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1 **CO₂ effects on diatoms: A Synthesis of more than a decade of ocean**

2 **acidification experiments with natural communities**

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12

13 **Abstract**

14 Diatoms account for ~40% of marine primary production and are considered to be key

15 players in the biological carbon pump. Ocean acidification (OA) is expected to affect

16 diatoms primarily by changing the availability of CO_2 as a substrate for photosynthesis

17 or through altered ecological interactions within the marine food web. Yet, there is little

18 consensus how entire diatom communities will respond to increasing CO_2. To address

19 this question, we synthesized the literature from over a decade of OA-experiments with

20 natural diatom communities to uncover: 1) if and how bulk diatom communities respond

21 to elevated CO_2; 2) if shifts within the diatom communities could be expected and how

22 they are expressed with respect to taxonomic affiliation and size structure. We found that

23 diatom communities responded to high CO_2 in ~60 % of the experiments and in this case

24 more often positively (56 %) than negatively (32 %; 12 % did not report the direction of

25   change). Shifts among different diatom species were observed in 65 % of the experiments.

26   Our synthesis supports the hypothesis that high CO_2 particularly favors larger species as

27   12 out of 13 experiments which investigated cell size found a shift towards larger species.

28   Unraveling winners and losers with respect to taxonomic affiliation was difficult due to

29   a limited database, but there is evidence that the genus *Pseudo-nitzschia* could be among

30   the losers. We conclude that OA-induced changes in diatom competitiveness and

31   assemblage structure must be classified as a "risk for ecosystem services" due to the

32   pivotal role diatoms play in trophic transfer and biogeochemical cycles.

33   **1. Introduction**

34   The global net primary production (NPP) of all terrestrial and marine autotrophs amounts

35   to approximately 105 petagrams (Pg) of carbon per year (Field et al., 1998). Marine

36   diatoms, a taxonomically diverse group of cosmopolitan phytoplankton, were estimated

37   to contribute up to 25 % (26 Pg C year^{-1}) to this number, which is more than the annual

38   primary production in any biome on land (Field et al., 1998; Nelson et al., 1995; Tréguer

39   and De La Rocha, 2013). Thus, diatoms are likely the most important single taxonomic

40   group of primary producers on Earth and any change in their prevalence relative to other

41   phytoplankton taxa could profoundly alter marine food web structures and thereby affect

42   ecosystem services such as fisheries or the sequestration of CO_2 in the deep ocean

43   (Armbrust, 2009; Tréguer et al., 2018).

44   The most conspicuous feature of diatoms is the formation of a silica shell, which is

45   believed to primarily serve as protection against grazers (Hamm and Smetacek, 2007;

46   Pančić and Kiørboe, 2018). Since the formation of this shell requires dissolved silicate,

47   diatoms are often limited by silicon as a nutrient rather than by nitrogen or phosphate

48   (Brzezinski and Nelson, 1996). However, when dissolved silicate is available, diatoms

49   benefit from their high nutrient uptake and growth rates, allowing them to outcompete

50   other phytoplankton and form intense blooms in many ocean regions (Sarthou et al.,

51   2005).

52   Diatoms display an enormous species richness, with recent estimates being in the range

53   of 30,000 species (Mann and Vanormelingen, 2013). Although only a fraction has been

54   morphologically described, known diatom taxa span a size range of several orders of

55   magnitude (<5 µm up to a few mm) with a wide range of morphologies and life strategies,

56   e.g. single cells and cell chains, pelagic and benthic habitats (Armbrust, 2009; Mann and

57   Vanormelingen, 2013; Sournia et al., 1991). Accordingly, they should not be treated as

58   one functional group, but rather as a variety of subgroups occupying different niches.

59   It is well recognized that the global importance of diatoms as well as their diversity in

60   morphology and life style is tightly linked to the functioning of pelagic food webs and

61   elemental cycling in the oceans. For example, iron enrichment experiments in the

62   Southern Ocean found that a shift in diatom community composition from thick- to thin-

63   shelled species ("persistence strategy" vs. "boom-and-bust strategy") can enhance carbon

64   and alter nutrient export via sinking particles (Assmy et al., 2013; Smetacek et al., 2012).

65   This may not only affect element fluxes locally but enhance nutrient retention within the

66   Southern Ocean and reduce productivity in the north which underlines how important

67   diatom community shifts can be on a global scale (Boyd, 2013; Primeau et al., 2013;

68   Sarmiento et al., 2004). Likewise, the cell size of diatoms can play an important role in

69   transferring energy to higher trophic levels, as the dominance of larger species is

70   generally considered to reduce the length of the food chain and lead to higher trophic

71   transfer efficiency (Sommer et al., 2002). Consequently, understanding impacts of global

72   change on diatom community composition is crucial for assessing the sensitivity of

73   biogeochemical cycles and ecosystem services in the world oceans.

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74   It has become evident that the sensitivity of diatoms to increasing pCO_2 is highly variable,

75   likely being related to specific traits such as cell size or the carbon fixation pathway, as

76   well as interactions with other environmental factors such as nutrient stress, temperature

77   or light (Gao et al., 2012; Hoppe et al., 2013; Wu et al., 2014). However, it is still rather

78   unclear how these species-specific differences in CO_2 sensitivities manifest themselves

79   on the level of diatom communities. This knowledge gap motivated us to compile the

80   presently available experimental data in order to reveal common responses of diatom

81   communities to high CO_2 and thereby assess potential scenarios of shifts in diatom

82   community composition under ocean acidification.

83   **2. Literature investigation**

84   **2.1. Approach**

85   Our original intention was to conduct a classical meta-analysis, which would have yielded

86   the benefit of a quantitative measure of diatom responses to OA, expressed as an overall

87   effect size (i.e. combined magnitude) such as the response ratio. However, our literature

88   analysis revealed a large variability in experimental pCO_2 ranges as well as measured

89   response variables, which cannot be directly compared among each other (e.g.

90   microscopic cell counts, pigment concentrations, genetic tools). These limitations impede

91   data aggregation as required for a classical meta-analysis. Furthermore, experimental

92   setups differed widely in terms of other environmental factors such as temperature, light,

93   and nutrient concentrations, all of which are known to modulate potential responses to

94   pCO_2 (Boyd et al., 2018), thereby further complicating data aggregation for meta-

95   analysis. Therefore, we chose an alternative, semi-quantitative approach where diatom

96   responses to increasing CO_2 are grouped in categories (see section 2.2) and also allows

97   to account for differences in experimental setups, e.g. with respect to container volume.

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98   While this approach excludes the determination of effect size, it provides an unbiased

99   insight on the direction of change of potential CO_2 effects.

100   **2.2. Data compilation**

101   We explored the response of diatom assemblages to high CO_2 (low pH) by searching the

102   literature for relevant results with Google Scholar (December 15, 2017) using the

103   following search query: diatom OR Bacillariophyceae AND "ocean acidification" OR

104   "high CO_2" or "carbon dioxide" OR "elevated CO_2" OR "elevated carbon dioxide" OR

105   "low pH" OR "decreased pH". The first 200 results were inspected and considered to be

106   relevant when they were published in peer-reviewed journals, contained a description of

107   the relevant methodological details, a statistical analysis or at least a transparent

108   description of variance and uncertainties, and tested CO_2 effects on natural plankton

109   assemblages (artificially composed communities were not considered). We then carefully

110   checked the cited literature in these relevant studies to uncover other studies that were

111   missed by the initial search. Furthermore, we checked the "Ocean Acidification news

112   stream provided by the Ocean Acidification International Coordination Centre" under the

113   tag "phytoplankton" (https://news-oceanacidification-icc.org/tag/phytoplankton/) for

114   relevant updates since December 2017 (last check on January 16, 2019).

115   There were two response variables of interest for the literature compilation:

116   1) The response of the "bulk diatom community" to high CO_2. For this we checked if the

117   abundance of diatoms, the biomass of diatoms, or the relative portion of diatoms within

118   the overall phytoplankton assemblage increased or decreased under high CO_2 relative to

119   the control. We distinguished between "positive", "negative", and "no effect" following

120   the statistical results provided in the individual references. When the CO_2 effect on the

121   bulk community was derived from abundance data we also checked if there are

122   indications for a concomitant shift in the biomass distribution among species. This is

123   relevant because, for example, an increase in bulk abundance could coincide with a

124   decrease in bulk biomass when the species driving the abundances is smaller. We found

125   no indications for conflicting cases but acknowledge that not every reference provided

126   sufficient data on morphological details to fully exclude this scenario.

127   2) The CO_2-dependent species shifts within the diatom community with respect to

128   taxonomic composition and/or size structure. Unfortunately, cell size of the species was

129   not reported for all experiments. Thus, we distinguished between "no shifts", "shifts

130   between species with unspecified size", as well as "shifts towards larger or smaller

131   species" when this information was provided. Furthermore, we noted the winners and

132   losers within the diatom communities when these were reported (on the genus level).

133   In case the data was taken from factorial multiple stressor experiments (e.g. CO_2 x

134   temperature) we only considered the control treatment at ambient conditions (e.g. at

135   control temperature). Furthermore, we extracted various metadata from each study

136   largely following the literature analysis of (Schulz et al., 2017). All bulk diatom

137   responses, community shifts, and metadata is compiled/described in Table 1 and most of

138   it is self-explanatory (e.g. incubation temperature). The habitats of the investigated

139   diatom communities were categorized according to water depth, salinity, or life style in

140   the case of benthic communities: "oceanic" = water depth > 200 m (unless the habitat lies

141   within a fjord or fjord-like strait), S > 30; "coastal" = water depth < 200 m, S > 30;

142   "estuarine" = water depth < 200 m, S < 30; "benthic" = benthic communities (diatoms

143   growing on plates) were investigated. We reconstructed the water depth in case it was not

144   provided in the paper using Google Earth Pro (version 7.3.2.5495). The coordinates

145   provided in some of the experiments conducted in land-based facilities were imprecise

146   and marked positions on land. In this case the habitats were set to coastal or estuarine

147   depending on salinity. If salinity was not given we checked the location on Google Earth

148   for potential fresh water sources and also checked the text for more cryptic indications

149   (e.g. "euryhaline" in a lagoon were strong indications for an estuarine habitat). The

150   methods with which responses of the bulk diatom communities to high OA were

151   determined varied greatly among studies and included light microscopy (LM), pigment

152   analyses (PA), flow cytometry (FC), genetic tools (PCR), and biogenic silica (BSi)

153   analyses (Table 1).

154   **2.3. Balancing the influence of smaller and larger scale experiments to account for**

155   **the "degree of realism"**

156   The most realistic OA experiment would be one where all aspects of the natural habitat

157   are represented correctly. Such setups are possible for benthic communities which can be

158   sampled *in situ* along a natural CO_2 gradient at volcanic CO_2 seeps (Fabricius et al., 2011;

159   Hall-Spencer et al., 2008; Johnson et al., 2011). However, this does not work easily for

160   the large majority of pelagic studies compiled herein due to water advection. Thus, OA

161   experiments with pelagic communities are performed in closed containers which

162   inevitably cause artefacts (Calvo-Díaz et al., 2011; Ferguson et al., 1984; Guangao, 1990;

163   Menzel and Case, 1977). However, the degree by which they are unrealistic will differ

164   from study to study depending on the experimental design (Duarte et al., 1997). Here, we

165   aimed to develop a metric that allows us to estimate the realism of experiments with

166   pelagic communities in order to balance their influence on the final outcome of the

167   literature analysis. Most certainly, we do not mean to devalue any studies but think that

168   the highly different scales of experiments should not be ignored when evaluating the

169   literature. In the following we will first derive the equation for the proposed metric –

170   termed the "relative degree of realism (RDR)" – and introduce the underlying

171   assumptions. Afterwards we describe aspects that were considered while conceptualizing

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172   the RDR.

173   The experimental design in the studies considered herein ranged from smaller bottle

174   experiments (e.g. 1 L) to *in situ* mesocosm studies with considerably larger incubation

175   volumes (e.g. 75000 L). While smaller differences in incubation volumes (e.g. 0.5 vs. 2

176   L) were shown to have no, or a minor, influence on physiological rates (Fogg and

177   Calvario-Martinez, 1989; Hammes et al., 2010; Nogueira et al., 2014; Robinson and

178   Williams, 2005), they can influence food web composition e.g. by excluding larger

179   grazers (Calvo-Díaz et al., 2011; Spencer and Warren, 1996). Larger differences of

180   incubation volumes (e.g. 10 vs. 10000 L) are considered to be important in all aspects

181   (Duarte et al., 1997), with the larger volume being more representative of natural

182   processes (Sarnelle, 1997). Therefore, our first assumption to conceptualize the RDR was

183   that larger incubation volumes represent nature generally better than smaller ones.

184   Plankton communities were pre-filtered in many experiments to exclude larger and often

185   patchily distributed organisms. This is a valid procedure to reduce noise and to increase

186   the likelihood to detect CO_2 effects but it also influences the development of plankton

187   communities as they modify the grazer/prey link within the food web (Ferguson et al.,

188   1984; Nogueira et al., 2014; Pomeroy et al., 1994). For example, (Nogueira et al., 2014)

189   compared plankton successions of pre-filtered (100 µm) and unfiltered communities and

190   found that the removal of larger grazers and diatoms gave room for green algae and

191   picophytoplankton to grow. Such manipulations make the experiment less representative

192   for a natural food web which brought us to the second assumption for the RDR: The

193   smaller the mesh size during the pre-filtration treatment, the less complete and thus the

194   less realistic is the pelagic food web.

195   To parameterize the two abovementioned assumptions we first converted the volume

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196   information provided in each experiment into a volume-to-surface ratio (V/S). The

197   underlying thought is that V increases with the third power to the surface area of the

198   incubator and is indicative for the relation of open space to hard surfaces (Ferguson et al.,

199   1984). Therefore we first converted V into a radius (r) assuming spherical shape:

200    $r = \sqrt[3]{\dfrac{3}{4}\dfrac{V}{\pi}}$ (1).

201   The surface (S) of the spherical volume was calculated as:

202    $S = 4\pi r^2$ (2)

203   Assuming spherical shape was necessary because there is generally no information about

204   the shape of the incubation containers available. Although shape can influence processes

205   within the container (Pan et al., 2015), it is probably a less important factor to consider in

206   light of the large volume differences compared herein (Table 1).

207   The influence of pre-filtration treatments of the investigated plankton community is

208   implemented by multiplying the V/S with the third root of the applied mesh size (d_{mesh} in

209   μm) so that the RDR is defined as:

210    $RDR = \dfrac{V}{S}\sqrt[3]{d_{mesh}}$ (3).

211   Thus, as for V/S, the influence of d_{mesh} on RDR does not linearly increase but dampens

212   with increasing d_{mesh}. The rationale for the non-linear increase is that incubations will still

213   have an increasing bias even if they do not have any pre-filtration treatment due to

214   generally increasing organism motility with size. For example, when collecting a

215   plankton community with a Niskin bottle, more motile organisms can escape from the

216   approaching sampler so that the food web composure is still affected even without

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217   subsequent pre-filtration. For this reason we also capped the maximum d_{mesh} to 10,000

218   µm when there was no pre-filtration treatment applied since none of the studies included

219   significantly larger organisms. Figure 1 illustrates the change of RDR as a function of V

220   and d_{mesh}. High RDRs are calculated for large-scale *in situ* mesocosm studies (~50 – 190)

221   while bottle experiments yield RDRs between ~1 – 12.

222   The key pre-requisite for an experimental parameter to be included in the RDR equation

223   (eq. 3) was that it is reported in all studies. Many parameters that we would have liked to

224   use for the RDR are either insufficiently reported (e.g. the light environment) or not

225   provided quantitatively at all (e.g. turbulence). We therefore had to work with very basic

226   properties related to the experimental setup rather than to the experimental conditions.

227   A particularly critical aspect of the RDR we had to deal with was the duration of the

228   experiments (Time). Time is a quantity, which is reliably reported in all studies and

229   therefore principally suitable for the RDR. Our first thoughts were that a realistic

230   community experiment should be long enough to cover relevant ecological processes

231   such as competitive exclusion and therefore also parameterized Time in the first versions

232   of the RDR equation. However, we decided to not account for it in the final version

233   because the factors that define the optimal duration of an experiment are poorly

234   constrained. For example, a 1 day experiment in a 10 L container could indeed miss

235   important CO_2 effects caused by food web interactions. On the other hand, a 30 days

236   experiment in the same container could reveal such indirect effects but at the same time

237   be associated with profound bottle effects and make the study unrepresentative for

238   simulated natural habitat. Thus, too long and too short are both problematic and the

239   optimum is hard to find. One such attempt to find the optimum was made by (Duarte et

240   al., 1997) who analyzed the plankton ecology literature between 1990 – 1995. By

241   correlating the experimental duration with the incubation volume of published

242   experiments they provided an optimal length for any given volume. However, as noted

243   by (Duarte et al., 1997), their correlation is based on publication success and therefore

244   rather reflects common practice in plankton ecology experiments and not necessarily a

245   mechanistic understanding of bottle effects. Thus, as there is no solid ground for a

246   parameterization of Time we ultimately decided to not consider it for the RDR.

247   **3. Results**

248   We found 54 relevant publications on CO_2 experiments with natural diatom assemblages.

249   Some publications included more than one experiment so that 69 experiments are

250   considered hereafter (Table 1). Most were done with diatom communities from coastal

251   environments (46 %) and oceanic (28%) environments. Estuarine and benthic

252   communities were investigated in 16 % and 6% of the studies, respectively (Figs. 2 and

253   3). 4 % of the studies did not provide coordinates where the samples were taken although

254   the region was reported (Table 1; Fig. 3).

255   One third (33 %) of all experiments revealed a positive influence of CO_2 on the "bulk

256   diatom community" (see section 2.2), while 19 % revealed a negative one. 7 % of the

257   studies found a CO_2 effect but did not specify whether it is a positive or negative one. 41

258   % found no effect (Fig. 4A; left column). Those experiments that revealed positive CO_2

259   effects on bulk diatom communities yielded the highest cumulative RDR score ($\sum$RDR)

260   of 605 while the $\sum$RDR for negative CO_2 effects was 266. No CO_2 effects yielded a score

261   of 768 while an "unspecified effect" yielded 266.

262   CO_2-dependent shifts in diatom species composition were investigated with light

263   microscopy except for (Endo et al., 2015) who used molecular tools,. Species shifts were

264   investigated in a subset of 40 of the 69 experiments (Fig. 4B). Within this subset of 40

265   studies, 12 (30 %, $\sum$RDR = 265) found a shift towards larger diatom species under high

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266   CO_2, 1 (2.5 %, $\sum RDR = 10$) found a shift towards smaller diatom species, and 13 (32.5

267   %, $\sum RDR = 103$) found no CO_2 effect on diatom community composition. 14 studies (35

268   %, $\sum RDR = 141$) reported a CO_2-dependent shift but did not further specify any changes

269   in the size-class distribution (Fig. 4C).

270   A taxon-specific assessment of potential winners and losers (on the genus level) was

271   possible only to a limited extent, because most genera were not present in enough

272   experiments to get useful results. Only *Chaetoceros*, *Cylindrotheca,* and *Pseudo-*

273   *Nitzschia* were explicitly investigated in at least 5 experiments, which we set as a

274   minimum threshold.   *Chaetoceros* responded positively to high CO_2 in 6 out of 9

275   experiments ($\sum RDR$ of winning = 84; $\sum RDR$ of losing = 61; Fig 5A). *Cylindrotheca*

276   responded positively in 2 out 5 experiments ($\sum RDR$ of winning = 5; $\sum RDR$ of losing =

277   9;Fig. 5B). *Pseudo-Nitzschia* responded positively in 2 out of 9 experiments ($\sum RDR$ of

278   winning = 3; $\sum RDR$ of losing = 77; Fig. 5C). Thus, *Pseudo-Nitzschia* is the only genus,

279   for which there seems to be a fairly consistent negative response to high CO_2.

280   **4. Discussion**

281   Numerous physiological studies have shown that diatom growth and metabolic rates can

282   be affected by seawater CO_2 concentrations, and that these responses vary widely among

283   different species (Gao and Campbell, 2014). Such inter-specific differences in pCO_2

284   sensitivity are an important feature as this could alter the composition of diatom

285   assemblages in a changing ocean. In this regard, it is interesting to note that

286   paleolimnologists have long been using diatom species composition as paleo-proxy to

287   reconstruct lake pH (Battarbee et al., 2010). Hence, there is ample evidence that high CO_2

288   conditions have the potential to change the diatom species composition.

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289   Indeed, our analysis revealed that CO_2-induced changes in diatom community

290   composition occurred in 27 out of 40 (i.e. 68 %) of community-level experiments which

291   investigated species composition (Fig. 4C). This is certainly a conservative outcome

292   because many studies have only looked at dominant species. In fact, one of the few

293   experiments that investigated the diatom assemblage with higher taxonomical resolution

294   found CO_2 effects also on subdominant species (Sommer et al., 2015) which may have

295   been overlooked in many other experiments.

296   **4.1 Winners and losers in the diatom community**

297   There was sufficient data (i.e. ≥ 5 experiments) for the genera *Chaetoceros*,

298   *Cylindrotheca*, and *Pseudo-Nitzschia* to determine common responses to high CO_2.

299   Among these 3, only *Pseudo-Nitzschia* was fairly consistently identified as a "loser"

300   within the investigated natural diatom communities. *Chaetoceros* was mostly winning

301   while *Cylindrotheca* was mostly losing but the trends were not strong. The relatively

302   weak performance of *Pseudo-Nitzschia* spp. was somewhat surprising because previous

303   monoclonal experiments with this genus often reported a sometimes pronounced positive

304   (Sun et al., 2011; Tatters et al., 2012), or no influence of high CO_2 on their growth rate

305   (Sugie and Yoshimura, 2013; Trimborn et al., 2013) but more rarely a negative one

306   (Tatters et al., 2013). Likewise, laboratory competition experiments between *Chaetoceros*

307   *debilis* and *Pseudo-Nitzschia subcurvata* saw the latter rather on the winning side under

308   high CO_2 although the difference between them was small (Trimborn et al., 2013). The

309   reasons for the inconsistency between our results and the impression derived from

310   controlled laboratory experiments could be manifold. Since our outcome is based on

311   "only" 9 experiments, it could still be coincidence. However, the pronounced difference

312   in the RDR value alleviate this concern to some extent (see numbers on top of Fig. 5C).

313   If the inconsistency is reflecting a true biological pattern than this would emphasize once

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314   more that ecological success within a natural community cannot be easily derived from

315   physiological studies.

316   **4.2 CO_2 effects on diatom assemblages originating from (direct) physiological**

317   **responses to high CO_2**

318   Most studies that found effects of pCO_2 on diatom communities related these changes to

319   CO_2 fertilization of photosynthesis. Concentrations of CO_2 in the surface ocean are

320   relatively low compared to other forms of inorganic carbon, especially bicarbonate ion

321   (HCO_3^-) (Zeebe and Wolf-Gladrow, 2001). However, RubisCO, the primary

322   carboxylating enzyme used in photosynthesis, is restricted to CO_2 for carbon fixation and

323   has a relatively low affinity for CO_2 compared to O_2 (Falkowski and Raven, 2007).

324   Therefore, diatoms (like many other phytoplankton species) operate a carbon

325   concentrating mechanism (CCM) to enhance their CO_2 concentration at the site of

326   fixation relative to external concentrations (e.g. by converting HCO_3^- to CO_2) and thereby

327   establish higher rates of carbon fixation than what would be possible when only

328   depending on diffusive CO_2 uptake (Giordano et al., 2005). It is well known that the

329   proportion of CO_2 uptake vs. HCO_3^- uptake for photosynthesis varies largely among

330   diatoms (Burkhardt et al., 2001; Rost et al., 2003; Trimborn et al., 2008) and is

331   theoretically also a function of cell size (Flynn et al., 2012; Wolf-Gladrow and Riebesell,

332   1997). Accordingly, increasing seawater pCO_2 may increase the proportion of diffusive

333   carbon uptake and/or lower the energy and resource requirements for CCM operation

334   (Raven et al., 2011). From a physiological point of view, these mechanisms could allow

335   for increased rates of photosynthesis and cell division.

336   So how do these theoretical considerations align with (A) the variable and species-

337   specific physiological responses of diatoms to increasing CO_2 (Dutkiewicz et al., 2015),

338   and (B) the results from community-level experiments compiled in this study? Regarding

339   the variability of physiological responses, progress has recently been made by (Wu et al.,

340   2014) who experimentally demonstrated a positive relationship between cell volume and

341   the magnitude of the CO_2 fertilization effect on diatom growth rates. Their findings agree

342   well with theoretical considerations, which predict that high CO_2 is particularly beneficial

343   for carbon acquisition by larger species as they are more restricted by diffusion gradients

344   due to lower surface-to-volume ratios than smaller cells (Flynn et al., 2012; Wolf-

345   Gladrow and Riebesell, 1997). The outcome of our literature analysis supports this

346   allometric concept (Fig. 4, Table 2). Twelve out of 13 experiments in which cell size was

347   taken into account found a shift towards larger species. This is reflected in the ∑RDR

348   score of 265 which is ~25 times higher than the opposite result (i.e. CO_2-induced shifts

349   towards smaller diatoms, Fig. 4C). An allometric scaling of CO_2 sensitivity is particularly

350   useful for modelling since cell size is a universal trait which is relatively easy to measure

351   and therefore frequently available (Ward et al., 2012). Accordingly, it may lead to

352   significant improvements of ecological and/or biogeochemical model projections under

353   CO_2 forcing when more than one size class for diatoms is considered.

354   However, although the (Wu et al., 2014) allometric approach constitutes a solid starting

355   point to help understanding the variable responses of different diatom species, it probably

356   also still needs some further refinements. For example, central components of CCMs

357   seem to be adapted to diatom cell sizes, thereby potentially alleviating a strict cell size

358   dependency of CO_2 limitation (Shen and Hopkinson, 2015). Furthermore, size

359   dependency alone cannot account for taxon-specific differences in the mode of carbon

360   acquisition (diffusive uptake of CO_2 vs. CCM-supported uptake of HCO_3^-) and how this

361   will affect the competitive ability of species under increasing CO_2. OA will lead to much

362   larger changes in dissolved CO_2 than in HCO_3^-. Thus, species that rely to a larger extent

363   on a resource-intensive CCM may benefit more from increasing pCO_2 on a cellular level,

364   as they could increase the proportion of diffusive CO_2 uptake. However, it is also possible

365   that the same species would be disadvantaged on the community-level, because their

366   niche (that is, being competitive at lower CO_2 due to an efficient CCM) is diminished

367   under high CO_2 conditions. Which of the scenarios occurs in nature would also depend

368   on how flexible species are in terms of switching carbon acquisition modes, as well as

369   resource allocation. In this regard, it is noteworthy that only few physiological studies on

370   OA effects have taken into account the role of changing nutrient concentrations or even

371   a transition to nutrient limitation. The available experimental evidence suggests that

372   increasing pCO_2 may reduce cellular nutrient requirements for CCM operations and

373   therefore free resources for elevated maximum diatom population densities, particularly

374   when running into nutrient limitation (Taucher et al., 2015). Unfortunately, however, the

375   relevance of this mechanism has so far only been investigated in monoclonal laboratory

376   experiments but not on the community-level.

377   These considerations illustrate that cell size is an important factor, but is not sufficient to

378   predict physiological or even community-level of diatoms to OA. Moreover, the

379   allometric concept as well as the additional mechanisms described above generally

380   presume positive effects of CO_2-fertilization, thus yielding no first order explanations for

381   observed negative responses of diatoms to changing carbonate chemistry. Obviously,

382   increasing CO_2 concentrations are accompanied by increasing proton (H^+) concentrations

383   under ocean acidification. High H^+ concentrations may reduce key metabolic rates above

384   certain thresholds and outweigh the positive influence of CO_2 fertilization as has been

385   observed in coccolithophores (Bach et al., 2011, 2015).

386   Another pathway by which ocean acidification may alter diatom communities is the pH

387   effect on silicification and silica dissolution. Low seawater pH should theoretically

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388   facilitate silicification as the precipitation of opal occurs in a cellular compartment with

389   low pH conditions (pH ~5) (Martin-Jézéquel et al., 2000; Vrieling et al., 1999). At the

390   same time, a lower pH should reduce chemical dissolution rates of the SiO_2 frustule

391   (Loucaides et al., 2012). While experimental evidence on this topic is still scarce and

392   partly controversial (Hervé et al., 2012; Mejía et al., 2013; Milligan et al., 2004), it is not

393   unlikely that OA-induced changes in the formation and dissolution of biogenic silica may

394   alter the strength of the frustule and therefore the palatability of diatoms to zooplankton

395   grazers (Friedrichs et al., 2013; Hamm et al., 2003; Liu et al., 2016; Wilken et al., 2011).

396   As for the other physiological effects e.g. on carbon fixation, it is likely that OA impacts

397   on silicification will vary among different diatoms species e.g. according to their species-

398   specific intrinsic buffering capacity, thereby leading to further taxonomic shifts within

399   diatom communities.

400   The response of diatoms to increasing pCO_2 in natural environments will be further

401   modified by multiple other environmental drivers changing simultaneously. Climate

402   change is expected to elevate ocean temperature, as well as also irradiance and nutrient

403   availability via changes in stratification. Physiological experiments have shown that

404   elevated pCO_2 may have beneficial effects under low and moderate irradiance, but this

405   effect may reverse under high light conditions due to enhanced photoinhibition (Gao

406   2012). Analogously, warming may have positive or negative effects on photosynthesis

407   and metabolism in general, depending on the thermal optima of the respective species

408   (Boyd et al., 2018). Altogether, these multiple additional drivers will also affect diatom

409   communities, leading to shifts in their taxonomic composition and size structure, which

410   will interact with the impacts of OA.

411   **4.3 Indirect CO₂ effects on diatom assemblages through food web interactions**

412   Diatom community responses can not only originate from a direct CO_2 effect on their

413   physiology but also be caused indirectly through CO_2 responses on other components of

414   the food web. For example, if a grazer of a diatom species is negatively affected by OA

415   then this may benefit the prey and indirectly promote its abundance. Direct OA impacts

416   on zooplankton communities are usually assumed to play a minor role, although there is

417   some experimental evidence that lower pH may have physiological effects at least on

418   some sensitive species or developmental stages (Cripps et al., 2016; Thor and Dupont,

419   2015; Thor and Oliva, 2015). Nevertheless, much of the currently available empirical

420   evidence indicates that zooplankton communities are affected by OA rather via bottom-

421   up effects, e.g. via changes in primary production or taxonomic composition of the

422   phytoplankton community (Meunier et al., 2017). However bottom-up effects on

423   zooplankton biomass, size structure, or species composition may in turn trigger feedbacks

424   on diatom communities, thereby leading to a feedback loop that may reinforce until a new

425   steady state is reached. Such considerations illustrate that also second or third order

426   effects need to be considered when assessing OA effects on the level of ecological

427   communities. Accounting for such indirect effects requires a holistic approach

428   considering all key players in of the food web (something that is beyond the scope of this

429   study). Therefore, interpretations about what the observed responses could mean for

430   entire plankton food webs or even biogeochemical element cycles (section 4.4) should

431   always be regarded with some healthy skepticism as they often neglect the potential for

432   indirect effects.

433   **4.4 Implications of changes in diatom community structure for pelagic food webs**

434   **and biogeochemical cycles**

435   The taxonomic composition and size structure of phytoplankton communities influences

436   the transfer of energy from primary production to higher trophic levels. In theory, larger

437   diatoms should support a more direct transfer because less trophic intermediates are

438   needed and therefore less respiration occurs until prey items are in an appropriate size

439   range for top predators (Azam et al., 1983; Pomeroy, 1974; Sommer et al., 2002).

440   Likewise a reduced abundance of the potentially toxic genus *Pseudo-Nitzschia* under high

441   CO_2 could further improve trophic transfer and growth of consumers in food webs where

442   *Pseudo-Nitzschia* exerts harmful impacts at present. Such changes at the bottom of a food

443   web might eventually lead to higher production in higher trophic levels such as fish.

444   Indeed, recent experimental evidence indicated that fish (including commercially

445   important species) could under certain constellations benefit from high CO_2 due to higher

446   food availability, although it was not tested if this response is somehow linked to the

447   diatom community (Goldenberg et al., 2018; Sswat et al., 2018).

448   Fluxes of elements through the oceans are (like fluxes of energy through food webs)

449   influenced by the composition of diatom communities (Sarmiento and Gruber, 2006).

450   This is particularly well recognized in the context of organic carbon export to the deep

451   ocean, for which diatoms are considered to play a pivotal role (Smetacek, 1985). Given

452   that high CO_2 favours large and perhaps more silicified diatoms over smaller ones

453   (section 4.2), we might expect accelerated sinking and thus a positive feedback on the

454   vertical carbon flux. This classical hypothesis is supported by observational evidence

455   from two consecutive years of the North Atlantic spring bloom where, despite similar

456   primary production, export was much higher in the year when the larger diatom species

457   dominated (Boyd and Newton, 1995). However, whether the positive relationship

458   between size and carbon export holds under all circumstances is by no means clear

459   (Tréguer et al., 2018) . It is possible that shifts towards larger sized species coincide with

460   shifts in other traits that feed back negatively on carbon export. For example, when the

461   size shift is associated with decreasing C:Si stoichiometry it may ultimately reduce carbon

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462   export (Assmy et al., 2013).

463   The abovementioned examples of trophic transfer and export fluxes illustrate the

464   importance of the factor "diatom community structure" in the context of marine food

465   production and biogeochemical fluxes. They also illustrate that our understanding of the

466   feedbacks induced through changes in diatom communities is highly incomplete. Hence,

467   with our limited understanding we must currently classify CO_2-induced changes in

468   diatom communities as "a potential risk" causing changes in key ecosystem services.

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475   **References**

476   Armbrust, E. V.: The life of diatoms in the world's oceans, Nature, 459(7244), 185–
477   192, doi:10.1038/nature08057, 2009.

478   Assmy, P., Smetacek, V., Montresor, M., Klaas, C., Henjes, J., Strass, V. H., Arrieta, J.
479   M., Bathmann, U., Berg, G. M., Breitbarth, E., Cisewski, B., Friedrichs, L., Fuchs, N.,
480   Herndl, G. J., Jansen, S., Kragefsky, S., Latasa, M., Peeken, I., Rottgers, R., Scharek,
481   R., Schuller, S. E., Steigenberger, S., Webb, a. and Wolf-Gladrow, D.: Thick-shelled,
482   grazer-protected diatoms decouple ocean carbon and silicon cycles in the iron-limited
483   Antarctic Circumpolar Current, Proc. Natl. Acad. Sci., 110(51), 20633–20638,
484   doi:10.1073/pnas.1309345110, 2013.

485   Azam, F., Fenchel, T., Field, J. G., Gray, J. S., Meyer-Reil, L. A. and Thingstad, F.: The
486   Ecological Role of Water-Column Microbes in the Sea, Mar. Ecol. Prog. Ser., 10, 257–
487   263, doi:10.3354/meps010257, 1983.

488   Bach, L. T., Riebesell, U. and Schulz, K. G.: Distinguishing between the effects of
489   ocean acidification and ocean carbonation in the coccolithophore *Emiliania huxleyi*,
490   Limnol. Oceanogr., 56(6), 2040–2050, doi:10.4319/lo.2011.56.6.2040, 2011.

491   Bach, L. T., Riebesell, U., Gutowska, M. A., Federwisch, L. and Schulz, K. G.: A

Ocean Science

Discussions

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492   unifying concept of coccolithophore sensitivity to changing carbonate chemistry
493   embedded in an ecological framework, Prog. Oceanogr., 135, 125–138,
494   doi:10.1016/j.pocean.2015.04.012, 2015.

495   Bach, L. T., Alvarez-Fernandez, S., Hornick, T., Stuhr, A. and Riebesell, U.: Simulated
496   ocean acidification reveals winners and losers in coastal phytoplankton, PLoS One,
497   12(11), e0188198, doi:10.1371/journal.pone.0188198, 2017.

498   Bach, L. T., Hernández-hernández, N., Taucher, J., Spisla, C., Sforna, C., Riebesell, U.
499   and Aristegui, J.: Effects of Elevated CO_2 on a Natural Diatom Community in the
500   Subtropical NE Atlantic, Front. Mar. Sci., 6(March), 1–16,
501   doi:10.3389/fmars.2019.00075, 2019.

502   Battarbee, R. W., Charles, D. F., Bigler, C., Cumming, B. F. and Renberg, I.: Diatoms
503   as indicators as surface-water acidity, in Diatoms: Applications for the Environmental
504   and Earth Sciences, edited by J. P. Smol and E. F. Stoermer, pp. 98–121, Cambridge
505   University Press, Cambridge., 2010.

506   Biswas, H., Cros, A., Yadav, K., Ramana, V. V., Prasad, V. R., Acharyya, T. and Babu,
507   P. V. R.: The response of a natural phytoplankton community from the Godavari River
508   Estuary to increasing CO_2 concentration during the pre-monsoon period, J. Exp. Mar.
509   Bio. Ecol., 407(2), 284–293, doi:10.1016/j.jembe.2011.06.027, 2011.

510   Biswas, H., Shaik, A. U. R., Bandyopadhyay, D. and Chowdhury, N.: CO_2 induced
511   growth response in a diatom dominated phytoplankton community from SW Bay of
512   Bengal coastal water, Estuar. Coast. Shelf Sci., 198, 29–42,
513   doi:10.1016/j.ecss.2017.07.022, 2017.

514   Boyd, P. and Newton, P.: Evidence of the potential influence of planktonic community
515   structure on the interannual variability of particulate organic carbon flux, Deep Sea Res.
516   Part I Oceanogr. Res. Pap., 42(5), 619–639, 1995.

517   Boyd, P. W.: Diatom traits regulate Southern Ocean silica leakage, Proc. Natl. Acad.
518   Sci., 110(51), 20358–20359, doi:10.1073/pnas.1320327110, 2013.

519   Boyd, P. W., Collins, S., Dupont, S., Fabricius, K., Gattuso, J. P., Havenhand, J.,
520   Hutchins, D. A., Riebesell, U., Rintoul, M. S., Vichi, M., Biswas, H., Ciotti, A., Gao,
521   K., Gehlen, M., Hurd, C. L., Kurihara, H., Mcgraw, C. M., Navarro, J. M., Nilsson, G.
522   E., Passow, U. and Pörtner, H. O.: Experimental strategies to assess the biological
523   ramifications of multiple drivers of global ocean change-A review, Glob. Chang. Biol.,
524   24, 2239–2261, doi:10.1111/gcb.14102, 2018.

525   Brzezinski, M. A. and Nelson, D. M.: Chronic substrate limitation of silicic acid uptake
526   rates in the western Sargasso Sea, Deep Sea Res. Part II Top. Stud. Oceanogr., 43(2–3),
527   437–453, doi:10.1016/0967-0645(95)00099-2, 1996.

528   Burkhardt, S., Amoroso, G. and Su, D.: CO_2 and HCO_3^- uptake in marine diatoms
529   acclimated to different CO_2 concentrations, , 46(6), 1378–1391, 2001.

530   Calvo-Díaz, A., Ďaz-Pérez, L., Suárez, L. Á., Morán, X. A. G., Teira, E. and Marañón,
531   E.: Decrease in the autotrophic-to-heterotrophic biomass ratio of picoplankton in
532   oligotrophic marine waters due to bottle enclosure, Appl. Environ. Microbiol., 77(16),

533   5739–5746, doi:10.1128/AEM.00066-11, 2011.

534   Cripps, G., Flynn, K. J. and Lindeque, P. K.: Ocean acidification affects the phyto-zoo
535   plankton trophic transfer efficiency, PLoS One, 11(4), 1–15,
536   doi:10.1371/journal.pone.0151739, 2016.

537   Davidson, A., McKinlay, J., Westwood, K., Thomson, P., van den Enden, R., de Salas,
538   M., Wright, S., Johnson, R. and Berry, K.: Enhanced CO_2 concentrations change the
539   structure of Antarctic marine microbial communities, Mar. Ecol. Prog. Ser., 552, 93–
540   113, doi:10.3354/meps11742, 2016.

541   Domingues, R. B., Guerra, C. C., Galvao, H. M., Brotas, V. and Barbosa, A. B.: Short-
542   term interactive effects of ultraviolet radiation, carbon dioxide and nutrient enrichment
543   on phytoplankton in a shallow coastal lagoon, Aquat. Ecol., 51(1), 91–105,
544   doi:10.1007/s10452-016-9601-4, 2017.

545   Donahue, K., Klaas, C., Dillingham, P. W. and Hoffmann, L. J.: Combined effects of
546   ocean acidification and increased light intensity on natural phytoplankton communities
547   from two Southern Ocean water masses, J. Plankton Res., 41(1), 30–45,
548   doi:10.1093/plankt/fby048, 2019.

549   Duarte, C. M., Gasol, J. M. and Vaqué, D.: Role of experimental approaches in marine
550   microbial ecology, Aquat. Microb. Ecol., 13(1), 101–111, doi:10.3354/ame013101,
551   1997.

552   Dutkiewicz, S., Morris, J. J., Follows, M. J., Scott, J., Levitan, O., Dyhrman, S. T. and
553   Berman-Frank, I.: Impact of ocean acidification on the structure of future phytoplankton
554   communities, Nat. Clim. Chang., 5(11), 1002–1006, doi:10.1038/nclimate2722, 2015.

555   Eggers, S. L., Lewandowska, A. M., Barcelos e Ramos, J., Blanco-Ameijeiras, S.,
556   Gallo, F. and Matthiessen, B.: Community composition has greater impact on the
557   functioning of marine phytoplankton communities than ocean acidification, Glob.
558   Chang. Biol., 20(3), 713–723, doi:10.1111/gcb.12421, 2014.

559   Endo, H., Yoshimura, T., Kataoka, T. and Suzuki, K.: Effects of CO_2 and iron
560   availability on phytoplankton and eubacterial community compositions in the northwest
561   subarctic Pacific, J. Exp. Mar. Bio. Ecol., 439, 160–175,
562   doi:10.1016/j.jembe.2012.11.003, 2013.

563   Endo, H., Sugie, K., Yoshimura, T. and Suzuki, K.: Effects of CO_2 and iron availability
564   on rbcL gene expression in Bering Sea diatoms, Biogeosciences, 12(7), 2247–2259,
565   doi:10.5194/bg-12-2247-2015, 2015.

566   Endo, H., Sugie, K., Yoshimura, T. and Suzuki, K.: Response of Spring Diatoms to CO_2
567   Availability in the Western North Pacific as Determined by Next-Generation
568   Sequencing, PLoS One, 11(4), e0154291, doi:10.1371/journal.pone.0154291, 2016.

569   Fabricius, K. E., Langdon, C., Uthicke, S., Humphrey, C., Noonan, S., De'ath, G.,
570   Okazaki, R., Muehllehner, N., Glas, M. S. and Lough, J. M.: Losers and winners in
571   coral reefs acclimatized to elevated carbon dioxide concentrations, Nat. Clim. Chang.,
572   1(6), 165–169, doi:10.1038/nclimate1122, 2011.

Ocean Science
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Open Access

573   Falkowski, P. G. and Raven, J. A.: Aquatic Photosynthesis, Princeton University Press,
574   Princeton., 2007.

575   Feng, Y., Hare, C. E., Leblanc, K., Rose, J. M., Zhang, Y., DiTullio, G. R., Lee, P. A.,
576   Wilhelm, S. W., Rowe, J. M., Sun, J., Nemcek, N., Gueguen, C., Passow, U., Benner, I.,
577   Brown, C. and Hutchins, D. A.: Effects of increased pCO_2 and temperature on the north
578   atlantic spring bloom. I. The phytoplankton community and biogeochemical response,
579   Mar. Ecol. Prog. Ser., 388, 13–25, doi:10.3354/meps08133, 2009.

580   Feng, Y., Hare, C. E., Rose, J. M., Handy, S. M., DiTullio, G. R., Lee, P. A., Smith, W.
581   O., Peloquin, J., Tozzi, S., Sun, J., Zhang, Y., Dunbar, R. B., Long, M. C., Sohst, B.,
582   Lohan, M. and Hutchins, D. A.: Interactive effects of iron, irradiance and CO_2 on Ross
583   Sea phytoplankton, Deep. Res. Part I Oceanogr. Res. Pap., 57(3), 368–383,
584   doi:10.1016/j.dsr.2009.10.013, 2010.

585   Ferguson, R. L., Buckley, E. N. and Palumbo, A. V.: Response of marine
586   bacterioplankton to differential filtration and confinement., Appl. Environ. Microbiol.,
587   47(1), 49–55, doi:0099-2240/84/010049-07$02., 1984.

588   Field, C. B., Behrenfeld, M. J., Randerson, J. T. and Falkowski, P. G.: Primary
589   Production of the Biosphere: Integrating Terrestrial and Oceanic Components, Science,
590   281(5374), 237–240, doi:10.1126/science.281.5374.237, 1998.

591   Flynn, K. J., Blackford, J. C., Baird, M. E., Raven, J. A., Clark, D. R., Beardall, J.,
592   Brownlee, C., Fabian, H. and Wheeler, G. L.: Changes in pH at the exterior surface of
593   plankton with ocean acidification, Nat. Clim. Chang., 2(7), 510–513,
594   doi:10.1038/nclimate1489, 2012.

595   Fogg, G. E. and Calvario-Martinez, O.: Effects of bottle size in determinations of
596   primary productivity by phytoplankton, Hydrobiologia, 173(2), 89–94,
597   doi:10.1007/BF00015518, 1989.

598   Friedrichs, L., Hörnig, M., Schulze, L., Bertram, A., Jansen, S. and Hamm, C.: Size and
599   biomechanic properties of diatom frustules influence food uptake by copepods, Mar.
600   Ecol. Prog. Ser., 481(2000), 41–51, doi:10.3354/meps10227, 2013.

601   Gao, K. and Campbell, D. A.: Photophysiological responses of marine diatoms to
602   elevated CO_2 and decreased pH: A review, Funct. Plant Biol., 41(5), 449–459,
603   doi:10.1071/FP13247, 2014.

604   Gao, K., Xu, J., Gao, G., Li, Y., Hutchins, D. A., Huang, B., Wang, L., Zheng, Y., Jin,
605   P., Cai, X., Häder, D. P., Li, W., Xu, K., Liu, N. and Riebesell, U.: Rising CO_2 and
606   increased light exposure synergistically reduce marine primary productivity, Nat. Clim.
607   Chang., 2(7), 519–523, doi:10.1038/nclimate1507, 2012.

608   Gazeau, F., Sallon, A., Pitta, P., Tsiola, A., Maugendre, L., Giani, M., Celussi, M.,
609   Pedrotti, M. L., Marro, S. and Guieu, C.: Limited impact of ocean acidification on
610   phytoplankton community structure and carbon export in an oligotrophic environment:
611   Results from two short-term mesocosm studies in the Mediterranean Sea, Estuar. Coast.
612   Shelf Sci., 186, 72–88, doi:10.1016/j.ecss.2016.11.016, 2017.

613   Giordano, M., Beardall, J. and Raven, J. A.: CO_2 concentrating mechanisms in algae:

Ocean Science
Discussions

614   mechanisms, environmental modulation, and evolution., Annu. Rev. Plant Biol., 56, 99–
615   131, doi:10.1146/annurev.arplant.56.032604.144052, 2005.

616   Goldenberg, S. U., Nagelkerken, I., Marangon, E., Bonnet, A. and Camilo, M.:
617   Ecological complexity buffers the impacts of future climate on marine animals
618   Corresponding author Keywords, Nat. Clim. Chang., 1–19, doi:10.1038/s41558-018-
619   0086-0, 2018.

620   Grear, J. S., Rynearson, T. A., Montalbano, A. L., Govenar, B. and Menden-Deuer, S.:
621   pCO_2 effects on species composition and growth of an estuarine phytoplankton
622   community, Estuar. Coast. Shelf Sci., 190, 40–49, doi:10.1016/j.ecss.2017.03.016,
623   2017.

624   Guangao, L.: Different types of ecosystem experiments, in Enclosed Experimental
625   Marine Ecosystems: A Review and Recommendations, edited by C. M. Lalli, pp. 7–20,
626   Springer-Verlag, New York., 1990.

627   Hall-Spencer, J. M., Rodolfo-Metalpa, R., Martin, S., Ransome, E., Fine, M., Turner, S.
628   M., Rowley, S. J., Tedesco, D. and Buia, M.-C.: Volcanic carbon dioxide vents show
629   ecosystem effects of ocean acidification, Nature, 454, 96–99, doi:10.1038/nature07051,
630   2008.

631   Hama, T., Inoue, T., Suzuki, R., Kashiwazaki, H., Wada, S., Sasano, D., Kosugi, N. and
632   Ishii, M.: Response of a phytoplankton community to nutrient addition under different
633   CO_2 and pH conditions, J. Oceanogr., 72(2), 207–223, doi:10.1007/s10872-015-0322-4,
634   2016.

635   Hamm, C. and Smetacek, V.: Armor: Why, when, and how, in Evolution of
636   Phytoplankton, edited by P. G. Falkowski and A. H. Knoll, pp. 311–332, Elsevier,
637   Boston., 2007.

638   Hamm, C. E., Merkel, R., Springer, O., Jurkojc, P., Maiert, C., Prechtelt, K. and
639   Smetacek, V.: Architecture and material properties of diatom shells provide effective
640   mechanical protection, Nature, 421(6925), 841–843, doi:10.1038/nature01416, 2003.

641   Hammes, F., Vital, M. and Egli, T.: Critical evaluation of the volumetric "bottle effect"
642   on microbial batch growth, Appl. Environ. Microbiol., 76(4), 1278–1281,
643   doi:10.1128/AEM.01914-09, 2010.

644   Hare, C. E., Leblanc, K., DiTullio, G. R., Kudela, R. M., Zhang, Y., Lee, P. A.,
645   Riseman, S. and Hutchins, D. A.: Consequences of increased temperature and CO_2 for
646   phytoplankton community structure in the Bering Sea, Mar. Ecol. Prog. Ser., 352, 9–16,
647   doi:10.3354/meps07182, 2007.

648   Hervé, V., Derr, J., Douady, S., Quinet, M., Moisan, L. and Lopez, P. J.:
649   Multiparametric Analyses Reveal the pH-Dependence of Silicon Biomineralization in
650   Diatoms, PLoS One, 7(10), e46722, doi:10.1371/journal.pone.0046722, 2012.

651   Hopkins, F. E., Turner, S. M., Nightingale, P. D., Steinke, M., Bakker, D. and Liss, P.
652   S.: Ocean acidification and marine trace gas emissions, Proc. Natl. Acad. Sci. U. S. A.,
653   107, 760–765, doi:10.1073/pnas.0907163107, 2010.

654   Hoppe, C. J. M., Hassler, C. S., Payne, C. D., Tortell, P. D., Rost, B. R. and Trimborn,
655   S.: Iron limitation modulates ocean acidification effects on Southern Ocean
656   phytoplankton communities, PLoS One, 8(11), doi:10.1371/journal.pone.0079890,
657   2013.

658   Hoppe, C. J. M., Schuback, N., Semeniuk, D. M., Maldonado, M. T. and Rost, B.:
659   Functional Redundancy Facilitates Resilience of Subarctic Phytoplankton Assemblages
660   toward Ocean Acidification and High Irradiance, Front. Mar. Sci., 4,
661   doi:10.3389/fmars.2017.00229, 2017a.

662   Hoppe, C. J. M., Schuback, N., Semeniuk, D., Giesbrecht, K., Mol, J., Thomas, H.,
663   Maldonado, M. T., Rost, B., Varela, D. E. and Tortell, P. D.: Resistance of Arctic
664   phytoplankton to ocean acidification and enhanced irradiance, Polar Biol., 41(3), 399–
665   413, doi:10.1007/s00300-017-2186-0, 2017b.

666   Hussherr, R., Levasseur, M., Lizotte, M., Tremblay, J. É., Mol, J., Thomas, H.,
667   Gosselin, M., Starr, M., Miller, L. A., Jarniková, T., Schuback, N. and Mucci, A.:
668   Impact of ocean acidification on Arctic phytoplankton blooms and dimethyl sulfide
669   concentration under simulated ice-free and under-ice conditions, Biogeosciences, 14(9),
670   2407–2427, doi:10.5194/bg-14-2407-2017, 2017.

671   James, R. K., Hepburn, C. D., Cornwall, C. E., McGraw, C. M. and Hurd, C. L.:
672   Growth response of an early successional assemblage of coralline algae and benthic
673   diatoms to ocean acidification, Mar. Biol., 161(7), 1687–1696, doi:10.1007/s00227-
674   014-2453-3, 2014.

675   Johnson, V. R., Brownlee, C., Rickaby, R. E. M., Graziano, M., Milazzo, M. and Hall-
676   Spencer, J. M.: Responses of marine benthic microalgae to elevated CO_2, Mar. Biol.,
677   160(8), 1813–1824, doi:10.1007/s00227-011-1840-2, 2011.

678   Kim, J. M., Lee, K., Yang, E. J., Shin, K., Noh, J. H., Park, K. T., Hyun, B., Jeong, H.
679   J., Kim, J. H., Kim, K. Y., Kim, M., Kim, H. C., Jang, P. G. and Jang, M. C.: Enhanced
680   production of oceanic dimethylsulfide resulting from CO_2-induced grazing activity in a
681   high CO_2 world, Environ. Sci. Technol., 44(21), 8140–8143, doi:10.1021/es102028k,
682   2010.

683   Kim, J.-M., Lee, K., Shin, K., Kang, J.-H., Lee, H.-W., Kim, M., Jang, P.-G. and Jang,
684   M.-C.: The effect of seawater CO2 concentration on growth of a natural phytoplankton
685   assemblage in a controlled mesocosm experiment, Limnol. Oceanogr., 51(4), 1629–
686   1636, doi:10.4319/lo.2006.51.4.1629, 2006.

687   Liu, H., Chen, M., Zhu, F. and Harrison, P. J.: Effect of Diatom Silica Content on
688   Copepod Grazing, Growth and Reproduction, Front. Mar. Sci., 3(June), 1–7,
689   doi:10.3389/fmars.2016.00089, 2016.

690   Loucaides, S., van Cappellen, P., Roubeix, V., Moriceau, B. and Ragueneau, O.:
691   Controls on the Recycling and Preservation of Biogenic Silica from Biomineralization
692   to Burial, Silicon, 4(1), 7–22, doi:10.1007/s12633-011-9092-9, 2012.

693   Mallozzi, A. J., Errera, R. M., Bargu, S. and Herrmann, A. D.: Impacts of elevated
694   pCO2 on estuarine phytoplankton biomass and community structure in two
695   biogeochemically distinct systems in Louisiana, USA, J. Exp. Mar. Bio. Ecol.,

696   511(September 2018), 28–39, doi:10.1016/j.jembe.2018.09.008, 2019.

697   Mann, D. G. and Vanormelingen, P.: An Inordinate Fondness ? The Number ,
698   Distributions , and Origins of Diatom Species, J. Eukaryot. Microbiol., 60, 414–420,
699   doi:10.1111/jeu.12047, 2013.

700   Martin-Jézéquel, V., Hildebrand, M. and Brzezinski, M. A.: Review Silicon Metabolism
701   in Diatoms: Implications for Growth, J. Phycol., 36, 821–840, 2000.

702   Maugendre, L., Gattuso, J.-P., Louis, J., de Kluijver, A., Marro, S., Soetaert, K. and
703   Gazeau, F.: Effect of ocean warming and acidification on a plankton community in the
704   NW Mediterranean Sea, ICES J. Mar. Sci., 72(6), 1744–1755,
705   doi:10.1093/icesjms/fsu161, 2015.

706   Mejía, L. M., Isensee, K., Méndez-Vicente, A., Pisonero, J., Shimizu, N., González, C.,
707   Monteleone, B. and Stoll, H.: B content and Si/C ratios from cultured diatoms
708   (*Thalassiosira pseudonana* and *Thalassiosira weissflogii*): Relationship to seawater pH
709   and diatom carbon acquisition, Geochim. Cosmochim. Acta, 123, 322–337,
710   doi:10.1016/j.gca.2013.06.011, 2013.

711   Menzel, D. W. and Case, J.: Concept and Design: Controlled Ecosystem Pollution
712   Experiment, Bull. Mar. Sci., 27(1), 1–7, 1977.

713   Meunier, C. L., Algueró-Muñiz, M., Horn, H. G., Lange, J. A. F. and Boersma, M.:
714   Direct and indirect effects of near-future pCO_2 levels on zooplankton dynamics, Mar.
715   Freshw. Res., 68(2), 373–380, doi:10.1071/MF15296, 2017.

716   Milligan, A. J., Varela, D. E., Brzezinski, M. A. and Morel, F. M. M.: Dynamics of
717   Silicon Metabolism and Silicon Isotopic Discrimination in a Marine Diatom as a
718   Function of pCO_2, Limnol. Oceanogr., 49(2), 322–329, 2004.

719   Nelson, D. M., Tréguer, P., Brzezinski, M. A., Leynaert, A. and Quéguiner, B.:
720   Production and dissolution of biogenic silica in the ocean: Revised global estimates,
721   comparison with regional data and relationship to biogenic sedimentation, Global
722   Biogeochem. Cycles, 9(3), 359–372, doi:10.1029/95GB01070, 1995.

723   Nielsen, L. T., Jakobsen, H. H. and Hansen, P. J.: High resilience of two coastal
724   plankton communities to twenty-first century seawater acidification: Evidence from
725   microcosm studies, Mar. Biol. Res., 6(6), 542–555, doi:10.1080/17451000903476941,
726   2010.

727   Nielsen, L. T., Hallegraeff, G. M., Wright, S. W. and Hansen, P. J.: Effects of
728   experimental seawater acidification on an estuarine plankton community, Aquat.
729   Microb. Ecol., 65(3), 271–285, doi:10.3354/ame01554, 2012.

730   Nogueira, P., Domingues, R. B. and Barbosa, A. B.: Are microcosm volume and sample
731   pre-filtration relevant to evaluate phytoplankton growth?, J. Exp. Mar. Bio. Ecol., 461,
732   323–330, doi:10.1016/j.jembe.2014.09.006, 2014.

733   Pan, Y., Zhang, Y., Peng, Y., Zhao, Q. and Sun, S.: Increases of chamber height and
734   base diameter have contrasting effects on grazing rate of two cladoceran species:
735   Implications for microcosm studies, PLoS One, 10(8), 1–14,

736   doi:10.1371/journal.pone.0135786, 2015.

737   Pančić, M. and Kiørboe, T.: Phytoplankton defence mechanisms: traits and trade-offs,
738   Biol. Rev., 92(2), 1269–1303, doi:10.1111/brv.12395, 2018.

739   Park, K. T., Lee, K., Shin, K., Yang, E. J., Hyun, B., Kim, J. M., Noh, J. H., Kim, M.,
740   Kong, B., Choi, D. H., Choi, S. J., Jang, P. G. and Jeong, H. J.: Direct linkage between
741   dimethyl sulfide production and microzooplankton grazing, resulting from prey
742   composition change under high partial pressure of carbon dioxide conditions, Environ.
743   Sci. Technol., 48(9), 4750–4756, doi:10.1021/es403351h, 2014.

744   Paul, A. J., Bach, L. T., Schulz, K.-G., Boxhammer, T., Czerny, J., Achterberg, E. P.,
745   Hellemann, D., Trense, Y., Nausch, M., Sswat, M. and Riebesell, U.: Effect of elevated
746   CO_2 on organic matter pools and fluxes in a summer Baltic Sea plankton community,
747   Biogeosciences, 12, 6181–6203, doi:10.5194/bg-12-6181/2015/, 2015.

748   Pomeroy, L. R.: The ocean food web - A changing paradigm, Bioscience, 24, 499–504,
749   1974.

750   Pomeroy, L. R., Sheldon, J. E. and Sheldon, W. M.: Changes in bacterial numbers and
751   leucine assimilation during estimations of microbial respiratory rates in seawater by the
752   precision winkler method, Appl. Environ. Microbiol., 60(1), 328–332, 1994.

753   Primeau, F. W., Holzer, M. and DeVries, T.: Southern Ocean nutrient trapping and the
754   efficiency of the biological pump, J. Geophys. Res. Ocean., 118(5), 2547–2564,
755   doi:10.1002/jgrc.20181, 2013.

756   Raven, J. A, Giordano, M., Beardall, J. and Maberly, S. C.: Algal and aquatic plant
757   carbon concentrating mechanisms in relation to environmental change., Photosynth.
758   Res., 109(1–3), 281–96, doi:10.1007/s11120-011-9632-6, 2011.

759   Reul, A., Muñoz, M., Bautista, B., Neale, P. J., Sobrino, C., Mercado, J. M., Segovia,
760   M., Salles, S., Kulk, G., León, P., van de Poll, W. H. D., Pérez, E., Buma, A. and
761   Blanco, J. M.: Effect of CO_2, nutrients and light on coastal plankton. III. Trophic
762   cascade, size structure and composition, Aquat. Biol., 22, 59–76, doi:10.3354/ab00585,
763   2014.

764   Robinson, C. and Williams, P. J. le B.: Respiration and its measurement in surface
765   marine waters, in Respiration in Aquatic Environments, edited by P. A. Del Giorgio and
766   P. J. le B. Williams, pp. 147–180, Oxford University Press, Oxford., 2005.

767   Roleda, M. Y., Cornwall, C. E., Feng, Y., McGraw, C. M., Smith, A. M. and Hurd, C.
768   L.: Effect of ocean acidification and pH fluctuations on the growth and development of
769   coralline algal recruits, and an associated benthic algal assemblage, PLoS One, 10(10),
770   1–19, doi:10.1371/journal.pone.0140394, 2015.

771   Rossoll, D., Sommer, U. and Winder, M.: Community interactions dampen acidification
772   effects in a coastal plankton system, Mar. Ecol. Prog. Ser., 486, 37–46,
773   doi:10.3354/meps10352, 2013.

774   Rost, B., Riebesell, U., Burkhardt, S. and Sültemeyer, D.: Carbon acquisition of bloom-
775   forming marine phytoplankton, Limnol. Oceanogr., 48(1), 55–67, 2003.

776   Sala, M. M., Aparicio, F. L., Balagué, V., Boras, J. A., Borrull, E., Cardelús, C., Cros,
777   L., Gomes, A., López-Sanz, A., Malits, A., Martínez, R. A., Mestre, M., Movilla, J.,
778   Sarmento, H., Vázquez-Domínguez, E., Vaqué, D., Pinhassi, J., Calbet, A., Calvo, E.,
779   Gasol, J. M., Pelejero, C. and Marrasé, C.: Contrasting effects of ocean acidification on
780   the microbial food web under different trophic conditions, Ices J. Mar. Sci., 73(3), 670–
781   679, doi:10.1093/icesjms/fsv130, 2015.

782   Sarmiento, J. L. and Gruber, N.: Ocean biogeochemical dynamics, Princeton University
783   Press, Princeton., 2006.

784   Sarmiento, J. L., Gruber, N., Brzezinski, M. A. and Dunne, J. P.: High-latitude controls
785   of thermocline nutrients and low latitude biological productivity, Nature, 427(6969),
786   56–60, doi:10.1038/nature10605, 2004.

787   Sarnelle, O.: Daphnia effects on microzooplankton: comparisons of enclosure and
788   whole-lake responses, Ecology, 78(3), 913–928, doi:10.1016/S0010-4655(02)00300-4,
789   1997.

790   Sarthou, G., Timmermans, K. R., Blain, S. and Tréguer, P.: Growth physiology and fate
791   of diatoms in the ocean: A review, J. Sea Res., 53, 25–42,
792   doi:10.1016/j.seares.2004.01.007, 2005.

793   Schulz, K. G., Riebesell, U., Bellerby, R. G. J., Biswas, H., Meyerhöfer, M., Müller, M.
794   N., Egge, J. K., Nejstgaard, J. C., Neill, C., Wohlers, J. and Zöllner, E.: Build-up and
795   decline of organic matter during PeECE III, Biogeosciences, 5, 707–718,
796   doi:10.5194/bg-5-707-2008, 2008.

797   Schulz, K. G., Bellerby, R. G. J., Brussaard, C. P. D., Büdenbender, J., Czerny, J.,
798   Engel, A., Fischer, M., Koch-Klavsen, S., Krug, S. A., Lischka, S., Ludwig, A.,
799   Meyerhöfer, M., Nondal, G., Silyakova, A., Stuhr, A. and Riebesell, U.: Temporal
800   biomass dynamics of an Arctic plankton bloom in response to increasing levels of
801   atmospheric carbon dioxide, Biogeosciences, 10, 161–180, doi:10.5194/bg-10-161-
802   2013, 2013.

803   Schulz, K. G., Bach, L. T., Bellerby, R., Bermudez, R., Boxhammer, T., Czerny, J.,
804   Engel, A., Ludwig, A., Larsen, A., Paul, A., Sswat, M. and Riebesell, U.: Phytoplankton
805   blooms at increasing levels of atmospheric carbon dioxide: experimental evidence for
806   negative effects on prymnesiophytes and positive on small picoeukaryotes, Front. Mar.
807   Sci., 4(64), 1–18, doi:10.3389/fmars.2017.00064, 2017.

808   Segovia, M., Lorenzo, M., Maldonado, M., Larsen, A., Berger, S., Tsagaraki, T.,
809   Lázaro, F., Iñiguez, C., García-Gómez, C., Palma, A., Mausz, M., Gordillo, F.,
810   Fernández, J., Ray, J. and Egge, J.: Iron availability modulates the effects of future CO_2
811   levels within the marine planktonic food web, Mar. Ecol. Prog. Ser., 565, 17–33,
812   doi:10.3354/meps12025, 2017.

813   Sett, S., Schulz, K. G., Bach, L. T. and Riebesell, U.: Shift towards larger diatoms in a
814   natural phytoplankton assemblage under combined high-CO_2 and warming conditions,
815   J. Plankton Res., 40(4), 391–406, doi:10.1093/plankt/fby018, 2018.

816   Shaik, A. U. R., Biswas, H. and Pal, S.: Increased CO_2 availability promotes growth of
817   a tropical coastal diatom assemblage (Goa coast, Arabian Sea, India), Diatom Res.,

818   32(3), 325–339, doi:10.1080/0269249X.2017.1379443, 2017.

819   Shen, C. and Hopkinson, B. M.: Size scaling of extracellular carbonic anhydrase
820   activity in centric marine diatoms, J. Phycol., 51(2), 255–263, doi:10.1111/jpy.12269,
821   2015.

822   Smetacek, V., Klaas, C., Strass, V. H., Assmy, P., Montresor, M., Cisewski, B., Savoye,
823   N., Webb, A., d'Ovidio, F., Arrieta, J. M., Bathmann, U., Bellerby, R., Berg, G. M.,
824   Croot, P., Gonzalez, S., Henjes, J., Herndl, G. J., Hoffmann, L. J., Leach, H., Losch, M.,
825   Mills, M. M., Neill, C., Peeken, I., Röttgers, R., Sachs, O., Sauter, E., Schmidt, M. M.,
826   Schwarz, J., Terbrüggen, A. and Wolf-Gladrow, D.: Deep carbon export from a
827   Southern Ocean iron-fertilized diatom bloom, Nature, 487(7407), 313–319,
828   doi:10.1038/nature11229, 2012.

829   Smetacek, V. S.: Role of sinking in diatom life-hystory: ecological, evolutionary and
830   geological significance, Mar. Biol., 84, 239–251, doi:10.1007/BF00392493, 1985.

831   Sommer, U., Stibor, H., Katechakis, A., Sommer, F. and Hansen, T.: Pelagic food web
832   confgurations at different levels of nutrient richness and their implications for the ratio
833   fish production:primary production, Hydrobiologia, 484, 11–20,
834   doi:10.1023/A:1021340601986, 2002.

835   Sommer, U., Paul, C. and Moustaka-Gouni, M.: Warming and ocean acidification
836   effects on phytoplankton - From species shifts to size shifts within species in a
837   mesocosm experiment, PLoS One, 10(5), 1–17, doi:10.1371/journal.pone.0125239,
838   2015.

839   Sournia, A., Chrétiennot-Dinet, M. J. and Ricard, M.: Marine phytoplankton: How
840   many species in the world ocean?, J. Plankton Res., 13(5), 1093–1099,
841   doi:10.1093/plankt/13.5.1093, 1991.

842   Spencer, M. and Warren, P. H.: The effects of habitat size and productivity on food web
843   structure in small aquatic microcosms, Oikos, 75(3), 419–430 [online] Available from:
844   http://www.jstor.org/stable/3545882?origin=crossref, 1996.

845   Sswat, M., Stiasny, M. H., Taucher, J., Algueró-Muñiz, M., Bach, L. T., Jutfelt, F.,
846   Riebesell, U. and Clemmesen, C.: Food web changes under ocean acidification promote
847   herring larvae survival, Nat. Ecol. Evol., 2(May), 1–5, doi:10.1038/s41559-018-0514-6,
848   2018.

849   Sugie, K. and Yoshimura, T.: Effects of pCO_2 and iron on the elemental composition
850   and cell geometry of the marine diatom *Pseudo-nitzschia pseudodelicatissima*
851   (Bacillariophyceae), J. Phycol., 49(3), 475–488, doi:10.1111/jpy.12054, 2013.

852   Sun, J., Hutchins, D. A., Feng, Y., Seubert, E. L., Caron, D. A. and Fu, F. X.: Effects of
853   changing pCO_2 and phosphate availability on domoic acid production and physiology of
854   the marine harmful bloom diatom *Pseudo-nitzschia multiseries*, Limnol. Oceanogr.,
855   56(3), 829–840, doi:10.4319/lo.2011.56.3.0829, 2011.

856   Tatters, A. O., Fu, F. X. and Hutchins, D. A.: High CO_2 and silicate limitation
857   synergistically increase the toxicity of *Pseudo-nitzschia fraudulenta*, PLoS One, 7(2),
858   doi:10.1371/journal.pone.0032116, 2012.

Ocean Science

Discussions

Open Access

859   Tatters, A. O., Roleda, M. Y., Schnetzer, A., Fu, F., Hurd, C. L., Boyd, P. W., Caron, D.
860   A., Lie, A. A. Y., Hoffmann, L. J. and Hutchins, D. A.: Short- and long-term
861   conditioning of a temperate marine diatom community to acidification and warming,
862   Philos. Trans. R. Soc. B Biol. Sci., 368, 20120437, doi:10.1098/rstb.2012.0437, 2013.

863   Tatters, A. O., Schnetzer, A., Xu, K., Walworth, N. G., Fu, F., Spackeen, J. L., Sipler,
864   R. E., Bertrand, E. M., McQuaid, J. B., Allen, A. E., Bronk, D. A., Gao, K., Sun, J.,
865   Caron, D. A. and Hutchins, D. A.: Interactive effects of temperature, CO_2 and nitrogen
866   source on a coastal California diatom assemblage, J. Plankton Res., 40(2), 151–164,
867   doi:10.1093/plankt/fbx074, 2018.

868   Taucher, J., Jones, J., James, A., Brzezinski, M. A., Carlson, C. A., Riebesell, U. and
869   Passow, U.: Combined effects of CO_2 and temperature on carbon uptake and
870   partitioning by the marine diatoms *Thalassiosira weissflogii* and *Dactyliosolen*
871   *fragilissimus*, Limnol. Oceanogr., 60(3), 901–919, doi:10.1002/lno.10063, 2015.

872   Taucher, J., Arístegui, J., Bach, L. T., Guan, W., Montero, M. F., Nauendorf, A.,
873   Achterberg, E. P. and Riebesell, U.: Response of Subtropical Phytoplankton
874   Communities to Ocean Acidification Under Oligotrophic Conditions and During
875   Nutrient Fertilization, Front. Mar. Sci., 5(September), 1–14,
876   doi:10.3389/fmars.2018.00330, 2018.

877   Thoisen, C., Riisgaard, K., Lundholm, N., Nielsen, T. G. and Hansen, P. J.: Effect of
878   acidification on an Arctic phytoplankton community from Disko Bay, West Greenland,
879   Mar. Ecol. Prog. Ser., 520, 21–34, doi:10.3354/meps11123, 2015.

880   Thor, P. and Dupont, S.: Transgenerational effects alleviate severe fecundity loss during
881   ocean acidification in a ubiquitous planktonic copepod, Glob. Chang. Biol., 21(6),
882   2261–2271, doi:10.1111/gcb.12815, 2015.

883   Thor, P. and Oliva, E. O.: Ocean acidification elicits different energetic responses in an
884   Arctic and a boreal population of the copepod *Pseudocalanus acuspes*, Mar. Biol.,
885   162(4), 799–807, doi:10.1007/s00227-015-2625-9, 2015.

886   Tortell, P. D., DiTullio, G. R., Sigman, D. M. and Morel, F. M. M.: CO_2 effects on
887   taxonomic composition and nutrient utilization in an Equatorial Pacific phytoplankton
888   assemblage, Mar. Ecol. Prog. Ser., 236, 37–43, doi:10.3354/meps236037, 2002.

889   Tortell, P. D., Payne, C. D., Li, Y., Trimborn, S., Rost, B., Smith, W. O., Riesselman,
890   C., Dunbar, R. B., Sedwick, P. and DiTullio, G. R.: CO_2 sensitivity of Southern Ocean
891   phytoplankton, Geophys. Res. Lett., 35, L04605, doi:10.1029/2007GL032583, 2008.

892   Tréguer, P., Bowler, C., Moriceau, B., Dutkiewicz, S., Gehlen, M., Aumont, O., Bittner,
893   L., Dugdale, R., Finkel, Z., Iudicone, D., Jahn, O., Guidi, L., Lasbleiz, M., Leblanc, K.,
894   Levy, M. and Pondaven, P.: Influence of diatom diversity on the ocean biological
895   carbon pump, Nat. Geosci., 11(1), 27–37, doi:10.1038/s41561-017-0028-x, 2018.

896   Tréguer, P. J. and De La Rocha, C. L.: The World Ocean Silica Cycle, Ann. Rev. Mar.
897   Sci., 5(1), 477–501, doi:10.1146/annurev-marine-121211-172346, 2013.

898   Trimborn, S., Lundholm, N., Thoms, S., Richter, K.-U., Krock, B., Hansen, P. J. and
899   Rost, B.: Inorganic carbon acquisition in potentially toxic and non-toxic diatoms: the

Ocean Science
Discussions

Open Access

EGU

900　effect of pH-induced changes in seawater carbonate chemistry., Physiol. Plant., 133(1),
901　92–105, doi:10.1111/j.1399-3054.2007.01038.x, 2008.

902　Trimborn, S., Brenneis, T., Sweet, E., Rost, B. and 10.1594/Pangaea.824406:
903　Sensitivity of Antarctic phytoplankton species to ocean acidification: growth, carbon
904　acquisition, and species interaction, Limnol. Oceanogr. , 58(3), 997–1007,
905　doi:10.4319/lo.2013.58.3.0997, 2013.

906　Trimborn, S., Brenneis, T., Hoppe, C. J. M., Laglera, L. M., Norman, L., Santos-
907　Echeandía, J., Völkner, C., Wolf-Gladrow, D. and Hassler, C. S.: Iron sources alter the
908　response of Southern Ocean phytoplankton to ocean acidification, Mar. Ecol. Prog. Ser.,
909　578, 35–50, doi:10.3354/meps12250, 2017.

910　Vrieling, E. G., Gieskes, W. W. C. and Beelen, T. P. M.: SILICON DEPOSITION IN
911　DIATOMS: CONTROL BY THE pH INSIDE THE SILICON DEPOSITION
912　VESICLE, J. Phycol., 35(3), 548–559, doi:10.1046/j.1529-8817.1999.3530548.x, 1999.

913　Ward, B. A., Dutkiewicz, S., Jahn, O. and Follows, M. J.: A size-structured food-web
914　model for the global ocean, Limnol. Oceanogr., 57(6), 1877–1891,
915　doi:10.4319/lo.2012.57.6.1877, 2012.

916　Wilken, S., Hoffmann, B., Hersch, N., Kirchgessner, N., Dieluweit, S., Rubner, W.,
917　Hoffmann, L. J., Merkel, R. and Peeken, I.: Diatom frustules show increased
918　mechanical strength and altered valve morphology under iron limitation, Limnol.
919　Oceanogr., 56(4), 1399–1410, doi:10.4319/lo.2011.56.4.1399, 2011.

920　Witt, V., Wild, C., Anthony, K. R. N., Diaz-Pulido, G. and Uthicke, S.: Effects of ocean
921　acidification on microbial community composition of, and oxygen fluxes through,
922　biofilms from the Great Barrier Reef, Environ. Microbiol., 13(11), 2976–2989,
923　doi:10.1111/j.1462-2920.2011.02571.x, 2011.

924　Wolf, K. K. E., Hoppe, C. J. M. and Rost, B.: Resilience by diversity: Large
925　intraspecific differences in climate change responses of an Arctic diatom, Limnol.
926　Oceanogr., 63(1), 397–411, doi:10.1002/lno.10639, 2018.

927　Wolf-Gladrow, D. and Riebesell, U.: Diffusion and reactions in the vicinity of plankton:
928　A refined model for inorganic carbon transport, Mar. Chem., 59(1–2), 17–34,
929　doi:10.1016/S0304-4203(97)00069-8, 1997.

930　Wu, Y., Campbell, D. A., Irwin, A. J., Suggett, D. J. and Finkel, Z. V.: Ocean
931　acidification enhances the growth rate of larger diatoms, Limnol. Oceanogr., 59(3),
932　1027–1034, doi:10.4319/lo.2014.59.3.1027, 2014.

933　Yoshimura, T., Nishioka, J., Suzuki, K., Hattori, H., Kiyosawa, H. and Watanabe, Y.
934　W.: Impacts of elevated CO2 on organic carbon dynamics in nutrient depleted Okhotsk
935　Sea surface waters, J. Exp. Mar. Bio. Ecol., 395(1–2), 191–198,
936　doi:10.1016/j.jembe.2010.09.001, 2010.

937　Yoshimura, T., Suzuki, K., Kiyosawa, H., Ono, T., Hattori, H., Kuma, K. and Nishioka,
938　J.: Impacts of elevated CO_2 on particulate and dissolved organic matter production:
939　Microcosm experiments using iron-deficient plankton communities in open subarctic
940　waters, J. Oceanogr., 69(5), 601–618, doi:10.1007/s10872-013-0196-2, 2013.

Ocean Science
Discussions

Open Access

EGU

941   Young, J. N., Kranz, S. A., Goldman, J. A. L., Tortell, P. D. and Morel, F. M. M.:
942   Antarctic phytoplankton down-regulate their carbon-concentrating mechanisms under
943   high CO_2 with no change in growth rates, Mar. Ecol. Prog. Ser., 532, 13–28,
944   doi:10.3354/meps11336, 2015.

945   Zeebe, R. E. and Wolf-Gladrow, D. A.: CO_2 in seawater: Equilibrium, kinetics,
946   isotopes, Elsevier O., Elsevier, Amsterdam., 2001.

947

948   **Tables and Figures**

949

950   **Table 1**. Response of diatom communities to high CO_2. 69 experiments from 54

951   publications were considered here. Location refers to the place where diatom

952   communities were collected. The RDR is dimensionless (see methods). T is the average

953   incubation temperature in °C. DoE are days of experiment with the number of samplings

954   given as the second number. Pre-filt. gives the mesh size in case the collected plankton

955   community was pre-filtered before incubation. Setup refers to the incubation style:

956   undiluted volumes (batch), repeatedly diluted volumes (s.-cont.), flow-through setups

957   (fl.-thr.; only benthos), chemostats (chem.; only pelagic), CO_2 vent sites (seep; only

958   benthos). Incubations can either be performed on deck (e.g. shipboards), *in situ* (e.g. *in*

959   *situ* mesocosms) or under laboratory conditions. V refers to the incubation volume.

960   Nutrient ammendments were made in some but not all studies. The element indicates

961   which nutrients were added. Asterisks indicate the presense of residual nutrients at the

962   beginning of the study. Manipulations were done with: CO_2 saturated seawater (SWsat),

963   acid additions (Acid), combined additions of acid and base (Comb.), CO_2 gas additions

964   (CO_2), Aeration at target pCO_2 (Aer.), Passing CO_2 gas through a diffusive silicone tubing

965   (Diff.). Meth. indicates the applied methodology to investigate diatom communities: light

966   microscopy (LM), pigment analyses (PA), flow cytometry (FC), genetic tools (PCR),

967   biogenic silica (BSi). The pCO_2 range of the experiment with the number of treatments

968   given in brackets. The response of the bulk diatom community to CO_2: no effect (~),

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969   positive (p), negative (n), not reported (N/A). The pCO$_2$ response indicates approximately

970   in between which treatments a CO$_2$ response was observed. Please note that this is based

971   on visual inspection of the datasets and therefore involves subjectivity. Please also note

972   that the range equals the treatment values in case only two treatments were set up. CO$_2$

973   induced shifts between diatom species can be: shift to larger species (large), shift to

974   smaller species (small), unspecified shift (shift), no species shift detected (~), not reported

975   (N/A). Winners or losers of the diatom community comprise: *Chaetoceros* (Chae), large

976   *Chaetoceros* (Chae I), medium *Chaetoceros* (Chae II), small *Chaetoceros* (Chae III),

977   *Neosyndra* (Neos), *Rhabdonema* (Rhab), *Eucampia* (Euca), *Cerataulina* (Cera),

978   *Thalassiosira* (Thals), *Proboscia* (Prob), *Pseudo-nitzschia* (Ps-n), *Thalassionema*

979   (Thalns), *Cylindrotheca* (Cyli), *Guinardia* (Guin), *Synedropsis* (Syned), *Dactyliosolen*

980   (Dact), *Toxarium* (Toxa), *Leptocylindrus* (Lept), *Grammatophora* (Gram), *Bacillaria*

981   (Baci), *Navicula* (Navi).

Reference	lat	long	RDR	S	T (°C)	Habitat	DoE/ # of sampl.	Pre-filt. (µm)	Setup	Incub.	V (L)	Nutr.	Manip.	Meth.	pCO$_2$ range (µatm)	CO$_2$ effect	pCO$_2$ response (µatm)	Intra-taxon effect	Winners	Losers
(Bach et al., 2017)	58.264	11.479	76.2	29	7	est.	113/57	1000	batch	in situ	50000	*none	SWsat	PA, LM	(2) 380, 760	p	380 - 760	large	Cosc	
(Bach et al., 2019)	27.990	15.369	59.6	37	18.5	coastal	32/21	3000	batch	in situ	8000	N,P,Si	SWsat	LM, BSi	(7) 380 - 1120	p	380 - 1120	large	Chae, Guin, Lept	Nitz
(Biswas et al., 2011)	16.750	81.100	2.1	25	29.5	est.	5/2	200	batch	Deck	5.6	*none/N, P	Comb.	PA	(4) 230 - 1860	n	650 - 1400	N/A		
(Biswas et al., 2017)	17.000	83.000	1.5	?	?	coastal	2/1	200	batch	Deck	2	*N,P,Si,F e,(Zn)	Comb.	LM	(2) 230, 2200	p	230 - 2200	shift	Skel	Thals
(Davidson et al., 2016)	-68.583	77.967	10.5	34	0.1	coastal	8/5	200	batch	Lab	650	*Fe	SWsat	LM	(6) 80 - 2420	n	1280 - 1850	small	Frag	Chae
(Domingues et al., 2017)	37.017	-8.500	7.4	?	23.5	est.	1/1	no	batch	Deck	4.5	N,P,Si,NH 4	Comb.	LM, PA	(2) 420, 710	~		~		
(Donahue et al., 2019)	-45.800	171.130	2.6	34	11	oceanic	14/5	200	batch	Lab	10	*Fe	Diff.	LM, FC	(2) 350, 620	~		N/A		
(Donahue et al., 2019)	-45.830	171.540	2.6	34	11	oceanic	21/4	200	batch	Lab	10	*Fe	Diff.	LM, FC	(2) 350, 630	p		N/A		
(Eggers et al., 2014)	38.633	27.067	1.9	36	15	coastal	9-10/3	200	batch	Deck	4	N,P,Si	Comb.	LM	(2) 380, 910	p	380 - 910	large	Chae III	Thals
(Eggers et al., 2014)	38.650	27.250	1.9	36	15	coastal	9-10/4	200	batch	Deck	4	N,P,Si	Comb.	LM	(2) 380, 910	p	380 - 910	large	Thals, Chae II	Chae I
(Eggers et al., 2014)	38.617	27.250	1.9	36	15	oceanic	9-10/5	200	batch	Deck	4	N,P,Si	Comb.	LM	(2) 380, 910	~		N/A		

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(Endo et al., 2013)	46.000	160.000	2.8	33	14	oceanic	14/3	197	batch	Deck	12	*none	Aer.	PA	(4) 230 - 1120	~		N/A		
(Endo et al., 2015)	53.083	-177.000	2.8	?	8.2	oceanic	5/3	197	batch	Deck	12	*none	Aer.	PA, PCR	(2) 360, 600	n	360 - 600	~		
(Endo et al., 2016)	41.500	144.000	2.8	?	5.4	oceanic	3/3	197	batch	Deck	12	*Fe	Aer.	PA, PCR	(4) 180 - 1000	n	350 - 1000	shift		
(Feng et al., 2009)	57.580	15.320	1.7	35	12	oceanic	14/1-2	200	s.-cont.	Deck	2.7	N,P	Aer.	LM, PA	(2) 390, 690	p	390 - 690	large	Ps-n	Cyli
(Feng et al., 2010)	-74.230	179.230	1.7	34	0	oceanic	18/1-14	200	s.-cont.	Deck	2.7	none	Aer.	LM, PA	(2) 380, 750	~		large	Chae	Cyli
(Gazeau et al., 2017)	43.697	7.312	125.8	38	14	coastal	18/14	5000	batch	in situ	45000	none	SWsat	PA	(6) 350 - 1250	p	600 - 1000	N/A		
(Gazeau et al., 2017)	42.580	8.726	125.8	38	23	coastal	27/18	5000	batch	in situ	45000	none	SWsat	PA	(6) 420 - 1250	~		N/A		
(Grear et al., 2017)	41.575	-71.405	9.3	?	9	est.	6/7	no	chem.	Deck	9.1	?none	Comb.	LM	(3) 220 - 720	~		~		
(Hama et al., 2016)	34.665	-138.940	7.1	?	?	coastal	29/11	100	batch	Deck	400	N,P,Si	Aer.	PA	(3) 400 - 1200	~		N/A		
(Hare et al., 2007)	56.515	-164.730	6.0	?	10.4	coastal	9-10/5	no	s.-cont.	Deck	2.5	Fe,N,P, Si	Aer.	LM, PA	(2) 370, 750	n	370 - 750	shift		Cyli
(Hare et al., 2007)	-55.022	179.030	6.0	?	10.4	oceanic	9-10/3	no	s.-cont.	Deck	2.5	Fe	Aer.	LM, PA	(2) 370, 750	n	370 - 750	N/A		
(Hopkins et al., 2010)	60.300	5.200	99.1	?	10	coastal	21/9	no	batch	in situ	11000	N, P	Aer.	LM	(2) 300, 600	n	300 - 600	N/A		
(Hoppe et al., 2013)	-66.833	0.000	1.9	34	3	oceanic	27-30/1	200	s.-cont.	Lab	4	*none	Aer.	LM	(3) 200 - 810	N/A	400 - 810	shift	Syned	Ps-n
(Hoppe et al., 2017b)	71.406	-68.601	1.9	33	9.5	oceanic	8/3	100	s.-cont.	Deck	8	N,P,Si	Aer.	PA, LM	(2) 320, 990	~		~		
(Hoppe et al., 2017a)	63.964	-60.125	1.9	32	7.9	oceanic	13-14/3	100	s.-cont.	Deck	8	N,P,Si	Aer.	LM	(2) 300, 960	n	300 - 960	shift	Frag	Ps-n
(Hussherr et al., 2017)	71.406	-70.188	2.6	33	4.3	oceanic	9/3-9	200	batch	Deck	10	*none	Comb.	LM, PA	(6) 510 - 3300	n	1040 - 1620	~		
(James et al., 2014)	-45.639	170.671		?	11.6	benthic	42/2		fl.-thr.	Lab	0	none	Comb.	pic	(2) 400, 1250	~		N/A		
(Johnson et al., 2011)	38.417	14.950		38	23.5	benthic	21/1	NA	seep	in situ	0	none	NA	PA, LM	(3) 420 - 1600	p	420 - 590	large	Toxa, Gram, Baci, Navi, Cocc	Cycl, Neos, Rhab, Nitz
(Kim et al., 2006)	34.600	128.500	4.3	?	14	coastal	14/?	60	batch	in situ	150	N,P	Aer.	LM	(3) 250 - 750	N/A	400 - 750	shift	Skel	Nitz
(Kim et al., 2010)	34.600	128.500	52.1	?	12	coastal	20/22	no	batch	in situ	1600	N,P,Si	SWsat/ Aer.	LM	(2) 400, 900	~		shift	Skel	Euca
(Mallozzi et al., 2019)	29.241	-90.935	2.4	12	21	est.	112/9	80	s.-cont.	Lab	20	*none	Aer.	PA, LM	(2) 400, 1000	~		shift	Cyli	
(Mallozzi et al., 2019)	29.272	-89.963	2.4	17	21	est.	112/9	80	s.-cont.	Lab	20	*none	Aer.	PA, LM	(2) 400, 1000	~		shift	Cyli	
(Maugendre et al., 2015)	43.667	-7.300	1.9	?	15	oceanic	12/4	200	batch	Deck	4	none	SWsat	PA	(2) 360, 630	~		N/A		
(Nielsen et al., 2010)	56.057	12.648	1.6	19	10.7	est.	14/4	175	s.-cont.	Lab	2.5	*none	Acid	LM, PA	(3) 500 - 1500	~		~		
(Nielsen et al., 2012)	-42.887	147.339	1.8	31	16	coastal	14/4	250	s.-cont.	Lab	2.5	*none	Acid	LM, PA	(3) 300 - 1200	~		~		
(Park et al., 2014)	34.600	128.500	59.6	?	17	coastal	19/17	no	batch	in situ	2400	N,P,Si	SWsat/ Aer.	LM, PA	(6) 160 - 830	p	160 - 830	N/A	Cera	

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(Paul et al., 2015)	59.858	23.258	112.7	6	11	est.	46/22	3000	batch	in situ	54000	none	SWsat	PA	(6) 370 - 1230	p	820 - 1000	N/A			
(Reul et al., 2014)	36.540	-4.600	3.3	?	21	coastal	7/6	200	batch	Deck	20	control/N,P	Aer.	LM, PA	(2) 500, 1000	p	500 - 1000	large			
(Roleda et al., 2015)	-45.639	170.671		34	10.8	benthic	112/?	NA	fl.-thr.	Lab	0.65	none	Comb.	PA	(2) 430, 1170	~		N/A			
(Rossoll et al., 2013)	54.329	10.149	29.8	18	18	est.	28/7	no	batch	Lab	300	N,P,Si	Aer.	LM	(5) 390 - 4000	~		N/A			
(Sala et al., 2015)	41.667	2.800	26.1	38	14	coastal	9/2	no	batch	Lab	200	none	CO2	LM	(2) 400, 800	~		N/A			
(Sala et al., 2015)	41.667	2.800	26.1	38	22	coastal	9/2	no	batch	Lab	200	none	CO2	LM	(2) 400, 800	~		N/A			
(Schulz et al., 2008)	60.267	5.217	133.7	31	10.5	coastal	25/18-23	no	batch	in situ	27000	N,P	Aer.	PA	(3) 350 - 1050	~		N/A			
(Schulz et al., 2013)	78.937	11.893	158.5	34	3	coastal	30/26 - 30	3000	batch	in situ	45000	N,P,Si	SWsat	LM, PA	(8) 185 - 1420	~		N/A			
(Schulz et al., 2017)	60.265	5.205	125.8	32	9	coastal	38/35	3000	batch	in situ	75000	*N, P	SWsat	LM, PA	(8) 310 - 3050	n	1165 - 1425	N/A			
(Segovia et al., 2017)	60.390	5.320	99.1	?	11	coastal	22/9	no	batch	in situ	11000	control	SWsat /Aer.	FC	(2) 300, 800	~		N/A			
(Sett et al., 2018)	54.329	10.149	49.8	20	5	est.	44/26	sand filter	batch	Lab	1400	*none	SWsat	LM, FC	(2) 540, 1020	~		~			
(Shaik et al., 2017)	15.453	43.801	5.6	35	29	coastal	2/1	no	batch	Deck	2	N,P,Si,Fe	CO2	LM	(2) 330, 1000	p	330 - 1000	~			
(Shaik et al., 2017)	15.453	43.801	5.6	36	29	coastal	9/1	no	s.-cont.	Deck	2	N,P,Si,Fe	CO2	LM	(2) 400, 1000	p	400 - 1000	~			
(Shaik et al., 2017)	15.453	43.801	5.6	35	29	coastal	2/1	no	batch	Deck	2	N,P,Si,Fe	CO2	LM	(2) 240, 780	p	240 - 780	~			
(Sommer et al., 2015)	54.329	10.149	49.8	20	9,15	est.	24/11	sand filter	batch	Lab	1400	*none	SWsat	LM	(2) 440, 1040	~		shift			Prob, Thaln, Guin, Ps-n, Chae
(Tatters et al., 2013)	-45.752	170.810	0.8	35	14	coastal	14/2	80	s.-cont.	Lab	0.8	N,P,Si,Fe	Aer.	LM	(3) 230 - 570	N/A	400 - 570	shift	Cosc, Ps-n	Navi, Chae	
(Tatters et al., 2018)	33.750	-118.215	12.1	?	19	coastal	10/1	no	chem.	Deck	20	N/urea,P,Si	Aer.	LM	380, 800	N/A		shift			
(Taucher et al., 2018)	27.928	-15.365	97.6	37	24-22	coastal	60/35	3000	batch	in situ	35000	N,P,Si	SWsat	LM, PA	(8) 350 - 1030	p	890 - 1030	large	Guin	Lept	
(Thoisen et al., 2015)	69.217	53.367	1.4	33	3	coastal	8-17/6-9	250	s.-cont.	Lab	1.2	*none	SWsat	LM	(4) 440 - 3500	n	440 - 900	shift	Navi I	Navi II	
(Tortell et al., 2002)	-6.600	81.017	7.1	?	?	oceanic	11/4	no	s.-cont.	Deck	4	*none	Aer.	PA, LM	(2) 150, 750	p	150 - 440	~			
(Tortell et al., 2008)	NA	NA	7.1	?	0	N/A	10-18/?	no	s.-cont.	Lab	4	*Fe	Aer.	LM, PA	(3) 100 - 800	p	100 - 400	large	Chae	Ps-n	
(Tortell et al., 2008)	NA	NA	7.1	?	0	N/A	10-18/?	no	s.-cont.	Deck	4	*Fe	Aer.	LM, PA	(3) 100 - 800	p	100 - 400	large	Chae	Ps-n	
(Tortell et al., 2008)	NA	NA	7.1	?	0	N/A	10-18/?	no	s.-cont.	Deck	4	*Fe	Aer.	LM, PA	(3) 100 - 800	p	100 - 400	large	Chae	Ps-n	
(Trimborn et al., 2017)	-53.013	10.025	1.9	34	3	oceanic	30/4	200	s.-cont.	Lab	4	none	Aer.	LM	420, 910	n	420 - 910	shift		Ps-n	
(Witt et al., 2011)	-23.450	151.917		?	24-25	benthic	11/4	NA	fl.-thr.	Deck	10	none	SWsat	LM	(4) 310 - 1140	p	560 - 1140	N/A			
(Wolf et al., 2018)	78.917	11.933	1.9	?	3	coastal	10 - 13/1	200	s.-cont.	Lab	4	none	Aer.	LM	(2) 400, 1000	N/A		~			
(Yoshimura et al., 2010)	49.500	148.250	2.7	33	13.5	oceanic	14/5	243	batch	Deck	9		Aer.	PA	(4) 150 - 590	n	150 - 280	N/A			

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| (Yoshimura et al., 2013) | 53.390 | 177.010 | 2.8 | ? | 8.4 | oceanic | 14/3 | 197 | batch | Deck | 12 | *none | Aer. | PA, LM | 4 (300 - 1190) | p | 960 - 1190 | N/A | | |
(Yoshimura et al., 2013)	49.020	174.020	2.8	?	9.2	oceanic	14/3	197	batch	Deck	12	*none	Aer.	PA, LM	(4) 230 - 1110	p	880 - 1110	N/A		
(Young et al., 2015)	-44.779	64.073	7.1	?	-1	coastal	21/21	no	s.-cont.	Deck	4	*none	Aer.	PA	(3) 100 - 800	~		N/A		
(Young et al., 2015)	-44.780	64.073	7.1	?	-0.5	coastal	16/16	no	s.-cont.	Deck	4	*none	Aer.	PA, LM	(3) 100 - 800	~		N/A		
(Young et al., 2015)	-44.780	64.073	7.1	?	1.5	coastal	20/20	no	s.-cont.	Deck	4	*none	Aer.	PA	(3) 100 - 800	~		N/A		

982

983
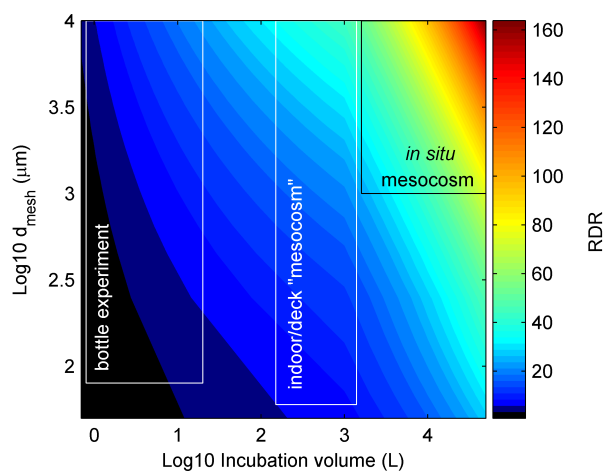
Figure 1. RDR as a function of incubation volume and size of the mesh that was used while filling the incubation volumes (d_{mesh}). The black and white boxes illustrate approximate ranges of the three main types of containers used in experiments. Please note that the general definition for mesocosms are volumes >1000 L (Guangao, 1990) but since most authors also use this term for open batch incubations with volumes between 150 – 1000 L we also stick to this term for the intermediate class.

991
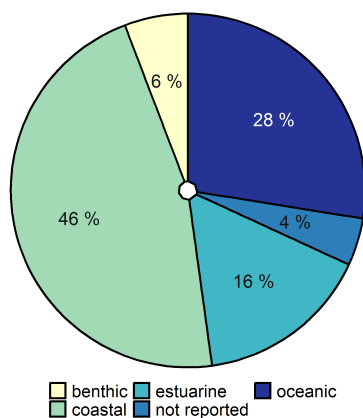
Figure 2. Habitats in which the ocean acidification experiments were conducted. The

total number of studies is 69. 'not reported' means that coordinates where the incubation

water was collected were not provided.



995
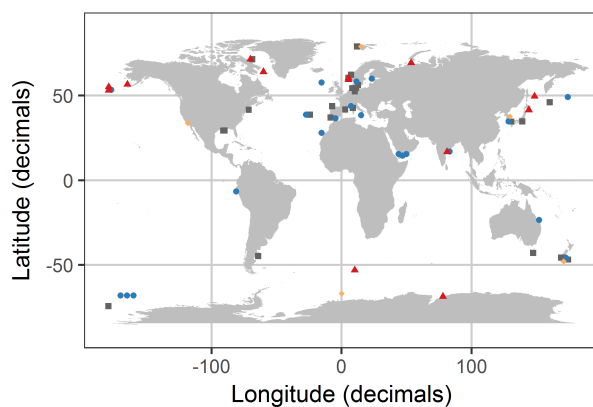
Figure 3. Distribution of diatom experiments with associated OA response of the bulk

communities as listed in Table 1. Blue circles = positive effect; red triangles = negative

response; grey squares = no response; orange diamonds = response not reported.

Locations were slightly modified in case of geospatial overlap to ensure visibility. Please

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1000   note that the three blue points in the Ross Sea at about -68, -165 are approximate locations

1001   because the reference did not provide coordinates.
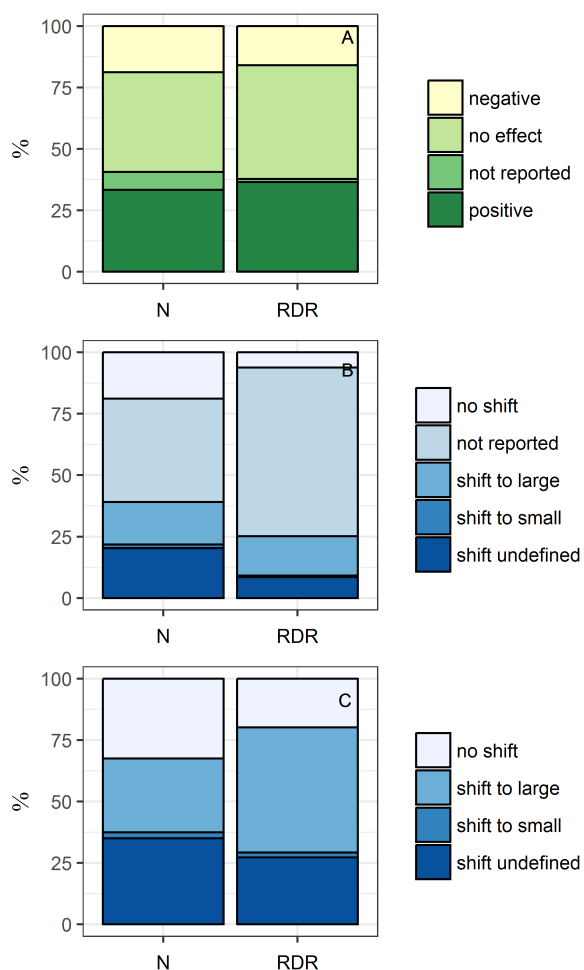
1002

1003   **Figure 4**. Summary of the literature analysis. (A) Response of the bulk diatom

1004   community to ocean acidification. (B) Shifts among different diatom species due to ocean

1005   acidification. 'Shift to large' and 'shift to small' indicate that the diatom community

1006   shifted towards the dominance of larger or smaller species, respectively. (C) Same data

1007   as in B but excluding studies where species shifts within the diatom community were not

1008   reported. This reduced the dataset from 69 to 40 studies. The left column is based on the

1009   number of studies. For example, the bulk diatom community was positively affected by

1010   OA in 29 out of 69 studies which is 33 %. The right column is based on the RDR values.

1011   For example, the ∑RDR value of all studies where the diatom community was positively

1012   affected by OA was 605 which is 36 % of the total ∑RDR.

1013
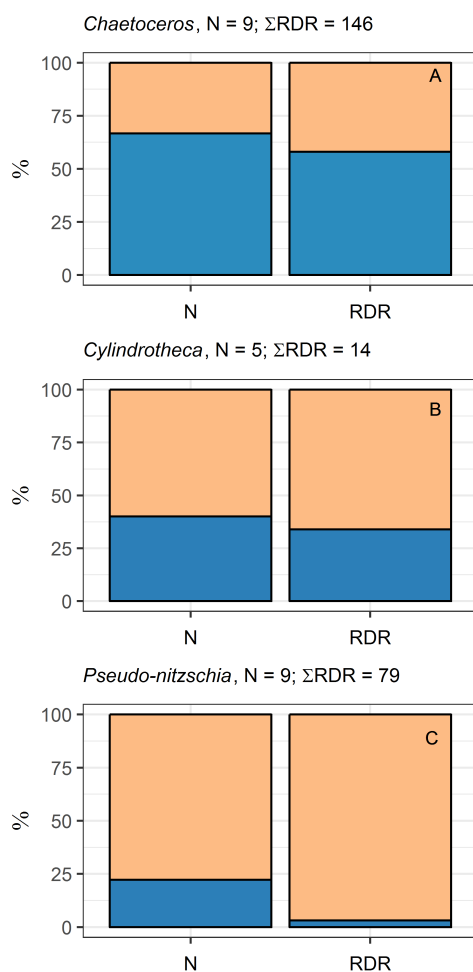
1014

1015   **Figure 5**. Winners and losers in diatom communities. The bar chart indicates the fraction

1016   of experiments where the respective genera benefitted from high CO_2 (blue) or were put

1017   at a disadvantage relative to the control treatment (orange). Shown here are diatom

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1018   genera that were microscopically identified in at least 5 experiments. The left bars are

1019   fractions based on the number of experiments (N, total number given above each plot).

1020   The right bars are fractions based on the RDR values of these experiments ($\sum$RDR of all

1021   experiments considered given above each plot). (A) *Chaetoceros*. (B) *Cylindrotheca*. (C)

1022   *Pseudo-nitzschia*. Please note that any such evaluation on the species level cannot be done

1023   at present due to too few data.