 2 | PRISMA diagram outlining article collection process for meta-analysis.



0.1935, $P = 0.0001$, 95% confidence interval 0.1268 – 0.2603), but decreased in juveniles and adults ($LnRR = -0.3701$, $P = 0.0058$, 95% confidence interval -0.6283 - -0.1118; $LnRR = -0.1715$, $P = 0.0404$, 95% confidence interval -0.3353 - -0.0078 respectively) (**Figure 4**).

Experimental design greatly influenced the observed impacts of organism responses to climate change stressors (**Supplementary Material**) as revealed by meta-regression. Study duration was important for responses of taxonomic groups while acclimation period mostly had no statistical significance suggesting that the current practise eliminates impacts on study design (**Supplementary Table**). Increased study duration period generally amplified responses, suggesting that European benthic organisms do not readily acclimate to acidification and/or warming within the same generation. Metabolic responses increased with study durations (**Table 1**). Survival was the only trait not significantly impacted by experimental duration or acclimation periods (**Table 1**).

The impact on taxa scales with the degree of environmental change with larger driver change resulting in higher impacts. There are expectations for example metabolic activity for molluscs and algae were metabolism decreased in response to OA (**Table 2**). Climate stress negatively impacted growth across all taxa except for polychaeta growth which showed an increase.

Interestingly, results suggest that larger organisms do not increase metabolisms in response to climate stressors as larger organisms grew more, while smaller organism's growth rate was lower (**Table 3**). Impacts on survival are not clear; for larger organisms determined by volume or weight (g) survival rates were negatively impacted by OA, but when organisms were measured by length larger organism had higher survival with increasing size.

4 DISCUSSION

While there have been meta-analyses of climate change impacts on marine organisms in the past, climate change is acting on a local to regional scale. Projected future risks originating from these changes make it increasingly important to identify regional signals of organismal responses to guide conservation strategy and governance. We chose European waters due to the geographic proximity of different biogeographic regions driven by environmental differences. Such analysis is fundamental to design effective conservation strategies by providing granularity that is not present in overarching datasets. In agreement with many experiments on individual taxa, we found highly variable impacts. Metabolic rates of molluscs, crustaceans, echinoderms, and calcifying algae increased under ocean warming and combined ocean acidification and warming, while mollusc and coral metabolic rates decreased under ocean acidification and ocean warming respectively (**Figure 2**). The physiology of calcifying organisms is significantly impacted with decreased growth rates of molluscs under all examined climate stressors and calcifying algae under ocean acidification, crustacean calcification decreased under combined ocean acidification and warming, while fleshy algal species appear resilient to the tested combinations of climate

stressors. Using meta-regression, we found against expectation that longer experimental periods generally amplified the effects of climate change and did not result in acclimation.

4.1 Impacts on Habitat Formers

Growth and reproduction of calcifying organisms in particular were reduced in response to warming and lowering of pH. However not all calcifying taxa experienced calcification reduction. Molluscs show negative impacts on calcification, growth and increases in metabolic costs, adding to the body of studies showing molluscs are a highly at-risk taxon globally (Parker et al., 2013; Kroeker et al., 2013; Goethel et al., 2017; Figuerola et al., 2021). Our findings contrast recent work on the Mediterranean Sea and a global analysis which suggested mollusc growth is unaffected by climate stressors (Zunino et al., 2017; Sampaio et al., 2021). Our results likely differs from the signal observed by Zunino et al. (2017) due to a larger sample size encompassing a wider range of taxa and growth responses. We interpret this apparent disagreement with the global analysis as indication that European mollusc species are particularly sensitive to climate stressors; a suggestion which is corroborated by global studies which have a strong bias towards temperate molluscan species in North Atlantic waters resulting in a similar interpretation (Kroeker et al., 2013; Harvey et al., 2013). European species have long been reported to be altering distributions in response to climate change (Helmuth et al., 2006) highlighting species at the edge of distributions are sensitive to climate stressors.

Reductions in growth rates will not only affect size and fitness, but also reduce molluscs ability to form biogenic structures, limiting their ability to support biodiversity (Strain et al., 2021). Many habitats created by these taxa are protected due to the associated high biodiversity (Donnarumma et al., 2018). Evidence suggests high food availability can buffer against climate stressors (Thomsen et al., 2013), but primary productivity globally is predicted to decrease by ~8.6% under business-as-usual scenarios (Bopp et al., 2013) thereby potentially amplifying the impacts depending on local habitat and other inputs into coastal ecosystems.

Reductions in mollusc growth rates and survival paired with reductions in crustacean survival and reproduction would impact commercial fishing in Europe by lowering catch potential and impacting livelihoods of European fishers. France, the Netherlands, and Spain annually produce approximately half of consumed European molluscs (Narita and Rehdanz, 2017) suggesting these regions are particularly susceptible to the economic repercussions of climate impacts on mollusc species. Additionally, the resilience of mollusc and crustacean populations against climate change has been reduced by destructive fishing and pollution for decades (De Groot, 1984). There are attempts to restore habitats in line with historical distribution, e.g., recreation of oyster beds around the UK (Harding et al., 2016) or red gorgonian in the Mediterranean (Linares et al., 2008). Restoring historical habitats that are reliant on calcifying organisms as keystone species may be a risky approach and not provide longevity due to observed impacts on growth rates, reproduction, and survival. Assessing local

TABLE 1 | Study duration period impact on effect size (LnRR) for biological traits and climate change stressor treatment.

Biological Trait	Mollusc			Crustacean			Coral			Algae		
	OA	OW	OA + OW	OA	OW	OA + OW	OA	OW	OA + OW	OA	OW	OA + OW
Calcification	-	-	-	-	-	↓↓↓	↑	↑	-	-	-	-
Growth	↓	↓	↓↓↓	-	↑↑	↓↓	-	-	-	↓↓↓	↓↓↓	↓↓↓
Metabolism	-	↑	-	-	↑↑↑	↑↑	-	-	-	↑	-	-
Photosynthesis	-	-	-	-	-	-	↓↓↓	↓	↓↓	-	-	-
Reproduction	-	-	-	-	↓	↓↓↓	-	-	-	-	-	-
Survival	-	-	-	-	-	-	-	-	-	-	-	-

Biological Trait	Echinoderm			Calcifying algae			Polychaete			Seagrass		
	OA	OW	OA + OW	OA	OW	OA + OW	OA	OW	OA + OW	OA	OW	OA + OW
Calcification	↑↑	-	↑↑	-	↑	-	-	-	-	-	-	-
Growth	-	↓↓↓	↑↑↑	↓	-	-	-	-	↑↑	-	-	↑↑
Metabolism	-	-	-	-	↑	-	-	-	-	-	-	-
Photosynthesis	-	-	-	↑	↑	-	-	-	-	-	↑↑	-
Reproduction	-	-	-	-	-	-	-	-	-	-	-	-
Survival	-	-	-	-	-	-	-	-	-	-	-	-

Red shades refer to negative signals, blue shades are positive signals. At the bottom of the tables, light green refers to Ocean Acidification, orange refers to Ocean Warming, and dark blue is Ocean Acidification and Warming. On **Tables 1 and 2**, gold/orange is meant to highlight "Biological trait"

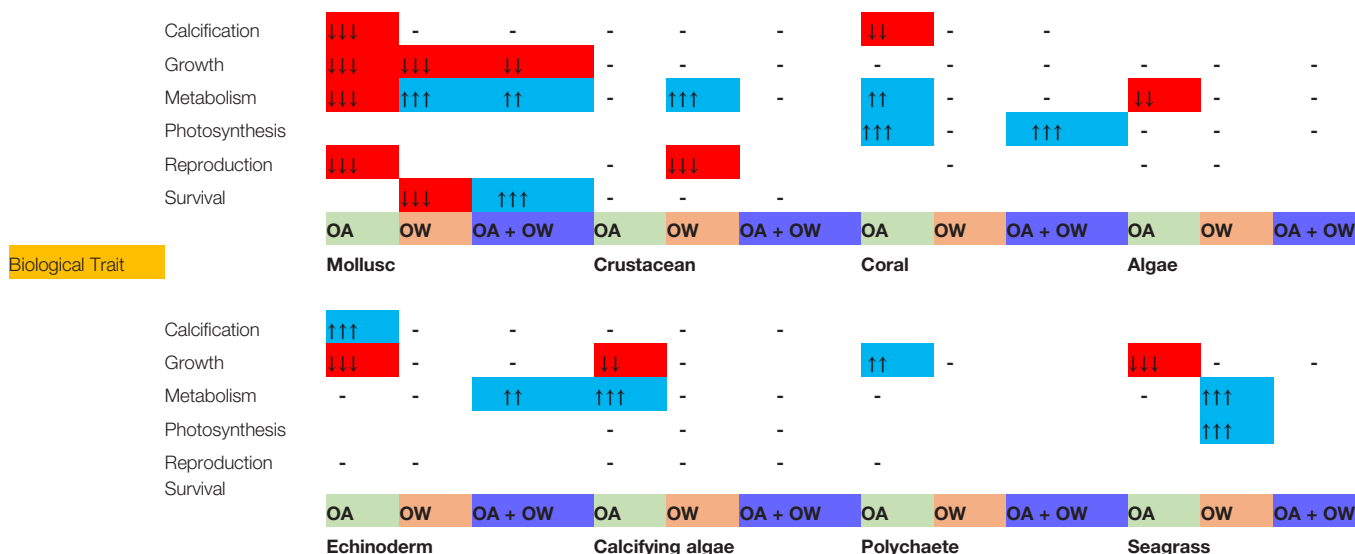
environmental conditions, the vulnerability of specific taxa, and options for reducing secondary local stressors are all needed to improve the long-term viability of these habitats.

Other ecosystem builders are similarly impacted, increasing the risk for coastal biodiversity. The decrease growth rates of calcifying algae are supported by other studies, highlighting the vulnerability of this group (Brodie et al., 2014; Chan et al., 2020). As they lose suitable environmental conditions (Simon-Nutbrown et al., 2020), calcifying algae are predicted to experience increased breakage due to increasingly intense weather, reducing structural complexity of Mearl beds (Melbourne et al., 2018). The reduced growth rates of calcifying algae suggested in our analysis will compound these problems (Ragazzola et al., 2013; Marchini et al., 2019). Furthermore, future sea level rise and changes in riverine input into coastal setting due to changes in precipitation and land use all threaten light attenuation in some habitats, for example where habitats cannot migrate landwards due to artificial coastal structures or cliffs, which exacerbates the impacts.

Our data suggest European corals are mostly unaffected by climate stressors, likely because most studies investigated the cold-water coral *Lophelia pertusa* which have been found in experiments to be resilient to projected end of century ocean conditions (Form and Riebesell, 2012; Wall et al., 2015; Büscher et al., 2017; Varnerin et al., 2020; Wang et al., 2021). While symbiont bearing tropical coral ecosystems are projected to be lost with only small amounts of additional warming (Hoegh-Guldberg et al., 2017), temperate deeper-water taxa appear more resilient (Kornder et al., 2018, this study). However, the 3D structure generated by deep water corals will be impacted by dissolution after death and thereby reduce the habitat and associated biodiversity (Hennige et al., 2020).

Our analysis suggests that autotrophic species, in our dataset mostly fleshy algae, will benefit from climate change. We echo the findings that algal species can display resilience to climate change stressors, in both regional (Strain et al., 2015; Phelps et al., 2017) and global analyses (Krumhansl et al., 2016). This finding is supported by field observations of intertidal habitats in Scotland which have observed increases in canopy-forming algal species (Burrows et al., 2017). However, the focus on the physiology masks species interactions which suggest that temperate algal communities may undergo simplification with decreases in structural complexity and diversity as climate change amplifies (Brodie et al., 2014; Agostini et al., 2021; King et al., 2021). Algal species frequently grow in high energy environments which experience rapid daily variations in tides and temperature. Therefore, they have evolved rapid growth responses to compensate frequent breakage in these environments (Rai and Gaur, 2012) which may also benefit under global change conditions. Due to their apparent resilience, associated ecosystem services like helping shoreline stabilisation and nutrient cycling may continue despite warming and acidification. However, the complexity of these systems is overlooked by our analysis of individual taxa as associated epifaunal species might be negatively impacted and thereby reduce biofilm production on the algae (Berner et al., 2015). It is important to note though that eutrophication, pollution and habitat destruction from shoreline protection, fishing or future sea level rise were not part of this assessment. This apparent resilience may support endeavours to grow kelp or seagrass for carbon sequestration (Unsworth et al., 2018; Bach and Boyd, 2021), or grow algae as part of the blue economy (Araújo et al., 2021). Our results suggest efforts to restore algal habitats, such as kelp beds around Norway (Hynes et al., 2021), might benefit from the suggested resilience to climate stressors.

TABLE 2 | Stressor severity impact on effect size (LnRR) for biological traits and climate change stressor treatment (OA = Ocean Acidification, OW = Ocean Warming, OA + OW = Ocean Acidification and Warming). Direction of response indicated by arrows, boxes with (-) indicate no statistically significant effect, blank boxes indicate insufficient/no data for meta-regression. P values denoted by number of arrows; <0.0001 = 3 arrows, < 0.001 = 2 arrows, <0.01 = 1 arrow.



Red shades refer to negative signals, blue shades are positive signals. At the bottom of the tables, light green refers to Ocean Acidification, orange refers to Ocean Warming, and dark blue is Ocean Acidification and Warming. On **Tables 1 and 2**, gold/orange is meant to highlight "Biological trait"

Our findings identify gaps in the experiments on some European benthic organisms. For example, while there is a high abundance of experiments on mollusc growth rates comparatively less is known for crustaceans or calcifying algae. This bias is replicated on a global scale (Kroeker et al., 2013; Harvey et al., 2013; Sampaio et al., 2021). Limited work on polychaetes and bryozoans hindered inclusion in our analysis expect for the generalised categories (calcifiers vs non-calcifiers, heterotrophs vs autotrophs). To gain a more differentiated understanding of what European seascapes may look like in the future and which services they can provide, greater efforts need to be taken to determine impacts on less studied taxonomic groups. Despite a clear importance of seasonal variation of environmental conditions, for example marine heat waves (Oliver et al., 2018), most studies were performed under stable environmental conditions resulting in insufficient data to analyse

potential seasonal impacts on organism physiology. Such extreme conditions and their projected increasing frequency will threaten communities as the reducing time periods between these extreme events reduce opportunities for communities to recover (Bednar-Friedl et al., 2022).

4.2 Physiological Responses

The observed increases in algal metabolism in our analysis show an increased demand for oxygen, indicating that climate change is increasing standard physiological rates (Pörtner, 2008). Whether these increases are beneficial or detrimental depends on the relative deviation from optimal environmental conditions for temperature and oxygen (Pörtner, 2002; Pörtner and Farrell, 2008). The detected impacts on the metabolic responses of calcifiers corroborate Lefevre (2016) who found calcifying organisms consumed significantly more oxygen when exposed

TABLE 3 | The effect of organism size at the start of an experiment on effect size (LnRR) for biological traits and climate change stressor treatment.



(OA = Ocean Acidification, OW = Ocean Warming, OA + OW = Ocean Acidification and Warming). Direction of response indicated by arrows, boxes with (-) indicate no statistically significant effect, blank boxes indicate insufficient/no data for meta-regression. P values denoted by number of arrows; <0.0001 = 3 arrows, < 0.001 = 2 arrows, <0.01 = 1 arrow. Red shades refer to negative signals, blue shades are positive signals. At the bottom of the tables, light green refers to Ocean Acidification, orange refers to Ocean Warming, and dark blue is Ocean Acidification and Warming.

to climate stressors. In contrast, previous meta-analysis suggested that ocean acidification does not impact metabolic responses (Kroeker et al., 2013; Sampaio et al., 2021) while warming increased them (Sampaio et al., 2021). One potential interpretation of this difference is the nature of the regional marine environment. European waters experience large temperature fluctuations and organisms in these environments have shown to have limited ability to acclimate to climate stressors (Seebacher et al., 2015). Increased physiological demands can be compensated, for example by higher food intake at warmer temperature or to facilitate calcification at lower pH. However, future oxygen losses in the ocean (Schmidt et al., 2017) could prevent organisms increasing their metabolic rates sufficiently. Therefore, interpretations on metabolic responses must be viewed in a wider biological context as increases in metabolism may result in negative responses in other parameters like growth rates (Kordas et al., 2011) and depend on the relative change in environmental conditions relative to critical and optimum values at their respective life stages (Pörtner and Farrell, 2008).

Organism size has been shown to greatly influence ectotherm survival (Peralta-Maraver and Rezende, 2021). Dynamic energy budget research shows organism metabolic rates generally decrease concurrently with size (Ren and Ross, 2001; Agüera et al., 2015). Increasing organism size decreases surface area to volume ratio, and oxygen uptake generally decreases relative to size as organism size increases (Lefevre et al., 2017). In general, metabolism increases in response to climate stressors. Meta-regression revealed that increasing organism size leads to negative metabolism responses (**Figure 3**), but this is likely an artifact of established metabolic theory. This result highlights the complexity of impacts on organisms, and potentially explains discrepancies between results of different studies. We were unable to explore this in greater detail due to studies infrequently reporting organism size and encourage experimentalist to make this part of their data reporting.

4.3 Increased Stressor Exposure Duration Amplifies Risk

Study duration (the period an organism was continuously exposed to a climate stressor) clearly impacts organism physiological responses to climate change. Using meta-regression to examine how study duration period changed trait responses to climate stressors suggests that impacts amplify the longer organisms are exposed. We expect effect size signals to shift towards zero if acclimation would occur. Our data though for growth and metabolism generally increased their response the longer experiments were conducted (**Table 1**). We suggest that European benthic organisms have limited capacity for acclimation over the time of the experiments. While we also detected many statistically insignificant signals, it is important to note that this does not indicate acclimation; it only suggests that study duration did not have a statistical relationship with effect size.

The mean experimental duration period across our data was only 86.3 days representing short-term exposure in contrast to climate change over decades. Long term experiments assessing acclimation are rare and typically conducted on organisms with fast reproduction time such as *Pseudokirchneriella* or *Emiliania huxleyi* (Schlüter et al., 2016; Limberger and Fussmann, 2021). Study length has not increased much since the meta-analysis Kroeker et al. (2013) clearly limiting our knowledge of the true long-term ecological impacts. Our selection of organisms may have a bias towards species which are adapted to deal with acute stress such as exposure to air, and highly variable environments. For example, photosynthetic performance of *Fucus serratus* in Spain when exposed to sudden thermal stress recovered within 24hrs, while populations from Norway, Denmark, and France did not recover (Jueterbock et al., 2014). Our results raise concerns that even organisms currently considered resilient and associated biological traits like algal growth rates can be overwhelmed by prolonged exposure to climate stressors. Chronic stress has been documented to lower the acclimation ability of marine organisms, reducing the upper thermal tolerances in mussels (Sorte et al., 2011) and coralline algae (Page et al., 2021).

Experiments used in this meta-analysis maintained stable conditions. Climate change will be associated with increasing frequency and duration of extreme events. Marine heat waves have led to mass mortality (Garrabou et al., 2009; Smale et al., 2019) and ecosystem restructuring (Wernberg et al., 2016; Ainsworth et al., 2020). Such extreme events have the potential to alter many currently statistically neutral responses) and are projected to increase in the future with climate change (Ranasinghe et al., 2021), thereby reducing time intervals which facilitate recovery (Cooley et al., 2022). Compounded by destructive fishing (Pedersen et al., 2017) and habitat fragmentation this increasing complexity of the currently observed risks (Simpson et al., 2021) highlights our still limited ability to project the true extent of the challenges marine ecosystems will face.

5 CONCLUSIONS

These results suggest European benthic organisms have highly variable responses to ocean acidification and warming. Future European benthic ecosystems will undergo restructuring based on current climate emission pathways. We highlight the vulnerability of calcifying organisms, and the potential resilience of fleshy algae. This study highlights the importance of experimental design parameters when investigating climate stressor interactions with marine organisms. Study duration in particular is highlighted as amplifying observed organism physiological responses to climate change, but average study durations are still limited in the context of decadal changes to ocean chemistry. Our understanding of how European marine ecosystems may evolve under future conditions are still limited due to focuses on specific organisms

like molluscs. Future experimental studies on marine organism responses to climate change need to expand to under represented groups like polychaetes.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**. Further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

GH, and DNS conceptualized and designed the study. GH collected the data and performed the statistical analysis. All authors contributed to manuscript revision, read, and

approved the submitted version. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.896157/full#supplementary-material>

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