

# OIKOS

## Meta-analysis

### Marine primary producers in a darker future: a meta-analysis of light effects on pelagic and benthic autotrophs



Maren Striebel<sup>1</sup>  <sup>1</sup>, Liisa Kallajoki<sup>1</sup>, Charlotte Kunze<sup>1</sup> , Jochen Wollschläger<sup>1</sup> , Anne Deininger<sup>2,3</sup> and Helmut Hillebrand<sup>1,4,5</sup> 

<sup>1</sup>Inst. for Chemistry and Biology of the Marine Environment, Carl von Ossietzky Univ. Oldenburg, Wilhelmshaven, Germany

<sup>2</sup>Centre for Coastal Research, Univ. of Agder, Kristiansand, Norway

<sup>3</sup>Norwegian Inst. for Water Research (NIVA), Oslo, Norway

<sup>4</sup>Helmholtz Inst. for Functional Marine Biodiversity (HIFMB), Univ. Oldenburg, Oldenburg, Germany

<sup>5</sup>Alfred Wegener Inst., Helmholtz Centre for Polar and Marine Research, Bremerhaven, Germany

Correspondence: Maren Striebel ([maren.striebe@uni-oldenburg.de](mailto:maren.striebe@uni-oldenburg.de))

Oikos

2023: e09501

doi: [10.1111/oik.09501](https://doi.org/10.1111/oik.09501)

Subject Editor: Peter Todd

Editor-in-Chief: Dries Bonte

Accepted 7 December 2022



The availability of underwater light, as primary energy source for all aquatic photoautotrophs, is (and will further be) altered by changing precipitation, water turbidity, mixing depth, and terrestrial input of chromophoric dissolved organic matter (CDOM). While experimental manipulations of CDOM input and turbidity are frequent, they often involve multiple interdependent changes (light, nutrients, C-supply). To create a baseline for the expected effects of light reduction alone, we performed a weighted meta-analysis on 240 published experiments (from 108 studies yielding 2500 effect sizes) that directly reduced light availability and measured marine autotroph responses. Across all organisms, habitats, and response variables, reduced light led to an average 23% reduction in biomass-related performance, whereas the effect sizes on physiological performance did not significantly differ from zero. Especially, pigment content increased with reduced light, which indicated a strong physiological plasticity in response to diminished light. This acclimation potential was also indicated by light reduction effects minimized if the experiments lasted longer. Nevertheless, the performance (especially biomass accrual) was reduced the more the less light intensity remained available. Light reduction effects were also more negative at higher temperatures if ambient light conditions were poor. Macrophytes or benthic systems were more negatively affected by light reduction than microalgae or plankton systems, especially in physiological responses were microalgae and plankton showed slightly positive

Synthesis

Underwater light availability for marine primary producers is changing in manifold ways. As experimental setups often include multiple factors that are changing in addition to light availability, a weighted meta-analysis on 240 published experiments that directly reduced light availability was performed to create a baseline for the expected effects of light reduction. Across all organisms, habitats, and response variables, reduced light led to an average 23% reduction in biomass-related performance, whereas the physiological performance did not significantly differ from zero. The strong log-linear relationship between remaining light and autotrophic performance observed in our study can be used to predict marine primary production in future light climate.



[www.oikosjournal.org](http://www.oikosjournal.org)

responses. Otherwise, the effect magnitudes remained surprisingly consistent across habitats and aspects of experimental design. Therefore, the strong observed log–linear relationship between remaining light and autotrophic performance can be used as a baseline to predict marine primary production in future light climate.

Keywords: climate change ecology, irradiance, macrophytes, meta-analysis, microphytobenthos, phytoplankton, primary producers, seagrass

## Introduction

Light is of central importance in aquatic ecosystems as primary energy source for aquatic photoautotrophs (Ryther 1956), essential condition for visually hunting predators (Mazur and Beauchamp 2003) and trigger of daily and seasonal behaviour as well as the life history of many plant and animal species (McFarland 1986). Changes in underwater light climate thus will have major consequences for species composition and ecosystem functioning (Winder et al. 2012, Lunt and Smee 2019, Luimstra et al. 2020). Such changes must be expected to occur with ongoing climate change and increased human activities on land (de Wit et al. 2016, Deining and Frigstad 2019, Dutkiewicz et al. 2019). The amount of light available in a certain depth is on the one hand determined by the radiation impinging on the sea surface, and on the other hand by the concentration and composition of light attenuating substances in the water. In the visible range, these are predominantly phytoplankton pigments, chromophoric dissolved organic matter (CDOM) and non-algal particles (e.g. mineral particles).

A predicted consequence of the climate change is a change in precipitation patterns. Particularly in higher latitude areas an increase of intense rain events (IPCC 2014) will result in a higher input of freshwater and terrestrial material in the aquatic, especially the coastal ecosystems. This material includes terrestrial CDOM, suspended sediments that increase turbidity, and nutrients fostering phytoplankton growth. In addition, higher precipitation does not only alter terrestrial run-off, but changes light conditions directly due to increased cloud coverage. Furthermore, freshening of marine ecosystems changes also other parameters controlling the growth of primary producers like the mixing regime, the vertical transport of nutrients and the depth of the nutricline (Ji et al. 2008, Aksnes et al. 2009, Wikner and Andersson 2012, Coupel et al. 2015).

Freshening is also a potential consequence of glacier melting, and meltwater additionally increases turbidity by transporting high concentrations of particles, altering biodiversity and species composition (Dierssen et al. 2002, Sommaruga 2015, Lunt and Smee 2019). Further reductions in light availability can be deduced from increasing particle resuspension in shallow areas related to increased storminess and dredging activity (Fettweis et al. 2011, Forsberg et al. 2019). Finally, also changes in autotrophic biomass and community composition itself alter light absorption, contributing to temporal trends of light availability (Opdal et al. 2019) with consequences for the relative role of benthic and pelagic primary producers (Vadeboncoeur et al. 2003, Griffiths et al. 2017).

Consequently, light availability in coastal areas is in a phase of rapid change, with multiple feedbacks between climate, biota and geomorphology. A darker coastal future is a likely emergent consequence of these interacting drivers, which motivates the need to provide a quantitative baseline of how photoautotrophic organisms will respond to reduced light availability. However, experimental manipulations of DOM input or sediment input not only alter light, but also provide nutrients or alter other chemical aspects of the habitat, which makes it difficult to separate light reduction effects from other consequences. Therefore, we performed a meta-analysis on direct light manipulation experiments to summarize the response of marine pelagic and benthic photoautotrophs to diminished light isolated from confounding factors. Meta-analyses are an excellent tool for such a synthesis as they allow us to derive quantitative estimates of average response magnitudes to environmental changes. Prominent examples include meta-analyses on warming (Lin et al. 2010, Wu et al. 2011, Gruner et al. 2017), precipitation changes (Wu et al. 2011, Liu et al. 2016), ocean acidification (Kroeker et al. 2013, Nagelkerken and Connell 2015) and altered nutrient availability (Elser et al. 2007, Gruner et al. 2008, Lu et al. 2011). In addition to reveal general tendencies, meta-analyses also allow to generate new hypotheses on the mechanisms driving these effects by analysing the heterogeneity of effect sizes, e.g. between habitats and organism groups.

Seagrasses, macroalgae, microphytobenthos and phytoplankton all contribute significantly to the total primary production of coastal zones and thus the global carbon cycle. Therefore, predictions of future primary production need to be informed by quantitative assessments of light reduction effects on both physiology and biomass production of these different groups. We compiled a database with 2500 effect sizes derived from 240 experiments in 108 studies, reflecting two broad types of responses: autotroph biomass (biomass, growth rate, abundance, cover, volume- or size-specific productivity) and physiology (biomass-specific productivity, photosynthesis, carbon or pigment content). We first quantified weighted overall effects of reduced light availability on marine primary producers and then examined sources of variation in effect sizes related to organism group, experimental approach, habitat and intensity of light reduction. Specifically, we hypothesize that light reduction will significantly reduce autotroph performance (H1a), but with potential different magnitudes for physiological responses and biomass production (H1b). We expect the response to be proportional to the amount of reduction (H2a) and more severe under conditions of higher growth rates (higher temperature, nutrient availability, shorter generation times, H2b). Further

variation in effect sizes will be related to habitats and aspects of experimental design (lab versus field, experimental unit, type of light manipulation) (H3a), and within that on the duration of the light reduction treatment (H3b), as longer-lasting experiments allow for acclimation.

## Methods

We followed the most recent recommendations for performing research synthesis and reporting meta-analysis in the setup, conduction and documentation of this meta-analysis (Koricheva and Gurevitch 2014, Nakagawa et al. 2017). We amend the description of the method below with a table of compliance to recommendations (Supporting information) and a detailed assessment of study selection (Supporting information) and publication bias (Supporting information).

### Data extraction

Relevant studies for the search were identified on ISI Web of Science (WOS) using the search term: '(light\* OR irradianc\* OR shadin\* OR light treatmen\*) AND (experimen\* OR manipul\* OR field experimen\* OR enclosure\* mesocosm\* OR treatment\*) AND (phytoplankt\* OR macroalga\* OR microphytobenth\*) AND (marin\* NOT freshwater)'. The search performed in December 2020 resulted in 1599 published studies. From these, we selected studies manipulating light availability with a clear definition of treatment and control (Supporting information). Consequently, 252 studies were selected for in-depth screening based on the abstracts. From this pre-selection, studies were excluded when 1) freshwater systems were addressed, or 2) they did not report mean and a measure of variance (standard deviation, standard error of mean) for an autotroph biomass or a physiological response to light availability. 108 studies remained reporting results of 240 experiments, for which data extraction was done directly from the manuscript or from the incorporated figures using WebPlot Digitizer (Rohatgi 2019). Because single studies reported multiple experiments and single experiments were sampled more than once, data extraction yielded 2500 effect sizes ( $k$ ). Multiple effect sizes from a single experiment create non-independence in the data, but as detailed below, we accounted for this by using multilevel statistical analyses. In the context of our hypotheses, this approach was needed as we explicitly test for difference in different response variables (hypotheses H1b), at different levels of light reduction (H2a) and with different timing and thus chance for acclimation (H3b).

Each experiment resulted in one or several estimates of the mean and standard deviation of the response variable for both treatment (reduced light) and control (ambient or higher light levels) as well as the respective number of replicates. Additionally, we extracted the following set of categorical and continuous variables (highlighted in bold) that detail the experiment, the habitat and organism group, potential covariates and the response variables:

### Experiment

Experiments were either done in the lab ( $k=1824$ ) or in the field ( $k=676$ ) (lab.field), the latter including all outdoor manipulations. More precisely, experimental types distinguished field measurements ( $k=228$ ), incubation experiments ( $k=177$ , mostly in situ), mesocosms ( $k=363$ ) and microcosms (predominantly in the lab, often with cultures,  $k=1832$ ). The type of light treatment by three categories depended on the used methodology: 1) shading screens ( $k=753$ ), 2) irradiance reduction by e.g. dimming light ( $k=1152$ ) and 3) gradients ( $k=568$ ). A fourth category 'other' ( $k=27$ ) covered a variety of rarely used approaches for light change. We quantified the strength of the light treatment by the remaining % light as continuous variable, ranging from 91% to almost complete darkness. We also recorded the duration of the experiment in days as continuous, ln-transformed moderator. The size of the experiment and the ambient irradiance were reported using different measures in the studies (area and volume in the former, instantaneous photon flux and daily light doses in the latter). To be able to use both aspects, we calculated instantaneous photon flux from the daily light doses assuming 12 h daylight and converted area-based sized to volume assuming a third dimension of 1 m, thus an area of 1 m<sup>2</sup> corresponds to 1000 l. The spatial distribution of the studies was surprisingly broad (Supporting information), covering a range from 73.21°N to 77.52°S. We used absolute latitude as a predictor in our analyses. We followed recommendations (Supporting information) in testing whether effect sizes changed with year of publication (publication year) to see whether there were systematic biases in the evolution of this research field.

### Organisms and habitats

We differentiated studies into pelagic ( $k=1844$ ) or benthic ( $k=656$ ) systems. Most studies were from coastal habitats ( $k=1467$ , both pelagic and benthic), which was contrasted to offshore ( $k=278$ ) and 'culture' for experiments dealing with laboratory cultures ( $k=755$ ) categories. With respect to organism groups, we reduced the comparison to macrophytes (seagrass, benthic macroalgae,  $k=550$ ) and microalgae ( $k=1950$ , microphytobenthos and phytoplankton).

### Covariates

The temperature (°C) measured during the experiment was used as a continuous moderator. Only a subset of studies reported nutrient availability in the form of total nitrogen and/or total phosphorus, which were highly correlated ( $r=0.90$ ,  $p < 0.001$ ). We therefore only used ln-transformed concentration of TN ( $\mu\text{mol l}^{-1}$ ).

### Responses

The variables used for quantifying the treatment effects were divided into two response types, biomass ( $k=1655$ ; standing stock in the form of abundance, biomass, biovolume or dry mass, primary production per area or volume, growth rates) and physiological responses ( $k=845$ ; cellular content of pigments, or primary productivity per unit

biomass or maximum electron transport rate). We used a second variable response category that detailed these types into four categories each: the response type biomass included 1) abundance ( $k=421$ ), 2) biomass (including biovolume, mass, chlorophyll per volume or area) ( $k=920$ ), 3) growth rate ( $k=155$ ) and 4) absolute productivity (per unit area or volume) ( $k=159$ ). The response type physiology comprised 1) specific productivity (per unit biomass) ( $k=219$ ), 2) cellular content of pigments ( $k=145$ ), 3) cellular content of other molecules (storage molecules, nutrients) ( $k=49$ ) and 4) the maximum quantum yield or electron transport ( $k=432$ ).

## Effect sizes

We calculated the log response ratio (LRR), which is among the most widely used effect size metrics used to quantify differences between treatment responses (LaJeunesse and Forbes 2003, Koricheva et al. 2013). Specifically, LRR represent relative changes in the response variable, as the treatment mean  $T$  is expressed as ln-transformed ratio to the control mean  $C$ .

$$\text{LRR} = \ln\left(\frac{T}{C}\right)$$

For each effect size, we used the inverse of the sampling variance var.LRR for weighting, which is based on the standard deviation (SD), number of replicates ( $N$ ) and means of treatment and control, respectively.

$$\text{var.LRR} = \left(\frac{\text{SD}_T^2}{T^2 \times N_T}\right) + \left(\frac{\text{SD}_C^2}{C^2 \times N_C}\right)$$

## Statistical methods

All analyses were performed in R ([www.r-project.org](http://www.r-project.org)) using the package metafor (Viechtbauer 2010). Following recommendations how to handle non-independent effect sizes (Konstantopoulos 2011, Cheung 2019), we performed a multi-level meta-analysis, with a nested random effect structure with unique experiments nested in unique studies. We chose this approach as studies differed how many experiments they reported.

We performed this multi-level weighted analysis without moderators ( $k=2500$ ) to test H1a (evaluating general light reduction effects on autotrophic performance) and as a multivariate weighted metaregression using moderators to test all other hypotheses. For the latter, we chose an additive model without interactions, equivalent to a main effect analysis. A fully interactive model was not possible as in our dataset, like in most meta-analyses, the distribution of studies across categories was highly unequal and non-orthogonal. This reflects that certain level combinations are either not possible or not used in experimental designs.

To produce unbiased average effect sizes and their confidence intervals, we used the multi-level weighted analysis

without moderators for a) all data, b) the biomass and physiology responses separately, and c) for all categorical groups in each predictor variable separately for physiology and biomass. Here, confidence intervals not including zero indicated significant positive or negative effects overall. For the complete model, the same random effect structure (experiments within studies) was used and amended by fixed effect moderators, for which we included response type, response category, lab. field, experiment unit type, habitat, system, organism group and type of light treatment as categorical variables and absolute temperature, duration, publication year and remaining % light as continuous variables. Significance of predictors rejected the null hypotheses corresponding to H2 and H3).

As not all studies reported all moderator values, the additive model comprised 2078 effect sizes. In order to evaluate whether this change in the data set and the presence of other moderators mattered, we also performed univariate multi-level meta-analyses and compared the outcome to the effect of the same moderator in the additive model (Supporting information). This comparison served three additional purposes. First, it allowed investigating whether collinearity between predictors changed the sign and significance of single moderators. As detailed, the effects were highly congruent between univariate and multivariate explanatory models. From 22 estimates in the complete model, only 2 estimates were significant in one analysis and changed sign in the other coinciding with becoming non-significant. Both these cases are detailed in the Results but overall the complete model was not strongly affected by collinearity or the reduction in  $k$ . Additionally, the univariate models provided predictor-specific intercepts in contrast to the complete model, which gives a single intercept for a certain combination of predictor groups at 0 (or 1 if log-transformed) values for continuous predictors.

For four variables, the amount of missing information was so high that their inclusion in the additive model would have caused massive reduction in the database by > 500 effect sizes. Therefore, we tested the moderating effects of incoming irradiance, experiment size, latitude and TN concentrations only in the univariate analyses (Supporting information).

## Results

The weighted mean effect size of light reduction across all organisms, habitats and response variables was significantly negative (mean LRR:  $-0.172$ ,  $p < 0.0001$ , 95% confidence interval (CI)  $-0.252$  to  $-0.092$ , number of effect size  $k=2500$ ). This corresponds to an average 16% reduction in performance, but with a large heterogeneity ( $Q=276$  296.4,  $p < 0.001$ ) indicating significant structuring of the effect sizes. The overall negative effect was driven by biomass responses (overall mean =  $-0.257$  corresponding to a 23% reduction, CI =  $-0.346$  to  $-0.168$ ,  $k=1655$ ) whereas for physiological responses the overall mean (0.042, 95% CI:  $-0.070$  to 0.154,  $k=845$ ) was not significantly different from zero (Fig. 1A). This difference between response types remained



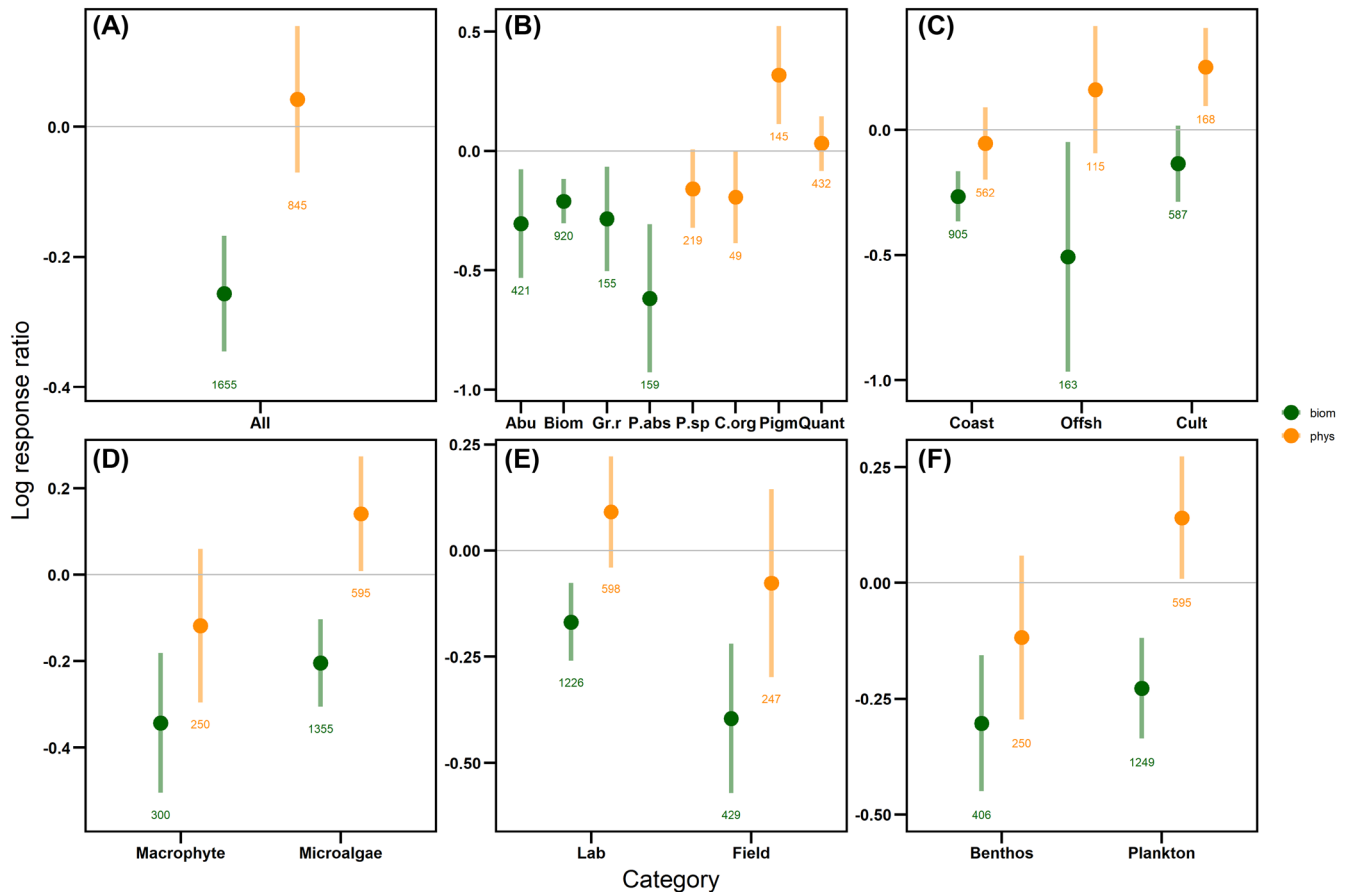


Figure 1. Effect size (log response ratios) of light reduction on marine autotroph biomass (green) and physiology (orange). Symbols represent mean effect size per category, whiskers represent 95% confidence intervals, both estimated from weighted random effects models for each specific group and separately for physiological and biomass response types. (A) Differentiation of all effect sizes between physiological and biomass response types. (B) Differentiation of effect sizes for response categories (Abu=abundance, Biom=biomass, Gr.r=growth rate, P.abs=absolute productivity (per unit area or volume), P.sp.=specific productivity (per unit C or size), Pigm=pigment content, Quant=quantum yield). (C) Differentiation of effect sizes for habitats coastal, offshore and lab cultures. (D) Differentiation of effect sizes for organism groups. (E) Differentiation of effect sizes for lab versus field experiments. (F) Differentiation of effect sizes for benthic and pelagic systems. Numbers are k, number of effect sizes.

significant in the complete multivariate model (Table 1) as in the univariate model (Supporting information).

The complete model explained significant heterogeneity in effect sizes (explained  $Q=32\ 577.3$ ,  $p < 0.001$ ), but substantial residual heterogeneity remained ( $Q=151\ 754.3$ ,  $p < 0.001$ ). Of this heterogeneity, 39.7% was contributable to differences between studies and 59.6% to different experiments within studies. Further detailing the response categories did not explain significant variance in the multivariate model (Table 1), but pigment content was the only response category deviating positively from zero (Fig. 1B) and significantly differed in the univariate model (Supporting information).

Effect sizes differed neither with habitat (Fig. 1C) nor between lab and field experiments (Fig. 1E). Consequently, both predictors were non-significant in the multivariate model (Table 1). Likewise, effect sizes were not significantly different between types of experimental unit or between methods

by which light was manipulated (Table 1, Supporting information). However, macrophytes were clearly more negatively affected by light reduction than microalgae, especially in physiological responses (Fig. 1D), such that organism group was a significant predictor in both multivariate (Table 1) and univariate (Supporting information) models. The difference between systems indicated a similar difference between phytoplankton and phytobenthos (Fig. 1F), which was captured in the univariate model, but in the complete model this turned into a negative deviation for the phytoplankton data.

Among the continuous moderators, light reduction effects on primary producers were mainly constrained by the remaining % light, the duration of the experiment and the temperature (Table 1, Supporting information). Effect sizes became significantly more negative if light was reduced more (Fig. 2A, Supporting information). The slope of the partial relationship in the complete model ( $b=0.075$ ) was remarkably consistent with the univariate model (Supporting

Table 1. Multi-level multivariate meta-analyses for all data, the heterogeneity explained by the model was significant (QM=32577, df=22,  $p < 0.001$ ), the fixed effects explained 11.6% of the variance (pseudo- $R^2$  through variance reduction between a model with and without moderators). Random variance components comprised 'study' (85 levels,  $\sigma=0.082$ ) and 'experiment within study' (186 levels,  $\sigma=0.128$ ). For fixed effects, parameter estimates and their standard errors (SE) are given for specified contrasts (categorical variables) or slopes (continuous variables). Significant outcomes ( $p < 0.05$ ) were highlighted in bold.

Factor (contrast)	Term	Estimate	SE	p value
Intercept		2.8779	15.5400	0.8528
Response type (physiology)	Biomass	<b>-0.4263</b>	<b>0.1443</b>	<b>0.0031</b>
Response category (abundance)	Biomass	0.0499	0.1227	0.6841
	Carbon content	-0.2758	0.2306	0.2317
	Pigment content	0.1362	0.1280	0.2871
	Growth rate	0.0573	0.1411	0.6848
	Absol. productivity	-0.3010	0.1936	0.1200
	Specific prod.	-0.2756	0.1526	0.0710
Habitat (offshore)	Coastal	-0.2621	0.2415	0.2781
	Cultures	-0.1122	0.2499	0.6534
Organism type (macrophytes)	Microalgae	<b>0.4452</b>	<b>0.2134</b>	<b>0.0370</b>
Lab-field (lab)	Field	-0.0973	0.1602	0.5432
System (benthos)	Plankton	<b>-0.4578</b>	<b>0.2162</b>	<b>0.0342</b>
Experimental unit (field plot)	Incubation	0.0608	0.3169	0.8479
	Mesocosm	0.1743	0.2111	0.4088
	Microcosm	0.2311	0.2345	0.3243
Light treatment (gradient)	Light reduced	-0.0857	0.1354	0.5267
	Other	-0.3734	0.3126	0.2323
	Shading screen	-0.1297	0.1907	0.4966
Remaining light (%)	Slope	<b>0.0075</b>	<b>&lt; 0.0001</b>	<b>0.0000</b>
Temperature (°C)	Slope	<b>-0.0048</b>	<b>0.0007</b>	<b>0.0000</b>
Duration (LN days)	Slope	<b>0.0660</b>	<b>0.0029</b>	<b>0.0000</b>
Publication year	Slope	-0.0015	0.0077	0.8501

information,  $b=0.072$ ). The significant positive relationship between experiment duration and effect size (Fig. 2B) was also consistently found in the multivariate model (Table 1) and in the univariate analysis (Supporting information), i.e. indicating less negative effects in longer-lasting experiments. Additionally, temperature affected the responses (Table 1), with more negative effects of light reduction found at higher temperatures (Fig. 2C, Supporting information). The multivariate model did not capture a significant change in effect sizes with publication year (Fig. 2D, Table 1). Only in the univariate analysis, we found that older studies tended to have more negative response magnitudes (Supporting information).

From the four additional continuous moderators, which were too rarely reported for inclusion in the full model, two explained significant variation in the effect sizes (Supporting information). Light reduction had less negative impacts at high incoming irradiance (Supporting information) and in smaller experiments (Supporting information). By contrast, neither the availability of nitrogen (total N, Supporting information) nor latitude (Supporting information) were significant moderators of light reduction effects.

## Discussion

In our meta-analysis across 240 experiments from 108 studies ( $k=2500$ ), we found a clear and significant reduction in marine autotroph performance with decreasing light

(accepting hypothesis H1a). The grand mean effect size corresponds to a 16% average reduction in performance, but we found a strong and significant difference between a significant decline in biomass production (on average by 23%) compared to a much weaker effect on physiological response variables which was not significantly different from zero (accepting H1b). Thus, recent and predicted future coastal darkening will primarily reduce biomass of marine autotrophic groups and the magnitude of the observed performance decline fuels concerns about the consequences of darkening effects for marine primary production and coastal food webs (Aksnes et al. 2009, Dutkiewicz et al. 2019, McGovern et al. 2019).

Further division of biomass and physiology responses into categories revealed that biomass responses were significantly negative independent of the actual metric used: Confidence intervals for abundance, biomass, growth rate and absolute productivity were all widely overlapping, but none of them included zero. The non-significant results for physiological variables, by contrast, were fuelled by a dichotomy between negative light reduction effects on specific productivity and organic C content, but positive effects on pigment content. This indicates that algal biomass as well as their C-fixation and storage tend to decrease with reductions in light availability, but their pigment concentrations per cell (or per carbon) tend to increase (Geider et al. 1998, Goericke and Montoya 1998, Henriksen et al. 2002). Pigments play key roles in the short- and long-term responses, thus, acclimation and adaptation, of phytoplankton to the variability of

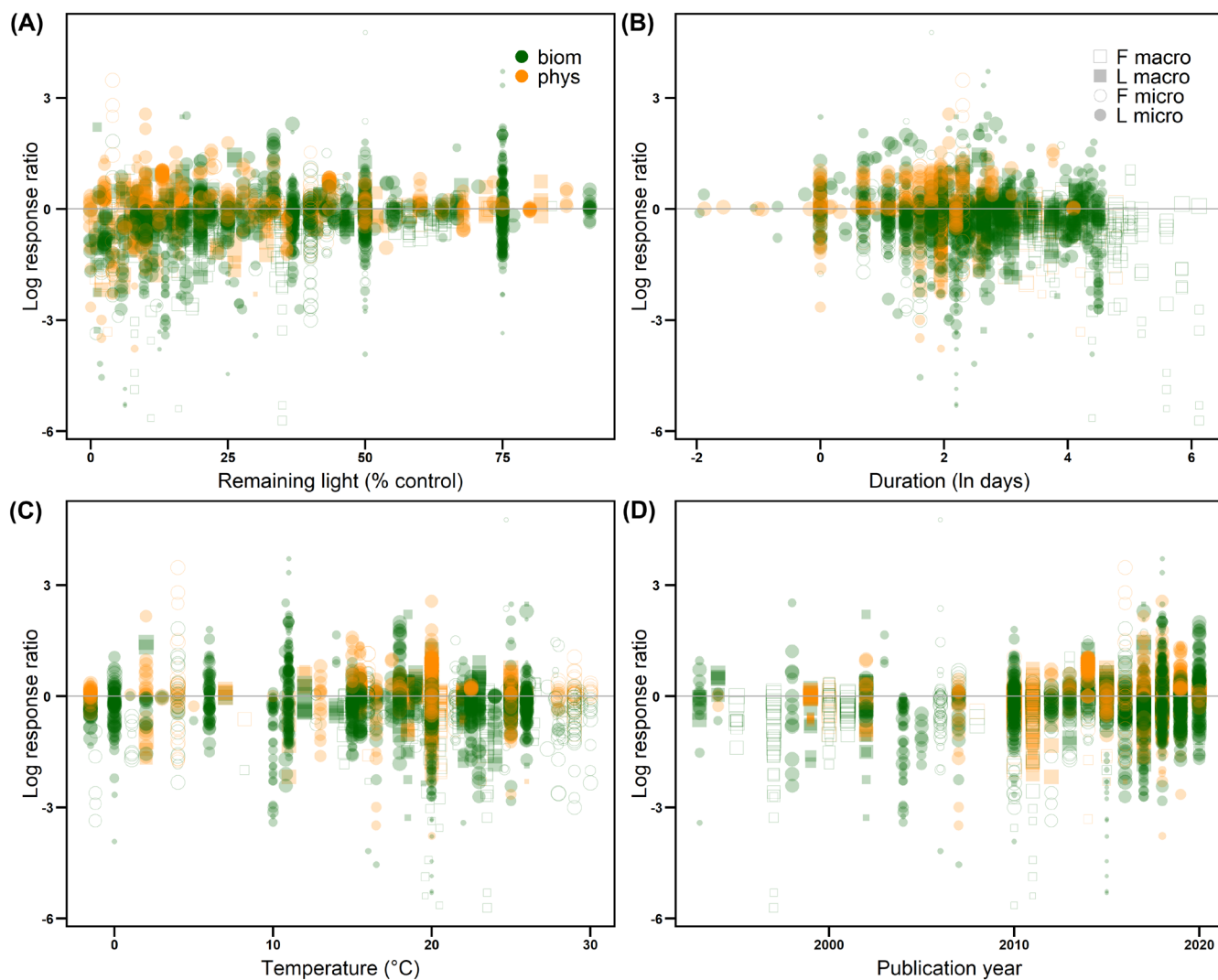


Figure 2. Effect size (log response ratios) of light reduction on marine autotroph biomass (green) and physiology (orange). Symbol size corresponds to individual weight of effect size, symbols differentiate between organism groups as well as field (F) and lab (L) experiments. Each panel correlates the log response ratios to remaining % light (A), log transformed duration of the experiment (B), ambient temperature ( $^{\circ}\text{C}$ ) (C), and publication year (D).

light and could have been increased under low light conditions to compensate for reduced light availability, albeit not resulting in similar biomass as under high light conditions. Furthermore, also the time-frame of the experiments could be an explanation as the increased pigment concentrations per cell might be the first response of the autotrophic cells to harvest light and allocate energy while the impact on biomass occurred later.

These results have potentially wide-reaching conclusions for monitoring programs that often use chlorophyll *a* as a simple biomass proxy (Andersen et al. 2006). Our data strongly suggest that under changing light conditions pigments do not suffice to monitor algal biomass. Especially under turbid, nutrient-rich conditions, changes in algal biomass may be underestimated when using chlorophyll *a* concentrations as sole proxy as increasing cellular concentrations

partly compensate the biomass reduction. Monitoring should include additional parameters (biovolume, primary production, carbon or cell counts), the more so as cellular pigment concentrations also depend on temperature, another factor currently changing. While the carbon to chlorophyll *a* ratio in phytoplankton increases with increasing light at constant temperature (= decreasing pigment concentration), it decreases exponentially (thus pigment concentration increases) with increasing temperature under constant light (Geider 1987).

Our analyses found a tight coupling between the amount of reduction in light intensity and the magnitude of performance loss (accepting H2a). Using the predictions for the complete model across all data, we found a clear dependence of the remaining performance on the remaining % light, with biomass-related performance always more negatively affected than physiology (Fig. 3). The relationship between % light

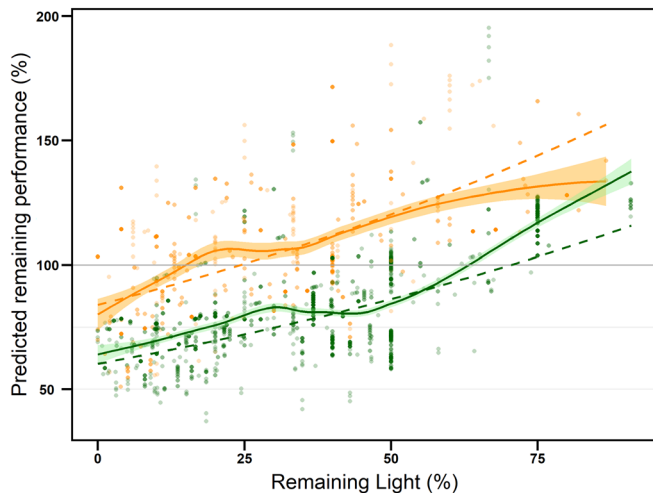


Figure 3. Predicted values from multi-level meta-analysis for the relationship between light reduction and autotroph performance. Points are predicted LRR values from the complete model, back-transformed to arithmetic space (LRR=0 equals no change in performance=100%). Solid lines provide a loess fit to these data including an error estimate. Dashed lines are a loess fit of the prediction from a model only including remaining light and response type, distinguished by color as biomass (green) and physiology (orange) respectively.

and % performance remained largely parallel for physiological and biomass responses, but negative impacts occur in the latter already at 25–30% reduction. The inclusion or exclusion of other moderators hardly changed the predictions along the remaining light gradient at all, indicating that this relationship can serve as a general baseline for predicting the effects of a darker future for aquatic systems.

Other ecological covariates had some but not consistent moderating influence on the effect sizes (partly rejecting H2b). More negative effects at higher temperatures and at higher incoming irradiance indicate that light reduction has a stronger effect under good growth conditions. However, neither the availability of nutrients nor latitude had significant effects on response magnitudes and habitat differences were absent as well. The results on organism type and system were less conclusive. In the univariate analyses, plankton systems and microalgae responded significantly less negative to light reduction than benthic systems or macrophytes, respectively (Supporting information). While the less negative effects for microalgae remained in the complete model, the difference between benthic and pelagic systems reversed to a more negative response of the pelagic. This can easily be explained by the interdependency of categorizations as all plankton are microalgae, but some microalgae are benthic. We had expected that benthic and pelagic organisms respond differently to light attenuation given the strong role of vertical light profile in the interaction between phytobenthos and phytoplankton (Vadeboncoeur et al. 2003). Moreover, Duarte (1991) showed that the distribution depth of seagrasses is highly light limited and their strong response to light reduction might reflect a high sensitivity of these marine angiosperms to underwater

light attenuation (Williams and Ruckelshaus 1993, Carr et al. 2010). Microphytobenthos on the other hand, is reportedly tolerant to shading (Barranguet et al. 1998, Gattuso et al. 2006). Fuelled by the univariate results, we expect that a darker coastal future will be especially detrimental to macrobenthic primary producers, as light climate close to the bottom is not only affected by more turbid waters but also by waves, erosion and trawling (Capuzzo et al. 2015, Wilson and Heath 2019).

Other moderators related to experimental design had no impact on the results (rejecting H3a) with the sole exception of experiment duration (accepting H3b). Here, we observed lower response magnitudes in longer-lasting experiments. This result strongly points to acclimation of photoautotrophs to altered light levels, which e.g. involves increasing the cellular pigment content (Falkowski and LaRoche 1991, Geider et al. 1998, Deiningner et al. 2016). The internal pigment content of algae grown under reduced light intensities may increase two- to five-fold (Richardson et al. 1983, Falkowski and LaRoche 1991, Deiningner et al. 2016), but this acclimation takes time and costs energy (Nicklisch 1998, Leeuwe et al. 2005). Aside from this duration effect, the findings were very consistent for different types of experiments, whether they were conducted in the field or the lab, how they manipulated the light availability, and of which size they were.

Therefore, we conclude that a reduction in light intensity will result in a significant reduction of marine photoautotrophic performance across all investigated habitats, organisms, experimental designs and conditions. Our study provides a quantitative baseline describing how autotrophic performance is declining and may further decline in a darker coastal future. For future steps, our study addressed only the effects of changing light quantities on coastal- and marine environments. Coastal darkening, however, also comprises changes in light quality. Determining the effects of altered light quality and light spectra on coastal on marine photoautotrophs will be a next crucial step to improve our understanding and prediction of coastal- and marine zones under potential future coastal darkening scenarios.

**Funding** – MS and HH received funding as part of the AQUACOSM\_plus project that received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement no. 871081. MS, LK and JW were funded by the project 'Coastal Ocean Darkening' by the Ministry for Science and Culture of Lower Saxony, Germany (project number: VWZN3175). HH was funded by Deutsche Forschungsgemeinschaft DFG HI848/26-1 and HIFMB, a collaboration between the Alfred-Wegener Institute, Helmholtz-Center for Polar and Marine Research, and the Carl-von Ossietzky University Oldenburg, initially funded by the Ministry for Science and Culture of Lower Saxony and the Volkswagen Foundation through the 'Niedersächsisches Vorab' grant program (grant number ZN3285). CK was funded by Deutsche Forschungsgemeinschaft DFG HI 848/29-1 and by the German Academic Exchange Service (DAAD: 91790542). The research exchange of AD at the University of Oldenburg was funded by a strategic institute program of the Norwegian Institute of Water Research on the topic land-ocean interactions (Project: DOMquality).



*Conflict of interest* – All authors disclose any potential sources of conflict of interest.

## Author contributions

**Maren Striebel:** Conceptualization (lead); Data curation (supporting); Formal analysis (supporting); Funding acquisition (equal); Writing – original draft (equal); Writing – review and editing (equal). **Liisa Kallajoki:** Conceptualization (equal); Data curation (lead); Writing – review and editing (equal). **Charlotte Kunze:** Data curation (lead); Formal analysis (supporting); Validation (supporting); Writing – review and editing (equal). **Jochen Wollschläger:** Data curation (supporting); Formal analysis (supporting); Validation (equal); Writing – review and editing (equal). **Anne Deininger:** Writing – original draft (equal); Writing – review and editing (equal). **Helmut Hillebrand:** Conceptualization (lead); Formal analysis (lead); Validation (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal).

## Data availability statement

Data and metadata, together with code to reproduce the figures and results, are uploaded to Dryad Digital Repository: <https://doi.org/10.5061/dryad.sxksn036w> (Striebel et al. 2022).

## Supporting information

The Supporting information associated with this article is available in the online version.

## References

- Aksnes, D. L., Dupont, N., Staby, A., Fiksen, Ø., Kaartvedt, S. and Aure, J. 2009. Coastal water darkening and implications for mesopelagic regime shifts in Norwegian fjords. – *Mar. Ecol. Prog. Ser.* 387: 39–49.
- Andersen, J. H., Schlüter, L. and Ærtebjerg, G. 2006. Coastal eutrophication: recent developments in definitions and implications for monitoring strategies. – *J. Plankton Res.* 28: 621–628.
- Barranguet, C., Kromkamp, J. and Peene, J. 1998. Factor controlling primary production and photosynthetic characteristics of intertidal microphytobenthos. – *Mar. Ecol. Prog. Ser.* 173: 117–126.
- Capuzzo, E., Stephens, D., Silva, T., Barry, J. and Forster, R. M. 2015. Decrease in water clarity of the southern and central North Sea during the 20th century. – *Global Change Biol.* 21: 2206–2214.
- Carr, J., D'Odorico, P., McGlathery, K. and Wiberg, P. 2010. Stability and bistability of seagrass ecosystems in shallow coastal lagoons: role of feedbacks with sediment resuspension and light attenuation. – *J. Geophys. Res. Biogeosci.* 115. <https://doi.org/10.1029/2009JG001103>
- Cheung, M. W. L. 2019. A guide to conducting a meta-analysis with non-independent effect sizes. – *Neuropsychol. Rev.* 29: 387–396.
- Coupe, P., Ruiz-Pino, D., Sicre, M. A., Chen, J. F., Lee, S. H., Schiffrine, N., Li, H. L. and Gascard, J. C. 2015. The impact of freshening on phytoplankton production in the Pacific Arctic Ocean. – *Prog. Oceanogr.* 131: 113–125.
- de Wit, H. A., Valinia, S., Weyhenmeyer, G. A., Futter, M. N., Kortelainen, P., Austnes, K., Hessen, D. O., Raike, A., Laudon, H. and Vuorenmaa, J. 2016. Current browning of surface waters will be further promoted by wetter climate. – *Environ. Sci. Technol. Lett.* 3: 430–435.
- Deininger, A. and Frigstad, H. 2019. Reevaluating the role of organic matter sources for coastal eutrophication, oligotrophication and ecosystem health. – *Front. Mar. Sci.* 6: 210.
- Deininger, A., Faithfull, C. L., Lange, K., Bayer, T., Vidussi, F. and Liess, A. 2016. Simulated terrestrial runoff triggered a phytoplankton succession and changed seston stoichiometry in coastal lagoon mesocosms. – *Mar. Environ. Res.* 119: 40–50.
- Dierssen, H. M., Smith, R. C. and Vernet, M. 2002. Glacial meltwater dynamics in coastal waters west of the Antarctic peninsula. – *Proc. Natl Acad. Sci. USA* 99: 1790–1795.
- Duarte, C. M. 1991. Seagrass depth limits. – *Aquat. Bot.* 40: 363–377.
- Dutkiewicz, S., Hickman, A. E., Jahn, O., Henson, S., Beaulieu, C. and Monier, E. 2019. Ocean colour signature of climate change. – *Nat. Commun.* 10: 578.
- Elser, J. J., Bracken, M. E. S., Cleland, E. E., Gruner, D. S., Harpole, W. S., Hillebrand, H., Ngai, J. T., Seabloom, E. W., Shurin, J. B. and Smith, J. E. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. – *Ecol. Lett.* 10: 1135–1142.
- Falkowski, P. G. and LaRoche, J. 1991. Acclimation to spectral irradiance in algae. – *J. Phycol.* 27: 8–14.
- Fettweis, M., Baeye, M., Francken, F., Lauwaert, B., Van den Eynde, D., Van Lancker, V., Martens, C. and Michiels, T. 2011. Monitoring the effects of disposal of fine sediments from maintenance dredging on suspended particulate matter concentration in the Belgian nearshore area (southern North Sea). – *Mar. Pollut. Bull.* 62: 258–269.
- Forsberg, P. L., Lumborg, U., Andersen, T. J., Kroon, A. and Erntsen, V. B. 2019. The relative impact of future storminess versus offshore dredging on suspended sediment concentration in a shallow coastal embayment: Rødsand lagoon, western Baltic Sea. – *Ocean Dyn.* 69: 475–487.
- Gattuso, J. P., Gentili, B., Duarte, C. M., Kleypas, J. A., Middelburg, J. J. and Antoine, D. 2006. Light availability in the coastal ocean: impact on the distribution of benthic photosynthetic organisms and their contribution to primary production. – *Biogeosciences* 3: 489–513.
- Geider, R. J. 1987. Light and temperature-dependence of the carbon to chlorophyll-a ratio in microalgae and cyanobacteria – implications for physiology and growth of phytoplankton. – *New Phytol.* 106: 1–34.
- Geider, R. J., MacIntyre, H. L. and Kana, T. M. 1998. A dynamic regulatory model of phytoplankton acclimation to light and nutrients. – *Limnol. Oceanogr.* 43: 679–694.
- Goericke, R. and Montoya, J. P. 1998. Estimating the contribution of microalgal taxa to chlorophyll a in the field – variations of pigment ratios under nutrient- and light-limited growth. – *Mar. Ecol. Prog. Ser.* 169: 97–112.
- Griffiths, J. R., Kadin, M., Nascimento, F. J. A., Tamelander, T., Törnroos, A., Bonaglia, S., Bonsdorff, E., Brüchert, V., Gärdmark, A., Järnström, M., Kotta, J., Lindegren, M., Nordström, M. C., Norkko, A., Olsson, J., Weigel, B., Žydelis, R., Blenckner, T., Niiranen, S. and Winder, M. 2017. The importance of benthic–pelagic coupling for marine ecosystem functioning in a changing world. – *Global Change Biol.* 23: 2179–2196.

- Gruner, D. S., Smith, J. E., Seabloom, E. W., Sandin, S. A., Ngai, J. T., Hillebrand, H., Harpole, W. S., Elser, J. J., Cleland, E. E., Bracken, M. E. S., Borer, E. T. and Bolker, B. M. 2008. A cross-system synthesis of consumer and nutrient resource control on producer biomass. – *Ecol. Lett.* 11: 740–755.
- Gruner, D. S., Bracken, M. E. S., Berger, S. A., Eriksson, B. K., Gamfeldt, L., Matthiessen, B., Moorthi, S., Sommer, U. and Hillebrand, H. 2017. Effects of experimental warming on biodiversity depend on ecosystem type and local species composition. – *Oikos* 126: 8–17.
- Henriksen, P., Riemann, B., Kaas, H., Sørensen, H. M. and Sørensen, H. L. 2002. Effects of nutrient-limitation and irradiance on marine phytoplankton pigments. – *J. Plankton Res.* 24: 835–858.
- IPCC 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. – IPCC, Geneva, Switzerland, 151 pp.
- Ji, R., Davis, C. S., Chen, C., Townsend, D. W., Mountain, D. G. and Beardsley, R. C. 2008. Modeling the influence of low-salinity water inflow on winter–spring phytoplankton dynamics in the Nova Scotian Shelf–Gulf of Maine region. – *J. Plankton Res.* 30: 1399–1416.
- Konstantopoulos, S. 2011. Fixed effects and variance components estimation in three-level meta-analysis. – *Res. Synth. Methods* 2: 61–76.
- Koricheva, J. and Gurevitch, J. 2014. Uses and misuses of meta-analysis in plant ecology. – *J. Ecol.* 102: 828–844.
- Koricheva, J., Gurevitch, J. and Mengersen, K. 2013. Handbook of meta-analysis in ecology and evolution. – Princeton Univ. Press.
- Kroeker, K. J., Kordas, R. L., Crim, R., Hendriks, I. E., Ramajo, L., Singh, G. S., Duarte, C. M. and Gattuso, J. P. 2013. Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. – *Global Change Biol.* 19: 1884–1896.
- Lajeunesse, M. J. and Forbes, M. R. 2003. Variable reporting and quantitative reviews: a comparison of three meta-analytical techniques. – *Ecol. Lett.* 6: 448–454.
- Leeuwe, M. A. V., Sikkelerus, B. V., Gieskes, W. W. C. and Stefels, J. 2005. Taxon-specific differences in photoacclimation to fluctuating irradiance in an Antarctic diatom and a green flagellate. – *Mar. Ecol. Prog. Ser.* 288: 9–19.
- Lin, D., Xia, J. and Wan, S. 2010. Climate warming and biomass accumulation of terrestrial plants: a meta-analysis. – *New Phytol.* 188: 187–198.
- Liu, L. L., Wang, X., Lajeunesse, M. J., Miao, G. F., Piao, S. L., Wan, S. Q., Wu, Y. X., Wang, Z. H., Yang, S., Li, P. and Deng, M. F. 2016. A cross-biome synthesis of soil respiration and its determinants under simulated precipitation changes. – *Global Change Biol.* 22: 1394–1405.
- Lu, M., Yang, Y. H., Luo, Y. Q., Fang, C. M., Zhou, X. H., Chen, J. K., Yang, X. and Li, B. 2011. Responses of ecosystem nitrogen cycle to nitrogen addition: a meta-analysis. – *New Phytol.* 189: 1040–1050.
- Luimstra, V. M., Verspagen, J. M. H., Xu, T., Schuurmans, J. M. and Huisman, J. 2020. Changes in water color shift competition between phytoplankton species with contrasting light-harvesting strategies. – *Ecology* 101: e02951.
- Lunt, J. and Smee, D. L. 2019. Turbidity alters estuarine biodiversity and species composition. – *ICES J. Mar. Sci.* 77: 379–387.
- Mazur, M. M. and Beauchamp, D. A. 2003. A comparison of visual prey detection among species of piscivorous salmonids: effects of light and low turbidities. – *Environ. Biol. Fishes* 67: 397–405.
- McFarland, W. N. 1986. Light in the sea – correlations with behaviors of fishes and invertebrates. – *Am. Zool.* 26: 389–401.
- McGovern, M., Evensen, A., Borgå, K., de Wit, H. A., Braaten, H. F. V., Hessen, D. O., Schultze, S., Ruus, A. and Poste, A. 2019. Implications of coastal darkening for contaminant transport, bioavailability and trophic transfer in Northern Coastal Waters. – *Environ. Sci. Technol.* 53: 7180–7182.
- Nagelkerken, I. and Connell, S. D. 2015. Global alteration of ocean ecosystem functioning due to increasing human CO<sub>2</sub> emissions. – *Proc. Natl Acad. Sci. USA* 112: 13272–13277.
- Nakagawa, S., Noble, D. W. A., Senior, A. M. and Lagisz, M. 2017. Meta-evaluation of meta-analysis: ten appraisal questions for biologists. – *BMC Biol.* 15: 18.
- Nicklisch, A. 1998. Growth and light absorption of some planktonic cyanobacteria, diatoms and Chlorophyceae under simulated natural light fluctuations. – *J. Plankton Res.* 20: 105–119.
- Opdal, A. F., Lindemann, C. and Aksnes, D. L. 2019. Centennial decline in North Sea water clarity causes strong delay in phytoplankton bloom timing. – *Global Change Biol.* 25: 3946–3953.
- Richardson, K., Beardall, J. and Raven, J. A. 1983. Adaptation of unicellular algae to irradiance: an analysis of strategies. – *New Phytol.* 93: 157–191.
- Rohatgi, A. 2019. WebPlotDigitizer. – ver. 4.6, Pacifica, California, USA. <https://automeris.io/WebPlotDigitizer>
- Ryther, J. H. 1956. Photosynthesis in the ocean as a function of light intensity. – *Limnol. Oceanogr.* 1: 61–70.
- Sommaruga, R. 2015. When glaciers and ice sheets melt: consequences for planktonic organisms. – *J. Plankton Res.* 37: 509–518.
- Striabel, M., Kallajoki, L., Kunze, C., Wollschläger, J., Deininger, A. and Hillebrand, H. 2022. Marine primary producers in a darker future – a meta-analysis of light effects on pelagic and benthic autotrophs. Dryad Digital Repository, <https://doi.org/10.5061/dryad.sxksn036w>.
- Vadeboncoeur, Y., Jeppesen, E., Vander Zanden, M. J., Schierup, H. H., Christoffersen, K. and Lodge, D. M. 2003. From Greenland to green lakes: cultural eutrophication and the loss of benthic pathways in lakes. – *Limnol. Oceanogr.* 48: 1408–1418.
- Viechtbauer, W. 2010. Conducting meta-analyses in R with the metafor package. – *J. Stat. Softw.* 36: 1–48.
- Wikner, J. and Andersson, A. 2012. Increased freshwater discharge shifts the trophic balance in the coastal zone of the northern Baltic Sea. – *Global Change Biol.* 18: 2509–2519.
- Williams, S. L. and Ruckelshaus, M. H. 1993. Effects of nitrogen availability and herbivory on eelgrass *Zostera marina* and epiphytes. – *Ecology* 74: 904–918.
- Wilson, R. J. and Heath, M. R. 2019. Increasing turbidity in the North Sea during the 20th century due to changing wave climate. – *Ocean Sci.* 15: 1615–1625.
- Winder, M., Berger, S. A., Lewandowska, A., Aberle, N., Lengfellner, K., Sommer, U. and Diehl, S. 2012. Spring phenological responses of marine and freshwater plankton to changing temperature and light conditions. – *Mar. Biol.* 159: 2491–2501.
- Wu, Z. T., Dijkstra, P., Koch, G. W., Penuelas, J. and Hungate, B. A. 2011. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. – *Global Change Biol.* 17: 927–942.